The understudied understory:
restoration with herbaceous species under climate change

A Thesis

SUBMITTED TO THE FACULTY OF THE

UNIVERSITY OF MINNESOTA

BY

Haley M Golz

IN PARTIAL FULFILLMENT OF THE REQUIERMENTS

FOR THE DEGREE OF

MASTER OF SCIENCE

Dr. Julie R. Etterson

December 2019

ABSTRACT

Herbaceous species are often overlooked in forest ecosystems. Even though understory species account for at least two thirds of species diversity in forested systems, the scientific literature is dominated by studies that exclusively focus on trees. This is an important oversight because of the vital functional role played by this species-rich layer. Knowledge is especially lacking in the realm of temperate forest restorations. In prairie ecosystems, extensive research has been conducted to support a detailed restoration methodology, while in forested ecosystems usually only tree species are planted, and research on the regeneration of the herbaceous understory layer is scant. To address these knowledge gaps, this research had two main parts. First, comparing intact to logged forest plots across Northeastern Minnesota to determine the regeneration of the herbaceous layer after logging. Overall, we found that logged plots had greater species richness and cover but were comprised of less even communities that saw some increase in non-native species. Observational evidence also suggests a lack of late-successional species. These results suggest that we may want to consider active plantings of the herbaceous layer in forest restorations to maintain the full diversity and functionality of these forests. Therefore, the second part of this research focused on the effect of simulated climate change on two herbaceous species from the boreal forest of NE MN; to help elucidate potential climate informed restoration techniques. A northern (ie. local) and a southern population of both *Symphyotrichum cilolatum* and *Maianthemum canadense* were grown in a factorial combination of temperature (ambient and +2°C) and water availability treatments (well-watered and -15% soil moisture). Size, leaf traits, and fitness metrics were recorded and analyzed between populations and treatments. The populations arrived with inherent trait differences in morphology, especially early in the season, but later on the treatment effects caused increases in size under elevated temperature and well-watered conditions. Most interesting was the indication of a negative effect of elevated temperature and low water availability on the northern population of both species. Across a number of traits, the northern population was shown to be at a unique disadvantage in this treatment combination. These results suggest that restoration plantings using southern seed sources may be more effective under a changing climate.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

Regeneration of the herbaceous layer after logging in Northeastern Minnesota Forests

INTRODUCTION

In forested systems herbaceous species are often understudied[1–4]. Especially in recovery from disturbance, it is often assumed that the herbaceous community will naturally reemerge if native tree species are established. However, Duffy and Meier 1992 found that the understory community in high elevation Appalachian forests hadn't fully recovered the species present in old growth areas 100 years after logging[5]. And Brudvig et. al 2011 document dispersal limitations of herbaceous species that translate into limited long-distance recruitment in Iowa forests after disturbance[6]. In the boreal forests of Northeastern Minnesota, it has been found that the understory recovers fairly well after disturbances, but that late-successional understory species are often absent from these areas[7,8].

Although small in stature, herbaceous species are an important component of diverse forested ecosystems, and diverse plant communities better provide a suite of important ecosystem services[4,9–12]. Herbaceous plants can be a source of food and shelter for animal species. It has been shown that the herbaceous layer plays an integral role in maintaining the hydrology of a region and influences water infiltration, filtration and total evapotranspiration[13]. Understory species are also critical components in watersheds as their roots hold soil and prevent erosion along streams and steep slopes[14]. And understory species impact tree recruitment, and therefore the ultimate health and make-up of the overstory tree community[15,16]. Importantly, diverse plant communities are thought to be more resilient in the face of disturbance and to the invasion by non-native species[17–19]. There is, therefore, ample indication that more consideration should be given to the herbaceous layer in general, but especially in relationship to its recovery after disturbance.

In northeastern Minnesota, heavy disturbance in the form of logging has impacted forests for the last 200 years. These forests were logged heavily in the late 1800s, early 1900s due to the preponderance of massive eastern white pines (*Pinus strobus*)[20–22]. After the majority of these ancient specimens were removed from the landscape the logging industry shifted to the next profitable venture, aspen harvest for pulp[20,21]. After harvest, forested areas are left bare, left to regenerate from the existing seed bank. Disturbance (eg. windthrow, fire, etc.) is an inherent part of the natural cycle in forests, however, the overutilization of forests in the last 200 years has removed the patchwork of old and young stands and replaced it with relatively homogenous young to mid-aged forests which lack the full complement of native understory species, especially late-successional species[8,23]. Additionally, in NE MN these areas are dominated by paper birch and aspen, early colonizing species[24–26], and as these trees have come to the natural end of their life-cycle[24–26] a dearth of tree recruitment has been documented, especially of long-lived conifers such as eastern white pine and white cedar (*Thuja occidentalis*)[26]. These trends in tree recruitment may further impact the successful establishment of understory species and further reduce the diversity of these systems. And finally, areas heavily disturbed by logging are more prone to invasion by non-native species[27], which can further impact the successful recruitment of native species[28,29].

On top of these impacts, the forests of NE MN are now experiencing the effects of climate change[30]. In this region the average annual temperature has increased by 0.6–1.7°C in the last 20 years compared to the early 1900s [31,32], and is predicted to rise another 1-3°C by mid-century[33]. Annual precipitation is also predicted to shift away from summer months, falling more in winter and less in summer[32], potentially causing drought like conditions during the growing season. Consequently, as NE MN forests work to regenerate after decades of logging, the communities native to this region now face the additional struggle of establishing in a novel climate[30,34]. This puts new stressors on communities and favors plant species that are more tolerant to warmer and drier environments[32,35–37]. This is especially concerning for the forests of NE MN that are adapted to cold, wet boreal conditions[38,39].

Increasing awareness of human-impacts, including climate change, has inspired a call to actively manage the regeneration of our forests with climate forward solutions[35,40–42]. Work has begun to probe whether native tree species sourced from drier, warmer climates may survive better than locally adapted material in restoration efforts[43–46]. In MN, surveys and modeling suggest that trees associated with southern mesic-hardwood forests, such as sugar maple (*Acer saccharum*), red pine (*Pinus resinosa*), and bur oak (*Quercus macrocarpa*), will increase in numbers across the state, while paper birch and balsam fir, species associated with northern boreal forests, will decline[20,36]. However, little work has gone into thinking about the re-establishment of the forest understory community, simply after logging or in response to a changing climate[1,9,47–49]. Therefore, it is imperative that we improve our understanding of forest understory dynamics to fully elucidate the impacts, and potential solutions, to climate change and other anthropogenic disturbances in forested ecosystems. Because almost no work has examined the response of the understory to these multiple stressors, we aimed to characterize the understory layer in logged openings as compared to intact areas in sites across Northeastern Minnesota. By gathering species composition data as well as environmental data, we aimed to explain the re-establishment dynamics of these forests after logging and in response to an already warming climate. Specifically, it is unknown how well the understory layer recovers after logging in NE MN. With our work we hoped to describe four major components of understory recovery: 1) To what extent do native herbaceous species naturally recover after logging? 2) What environmental characteristics drive community composition? 3) Are certain functional groups being increased under changing climate conditions? and 4) Are non-native species being given a foothold in logged areas? By gathering this data, we will provide a baseline against which to assess future changes in forest management techniques.

MATERIALS AND METHODS

Study Area

This study was conducted in northeastern Minnesota forests. Climate change is occurring rapidly in this region, which has altered patterns of tree mortality and recruitment[26,30]. This study was conducted in post-logging forest restoration sites that had been replanted with specific tree species which are predicted to thrive in future climates, such as bur oak and northern red oak (*Quercus rubra*)[50,51]. These logged openings were on average 40m wide and 40m long. To understand patterns of forest understory species recovery after logging and restoration and their relationship to environmental variables such as climate, topography, and forest composition (Table 1.2), we compared plant survey data in the restoration sites to adjacent intact forest and report differences in species richness, diversity, and evenness, as well as the effect of various environmental metrics on overall herbaceous community composition, a common technique to encourage the growth of the planted trees.

Research was conducted on a total of 16 sites located in northeastern Minnesota (Fig. 1.1). Sixteen previously logged and 16 adjacent but intact plots were surveyed (32 total plots). Intact plots were located as close to logged plots as possible, with the distance varying based on the availability of intact habitat, but on average were 370 m from logged plots and at least 50m from any roads, trails or the logged plots themselves to avoid edge effects. Intact plots were chosen that had similar characteristics such as elevation, slope, aspect and soil texture to the corresponding logged plots, and which had trees species similar to the remaining trees in the logged plot. The logged plots had been logged 1-5 years before being surveyed, with most sites having been logged three years prior to surveying. The logged plots had also been restored with a mix of eastern white pine, northern red oak and bur oak seedlings. Additionally, in the fall of 2014, the logged plots were cleared using a brush saw treatment to reduce the populations of woody competitors.

Plant surveys

Logged plots were surveyed in the summer of 2015 and intact plots in the summer of 2017. In both instances the same survey method was used. Round subplots (2m diameter) located every 5m along 20m N-S transects were used to collect data on herbaceous species composition using the Braun-Blanquet system[52]. The average number of transects per site was three, with successive transects located 10m apart and at least 10m from the cut edge if located in logged plots, or at least 50m from the forest edge in intact plots. However, in logged plots the number of transects varied depending on the size of the cut opening. Of note is that percent cover under this method can exceed 100%. Because the Braun-Blanquet method estimates species cover in broad categories, if percent cover is high in an area, adding up the broad category for each species can put you over 100%.

At each site the following environmental attributes were also obtained: the aspect, slope, soil family and texture, topography, and microtopography. The topography was defined as flat, or located on the toe, lower, middle, shoulder or summit of the slope. The microtopography was defined by the amount and size of mounds approximately 1 meter in size or less. Finally, the latitude, longitude, MN DNR seed zone and growing degree days were also determined for each site.

Data analysis

Non-metric Multidimensional Scaling

To assess correlations between environmental variables and herbaceous community composition as a whole, Non-metric Multidimensional Scaling (NMS) ordination analysis was employed (PC-ORD, Version 7, Released 2016, MjM Software Design)[53].

The parameters for the analysis were “Slow-and-thorough”. This type of analysis was run for the entire data set as well as a subset that only included coastal sites because previous work has shown that coastal plant communities on the north shore of Lake Superior are uniquely impacted by environmental conditions driven by proximity to the lake that shape community composition and dynamics[54,55]. This multivariate statistical method uses a reiterative process to find the local minima when correlating a large set of environmental data and species abundance data. Data is then plotted in a multidimensional space with data displayed according to the two main axes that account for the greatest variation in the data. Joint-plot outputs were used to determine how environmental variables correlate with species abundance data. And environmental correlations were deemed significant if their Pearson and Kendall correlations with the ordination axes had r-squared values greater than 0.1, the PC-ORD standard setting for environmental associate scores.

ANOVA

Mixed model ANOVAs were employed (JMP®, Version *13*. SAS Institute Inc., Cary, NC, 1989-2019.)[56] to analyze the difference in cover, species richness, Shannon’s diversity and Pielou’s evenness between logged and intact plots. These metrics were also run separately for the following plant functional groups which represented the majority of species found in both intact and logged plots: forbs, grasses, shrubs and vines. The difference in native and invasive cover between logged and intact plots, as well as the native and invasive cover for each major functional group, was also analyzed. In each analysis the history of the plot (intact or logged) was used as a fixed effect, with site – a unique identifier for each pair of plots – and its interaction with history as random effects. Data were alternately log or square root transformed, when necessary. Any data that was logged transformed also had 1 added to the original value to meet the model assumptions of normality and equal variance. However, for ease of interpretation, all figures display the original metrics of the data.

RESULTS

After 3 years of forest recovery, the herbaceous layer of logged plots in NE MN differed significantly from intact forest plots in several important respects. In general, logged plots had a greater percent herbaceous species cover and higher species richness, whereas the adjacent intact plots were characterized by higher species evenness as detailed below.

Percentage herbaceous cover

The total percentage cover of the herbaceous layer was significantly higher in logged plots compared to intact forest plots, 100% vs. 40%, respectively (Fig. 1.2A, Table 1.1). However, the extent of herbaceous cover differed according to other site attributes (i.e. logging history x site interaction, Fig. 1.2B). Although all logged plots had higher percent herbaceous cover than their intact counterparts, the herbaceous cover was greater in some logged sites (maximum 130%) than others (minimum 90%). Interestingly, sites with the lowest percentage cover in intact plots (~30%) showed the highest cover in logged plots (~125%). Sites with moderate herbaceous cover in intact areas (~50%) also had more modest levels of herbaceous cover in logged plots (~95%). Percent cover of forbs, grasses, and shrubs were also significantly higher in logged plots, although none of these functional groups responded uniquely to the combination of site and logging history (Table 1.1). In contrast, the percentage cover of vines, which was generally low on average (<1%), was significantly affected by the combination of logging history and site. Most sites had few or no vines in either intact or logged plots, but two sites had some vine cover in logged plots (5:5% & 6:1%) with only one exception that had more vines present in the intact plot (15: 1% intact vs. 0% logged).

Percentage cover of natives

Difference in the percentage cover of native species in logged and intact plots paralleled the patterns in overall percentage cover (~100% in logged plots vs. 40% in intact plots, Fig. 1.3A, Table 1.1). Percentage cover of natives also differed according to the logging history by site interaction. Sites with the lowest percentage cover of natives in intact plots (~25%) showed the highest cover in logged plots (~120%), while sites with moderate native cover in intact areas (~45%) also had more modest levels of native cover in logged plots (~90%). Native forbs, grasses, and shrubs also had greater percent cover in logged plots, although none of these functional groups responded uniquely to the combination of site and logging history (Table 1.1). In contrast, the percentage cover of native vines, which was generally low on average (<1%), was significantly affected by the combination of logging history and site. Most sites had few or no native vines present in either intact or logged plots, but two sites had some vine cover in logged plots (5:5% & 6:1%) with only one exception (15) that had greater native vine cover in its intact plot (15:1% intact vs. 0% logged).

Percentage cover of non-natives

Non-native species cover was significantly higher in logged plots. Intact plots had an average cover of 0.04±1.6% for non-native species, while logged plots had an average non-native cover of 4.1±0.3%% (Fig. 1.3B, Table 1.1). However, the extent of non-native cover was also affected by site, with some sites having more non-native cover than others (max: 2.8±1.2% Site 15, min: 1.9±0.6% Site 2). Accordingly, non-native cover also responded to the interaction between site and logging history (Table 1.1). Although percent non-native cover was similar across intact plots, percent cover of non-natives varied greatly in logged plots (12% to ~0%). In contrast, one site had more non-native cover in the intact plot than logged plot (15: 1% intact vs. 0% logged). Only two functional groups had non-native species recorded during surveying; grasses and forbs. Akin to overall non-native cover, there were significantly more non-native grasses in logged plots (2.0±0.4%) than intact plots (0.03±0.4%) (Table 1.1). In contrast, non-native forb cover wasn't different between logged and intact plots but did respond to the interaction between logging history and site (Fig. 1.4, Table 1.1). Intact plots across all sites had ~0% cover of non-native forbs, while logged plots had more variation; most had low to no non-native forb cover (0-3%) while two sites had significant non-native forb cover (7&30%). The site showing the greatest increase in non-native forbs (30%) was the most southern site closest to population centers (15), with site 10 being the next closest and having 7% cover of non-native forbs in logged plots.

Species Richness

Species richness was higher in logged plots than intact plots. Logged plots had an average of 38 species present, while intact plots had an average of 22 (Fig. 1.5A). Species richness was also higher in logged plots for all functional groups except vines, which had too few occurrences to run this type of analysis (Table 1.1). Interestingly, the species richness of grasses also differed significantly between sites, where there tended to be one more grass species in more south-western sites (~7.3, 11,12,15,17,18, 20,21) than northern and eastern sites (~6.4). Accordingly, grass species richness also differed by the interaction of logging history and site. Although all logged plots had higher species richness of grasses than their intact counterparts, the species richness was greater in some logged sites (maximum: 12.6) than others (minimum 8.7). Interestingly, sites with the lowest species richness of grasses in intact plots showed the highest richness in logged plots (eg. Site 1: 1.2 intact vs. 12.6 logged), while sites with moderate grass richness in intact areas also had more modest levels of grass richness in logged plots (eg. Site 11: 4.9 intact vs. 8.7 logged). The species richness of shrubs was also impacted significantly by site, with southern sites (2,8,10,11,15,17,18,20) having on average half the shrub species richness (~4) than northern sites (~8; 1,4,5,6,7,9,12,21) (Fig. 1.5B).

In general, logged and intact plots had similar plant communities, however numerous species were only recorded in logged plots, although this finding may be skewed by the significantly larger number of logged plots as compared to intact ones. A few species were only found in intact plots; *Carex spicata, Clematis occidentalis, Corallorhiza maculata, Lathyrus palustris, Monotropa uniflora, Phegopteris connectilis, and Rhododendron groenlandicum.* Although the most common species found in intact plots were also common in logged plots, the five most common species varied between logged and intact plots. In intact plots *Aralia nudicaulis, Clintonia borealis, Eurybia macrophylla, Maianthemum canadense* and *Pteridium aquilinum* were the most abundant species. In logged plots *Aralia nudicaulis, Eurybia macrophylla, Pteridium aquilinum, Rubus pubescens* and *Rubus strigosus* were the most abundant species.

Shannon's Diversity

Shannon's Diversity wasn't significantly different between logged and intact plots (Fig. 1.6A, Table 1.1). For grasses, however, there was significantly higher Shannon's Diversity in logged sites (1.7±0.1) than intact ones (0.8±0.1, Fig. 1.6B). Finally, although logging history didn't impact the Shannon's Diversity of shrubs, the site did have a significant influence, where sites 8, 10, 11, 15, 20 had much lower diversity of shrubs than other sites (~0.4 vs. 1.3)

Pielou's Evenness

Intact plots had significantly greater Pielou's Evenness (0.74), than logged plots (0.67, Fig. 1.7, Table 1.1). At the functional group level, only forbs had greater Pielou's Evenness in intact plots (0.7± 0.02) than logged plots (0.6± 0.02), while the other groups showed no differences between intact and logged plots (Table 1.1). Interestingly, grasses did differ according to the interaction between site and logging history. Although intact plots varied widely in their evenness scores for grasses (0.1-0.9), the corresponding logged plots converged to similar Pielou's evenness scores (0.6-0.8), meaning some sites had decreased grass evenness in logged plots, while others showed increases in grass evenness in logged plots.

Environmental correlations

Non-metric multidimensional scaling (NMDS) analysis was used to find correlations between environmental data and herbaceous species composition (Fig. 1.8). The correlation scores with the major axes showed that latitude, longitude and growing degree days (GDD) had the greatest influence on herbaceous community composition. Additionally, slope and aspect of the plot, as well as, acres of the logged opening were less significant, but still exerted an influence on community composition. Of note, coastal sites (Figs. 1.8C, D) showed significantly increased influence of GDD on community composition. Environmental correlations were deemed significant if their correlations with the ordination axes had Pearson and Kendall r-squared values greater than 0.1, the PC-ORD standard setting for environmental association scores.

DISCUSSION

This experiment was designed to determine which species recolonize logged plots and to what extent do logged plots reflect adjacent intact plots in Northeastern Minnesota under a changing climate. Specifically, noting the dearth of research on the understory layer, this research focused on the establishment dynamics of the understory component of Northern Boreal forests. Tree species are often the focus of both research as well as land management practices[1,47,57], with the assumption that the understory layer will naturally regenerate if the canopy is well established. Although northern boreal forests have shown to be somewhat resilient to intense disturbances such as prolonged logging[58–61], this assumption may fail under a changing climate[5]. This may be especially true of understory species, some of which require moist, cool conditions under dense canopies to thrive[60,62], and which are rarely included in restoration efforts aimed at reestablishing these communities.

NMDS analysis of the environmental attributes that shape understory community composition indicate that latitude, longitude and acres had the greatest influence on herbaceous community composition (Fig. 1.8). Different groups of species were found to associate with southern latitudes and western longitudes, while others associated with northern latitudes and eastern longitudes. Our study sites are contained within the Laurentain Mixed Forest Province of Minnesota as defined by the Minnesota Department of Natural Resources [63]; This province contains cool, wet conifer-dominated forests in the north-east and warm, dry mixed hardwood and conifer forests in the south-west. The driving influence of latitude and longitude in NMDS analysis is consistent with this broader trend. In comparison, when the analysis was restricted to coastal sites, they were most influenced by latitude, longitude and Growing Degree Days. The importance of Growing Degree Days is consistent with the fast transition of climate zones as you move away from the lake shore, which is controlled by the temperature regulating nature of the lake[64].

Comparison of logged plots to intact plots in Northeastern Minnesota revealed that the greatest changes to the understory after logging were likely related to increased light levels. Logged plots had significantly higher cover (~100% vs 40%) and 38 more species present than their intact counterparts (Figs. 1.2A & 1.5A). This is consistent with other research in boreal forests, where it has also been found that a primary driver of community changes after logging is a drastic increase in light levels which facilitates growth[9,59,65]. Additionally, because most logging in Minnesota happens in winter when the soil is frozen[66], there was little evidence of soil erosion or disturbance across these sites, another potential cause of increased growth of early successional species. Interestingly, increases in cover from intact to logged plots had different magnitudes depending on the site. Sites with high cover in intact plots showed the lowest cover of the logged plots and visa versa (Fig. 1.2B). This suggests that species already established in the understory of boreal forests may outcompete other species in event of canopy openings[67–69].

Although logged plots had more species present and more overall cover, logged and intact plots had the same average Shannon Diversity scores, while intact plots had 10% greater Pielou’s Evenness scores. These results suggest that the increase in growth and cover in logged plots is primarily driven by the expansion of early successional species that are present throughout the intact forest community but expand in abundance in the presence of increased light levels[70,71]. More importantly, they suggest that these increases in growth don’t translate into more diverse communities and result in less even communities. Boch et al. 2013 argue that species richness is not a good indicator of conservation importance, and is rather an indicator of successional status[72], a finding consistent with this research. Although intact forests tend to have fewer overall species, they harbor late-successional species and are crucial reservoirs for adjacent forests in the final stages of recovery from disturbances such as logging[7,9,73,74].

Another finding of interest is the trajectory and characteristics of the grass community, whose responses across treatments and sites were often different than other functional groups. The Species Richness of grasses was significantly different between sites, even though the overall species richness was not, with the more south-western sites having 1 more grass species than the north-eastern sites. And although the Shannon's Diversity also wasn't different between logged and intact sites for overall cover, the Shannon's Diversity of grasses was significantly higher in logged plots (1.7 vs. 0.8). Grasses also had different trends between logged and intact plots for Pielou's Evenness, showing a significant response to logging history only at specific sites, but showing no overall response of evenness to logging history or site as broad categories. This occurred because evenness scores varied widely in intact plots (0.1-0.9) but converged in logged sites (0.6-0.8) meaning some sites decreased in grass evenness in logged plots, while others increased. All these results taken together suggest that grasses thrive in southern and western sites and after logging, which is consistent with other research on disturbance in boreal forests[65,69,75]. These trends are particularly important to note in reference to a changing climate. As the climate warms and dries we may see a shift to plant species that can tolerate warmer, drier conditions, such as graminoids[37,76–78]. These hypotheses are also supported by the findings in this study that boreal shrub dominated communities are associated with the opposite characteristics of grasses. Species richness of shrubs in southern sites was half that of northern sites (Fig. 1.5B). The Shannon Diversity of shrubs was also significantly lower in southern vs. northern sites (~0.4 vs. 1.3).

Although increased light levels resulting from disturbance can benefit understory species, disturbance also can open niches for the invasion of harmful exotic species[79]. This research suggests that the current threat of invasive species in Northern Boreal forests is low, however, we hypothesize that the threat may increase as human activities expand in the area. Intact vs. logged plots had similar, low abundances of non-native species. In intact sites, the average non-native cover was ~0%, while logged sites had higher non-native cover (4%, Fig. 1.3B), but because logged sites also had higher overall cover the ratio of native to non-native species was consistent from logged to intact plots. However, percent non-native cover was also significantly different across sites, with sites closest to population centers or roads having the greatest non-native cover (Site 15: 2.8%), while sites furthest from roads and towns showed the lowest non-native cover (Site 2: 1.9%), suggesting that the current low threat of invasive species across these sites may be related to the relatively remote nature of the forests of NE MN. Accordingly, percent cover of non-native forbs was highest in the logged plots of sites 10, 15 and 20 (Fig. 1.4), which are the three sites closest to population centers and well-trafficked roads. A similar result was found for the cover of vines. Although most plots, intact or logged, had no vines present, three logged plots in sites 5, 6, and 15 had 1-5% cover of vines. Again, these sites are proximal to roads and extensive disturbance from logging. Visual observations suggest that the vines present at this site may result from seed transportation by logging equipment. All of these results suggest that the forests of Northeastern Minnesota have had a historically low threat from invasive non-native species, but that as human activities continue to spread into this area, we may see non-native species become more of a problem. It is important to note that the current low cover of non-natives in the forests of Northeastern Minnesota also offers a promising opportunity. It is substantially easier to manage small emergent populations of harmful non-natives than it is large well-established ones. Therefore, we would all benefit substantially if agencies and local partners across the region implemented an aggressive early-detection-rapid-response program that would help keep non-natives at a low level. In the face of a changing climate and other human pressures, this would reduce the stressors on the unique boreal forests of NE MN and give them a better chance to adapt and persist.

Overall these results indicate that the logged forests of Northeastern Minnesota currently maintain a lot of the characteristics of adjacent intact forests, however, there is mounting evidence that human activities and climate change could change these dynamics for the worse. Although these results indicate that the diversity of logged plots was equivalent to those of intact plots, observational evidence suggests that slow-growing late-successional species such as clubmosses are absent in the logged plots throughout this study. Newaz et al. 2019 observed similar trends in forests surrounding headwater streams in Ontario; although diversity between clear-cut and intact forests wasn't different, they found that overall species composition was altered in favor of early-successional species and ruderal invasives, and that certain late-seral understory species seemed to be locally extirpated. These observations combined with the results that grasses were associated with logging and warmer and drier sites, indicate that, as the climate continues to change, we may see a state shift away from late-successional boreal species and towards species that thrive under disturbance and warmer, drier conditions. A trend in this direction has already been documented for tree species in boreal forests[32,50,51,80,81] and a few researchers have documented this trend in the understory as well[37,76–78]. As other studies have shown that the understory layer is slow to recover from disturbance[5,82], this evidence suggests that if we hope to retain the characteristic boreal forest in some portions of NE MN we should consider active understory plantings in restoration efforts. Since NE MN forests have been heavily logged for 200 years[21] there are fewer and fewer areas that harbor the full range of boreal species[83], and active plantings may help retain some of our charismatic boreal species by allowing them to persist and adapt in the face ongoing disturbance, fragmentation and climate change[6,84].

We know that our boreal forests are facing multiple stressors; disturbance from resource extraction, human activities that spread non-native species, and a changing climate. All of these impact our northern forests in unique but additive ways. If we hope to retain healthy intact boreal forests in the face of these stressors we may need to implement active strategies. Although the current evidence suggests that these forests have been relatively resilient to disturbance in the past, there is some evidence that climate change may push this region past unprecedent thresholds and that we should take steps to retain healthy and resilient boreal forests[85–87]. Although tree species are often the focus of community analysis and restoration, we should consider the important contributions of understory species to the provision of ecosystem services such as pollination, water filtration and soil retention. If we can limit the spread of non-natives while simultaneously planting full components of tree and understory species in restoration efforts, we can help maintain as well as expand current boreal forest areas, ensuring the delivery of important ecosystem services while maintaining this rare and charismatic plant community for future generations.

Table 1.1. Results of a mixed model analysis of variance (ANOVA) for the plant community composition between paired logged and intact forest plots across Northeastern Minnesota. 16 sites were surveyed using the Braun-Blanquet method. Site and its interaction with logging history (logged vs. not logged) was included as a covariate due to the large geographical spread of the sites.

		Fixed Effect			Covariates			
		Logging History (LH)			Site (S)		LH*S	
		df	*F*	*p*	*df*	*Wald-p*	*df*	*Wald-p*
Cover	Overall	1, 15	57.02	**<0.0001**	1	0.69	1	**0.04**
	Forbs	1, 16	20.26	**0.0004**	1	0.29	1	0.13
	Grass	1, 15	56.09	**<0.0001**	1	0.33	1	0.22
	Shrubs	1, 13	74.08	**<0.0001**	1	0.26	1	0.86
	Vines	1, 16	1.44	0.25	1	0.98	1	**0.005**
Native Cover	Overall	1, 15	49.90	**<0.0001**	1	0.80	1	**0.01**
	Forbs	1, 13	15.53	**0.002**	1	0.75	1	0.96
	Grass	1, 15	40.04	**<0.0001**	1	0.76	1	0.36
	Shrubs	1, 13	23.48	**0.0003**	1	0.86	1	0.85
	Vines	1, 16	1.44	0.25	1	0.98	1	**0.005**
Non-Native Cover	Overall	1, 31	41.40	**<0.0001**	1	**<0.0001**	1	**<0.0001**
	Forbs	1, 15	2.27	0.15	1	0.97	1	**0.01**
	Grass	1, 13	10.74	**0.006**	1	0.92	1	0.21
	Shrubs	--	--	--	--	--	--	--
	Vines	--	--	--	--	--	--	--
Species Richness	Overall	1, 16	44.00	**<0.0001**	1	0.71	1	0.80
	Forbs	1, 15	16.9	**0.0009**	1	0.91	1	0.33
	Grass	1, 51	12.91	**0.0007**	1	**<0.0001**	1	**<0.0001**
	Shrubs	1, 15	8.16	**0.01**	1	**0.02**	1	0.44
	Vines	--	--	--	--	--	--	--
Shannon's Diversity	Overall	1, 15	2.03	0.17	1	0.47	1	0.71
	Forbs	1, 15	0.30	0.59	1	0.24	1	0.10
	Grass	1, 15	37.26	**<0.0001**	1	0.81	1	0.35
	Shrubs	1, 15	0.17	0.69	1	**0.02**	1	0.99
	Vines	--	--	--	--	--	--	--
Pielou's Evenness	Overall	1, 15	9.81	**0.007**	1	0.84	1	0.97
	Forbs	1, 15	11.84	**0.004**	1	0.46	1	0.11
	Grass	1, 15	0.58	0.46	1	0.81	1	**0.02**
	Shrubs	1, 15	1.52	0.24	1	0.33	1	0.52
	Vines	--	--	--	--	--	--	--

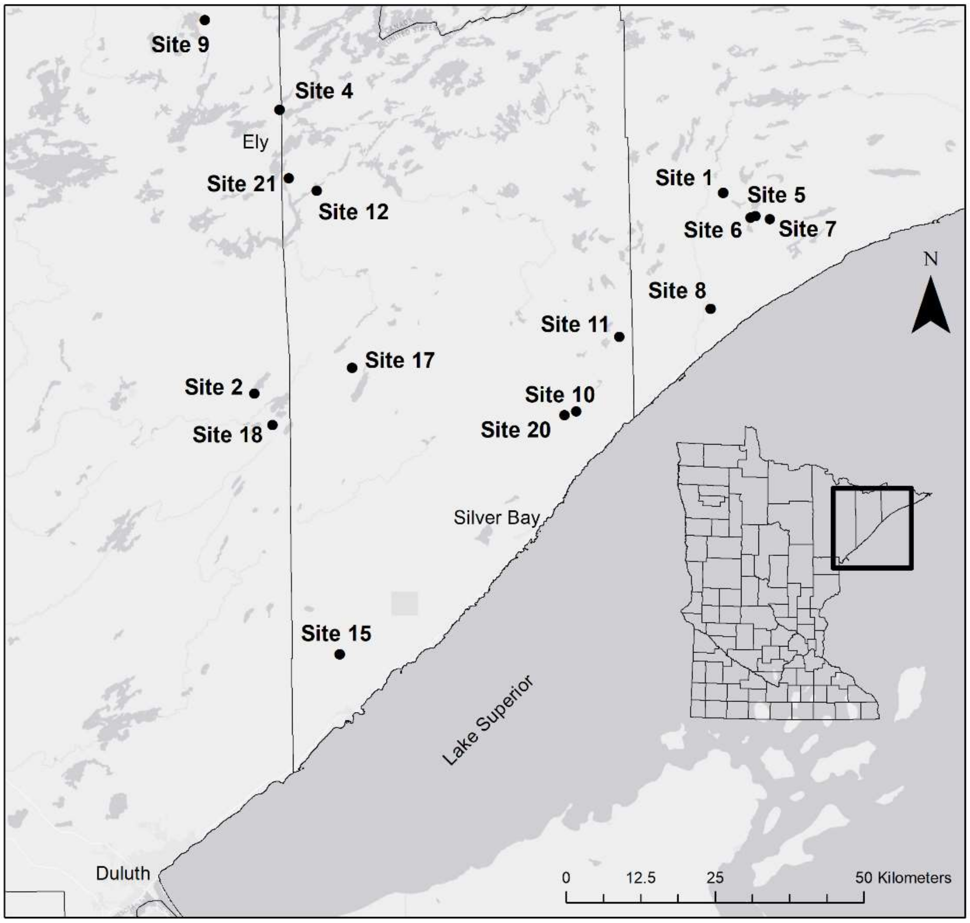

Figure 1.1. Location of 16 survey sites in Northeastern Minnesota. Each site was comprised of two plots, one logged plot and one intact plot. Plots were chosen so that intact plots had similar characteristics (such as elevation, slope, aspect and soil moisture) to the corresponding logged plots. Logged plots had been identified as part of the Adaptation Forestry project between the Etterson lab at the University of Minnesota Duluth and the Nature Conservancy.

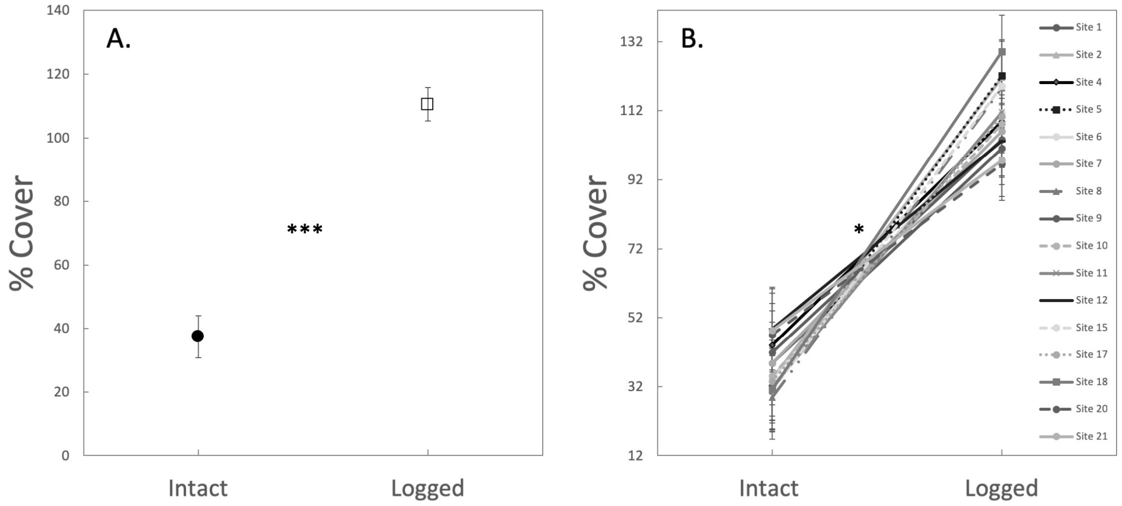

Figure 1.2. Average percent cover between intact and logged plots. Pairs of intact and logged plots were surveyed via the Braun-Blanquet method across Northeastern Minnesota. Values reported are least square means with standard error. Significant effects for population are reported as: * $p<0.05$, ** $p<0.01$ and ***$p<0.001$.

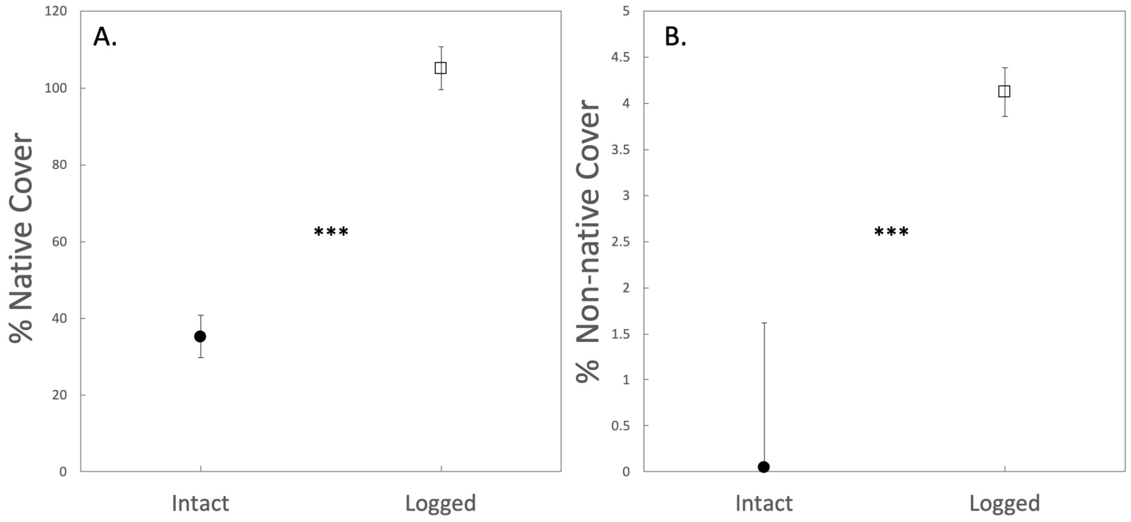

Figure 1.3. Average percent cover of a) native and b) non-native species between intact and logged plots. Pairs of intact and logged plots were surveyed via the Braun-Blanquet method across Northeastern Minnesota. Values reported are least square means with standard error. Significant effects for population are reported as: * $p<0.05$, ** $p<0.01$ and ***$p<0.001$.

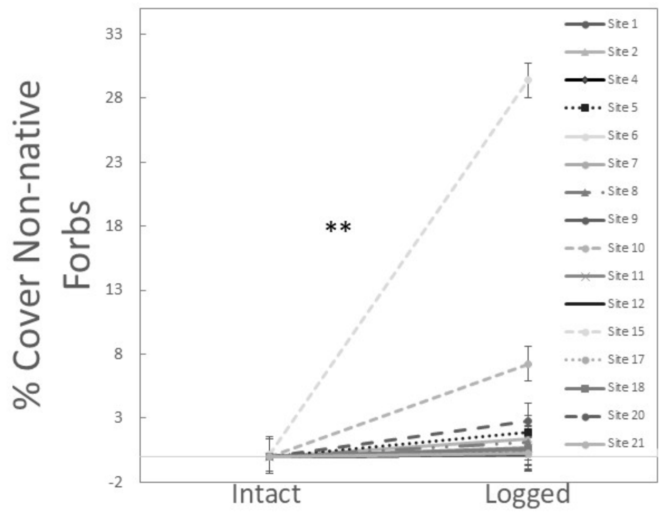

Figure 1.4. Average percent cover of non-native forb species between intact and logged plots. Pairs of intact and logged plots were surveyed via the Braun-Blanquet method across Northeastern Minnesota. Values reported are least square means with standard error. Significant effects for population are reported as: * p<0.05, ** p<0.01 and ***p<0.001.

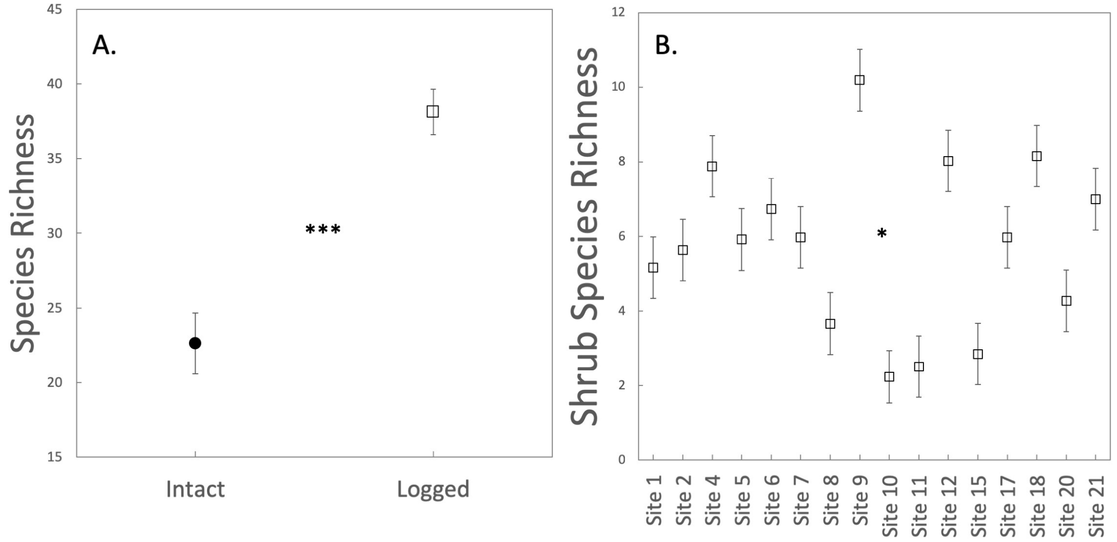

Figure 1.5. Average species richness between a) intact and logged plots and b) individual sites in the study (each site have one logged and one intact plot). Pairs of intact and logged plots were surveyed via the Braun-Blanquet method across Northeastern Minnesota. Values reported are least square means with standard error. Significant effects for population are reported as: * p<0.05, ** p<0.01 and ***p<0.001.

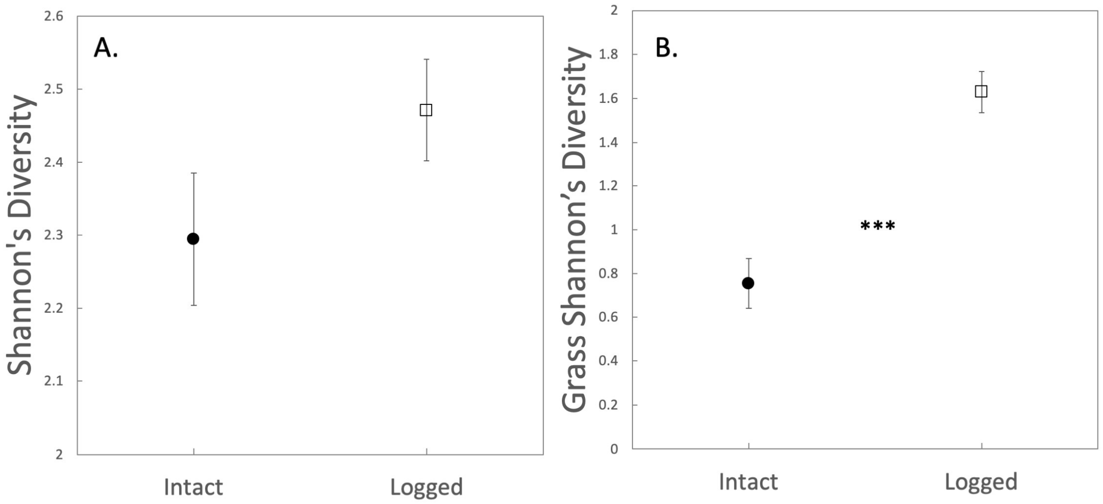

Figure 1.6. Average Shannon's Diversity between intact and logged plots. A) Shannon's diversity of the whole plant community and b) Shannon's diversity of the grass community. Pairs of intact and logged plots were surveyed via the Braun-Blanquet method across Northeastern Minnesota. Values reported are least square means with standard error. Significant effects for population are reported as: * p<0.05, ** p<0.01 and ***p<0.001.

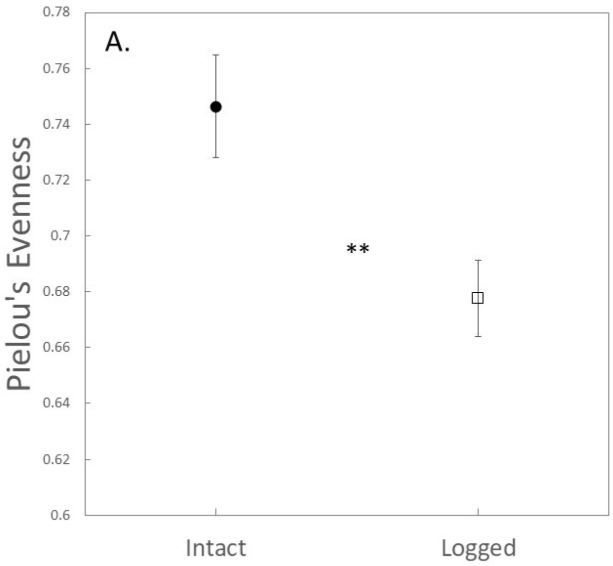

Figure 1.7. Average Pielou's evenness between intact and logged plots. Pairs of intact and logged plots were surveyed via the Braun-Blanquet method across Northeastern Minnesota. Values reported are least square means with standard error. Significant effects for population are reported as: * p<0.05, ** p<0.01 and ***p<0.001.

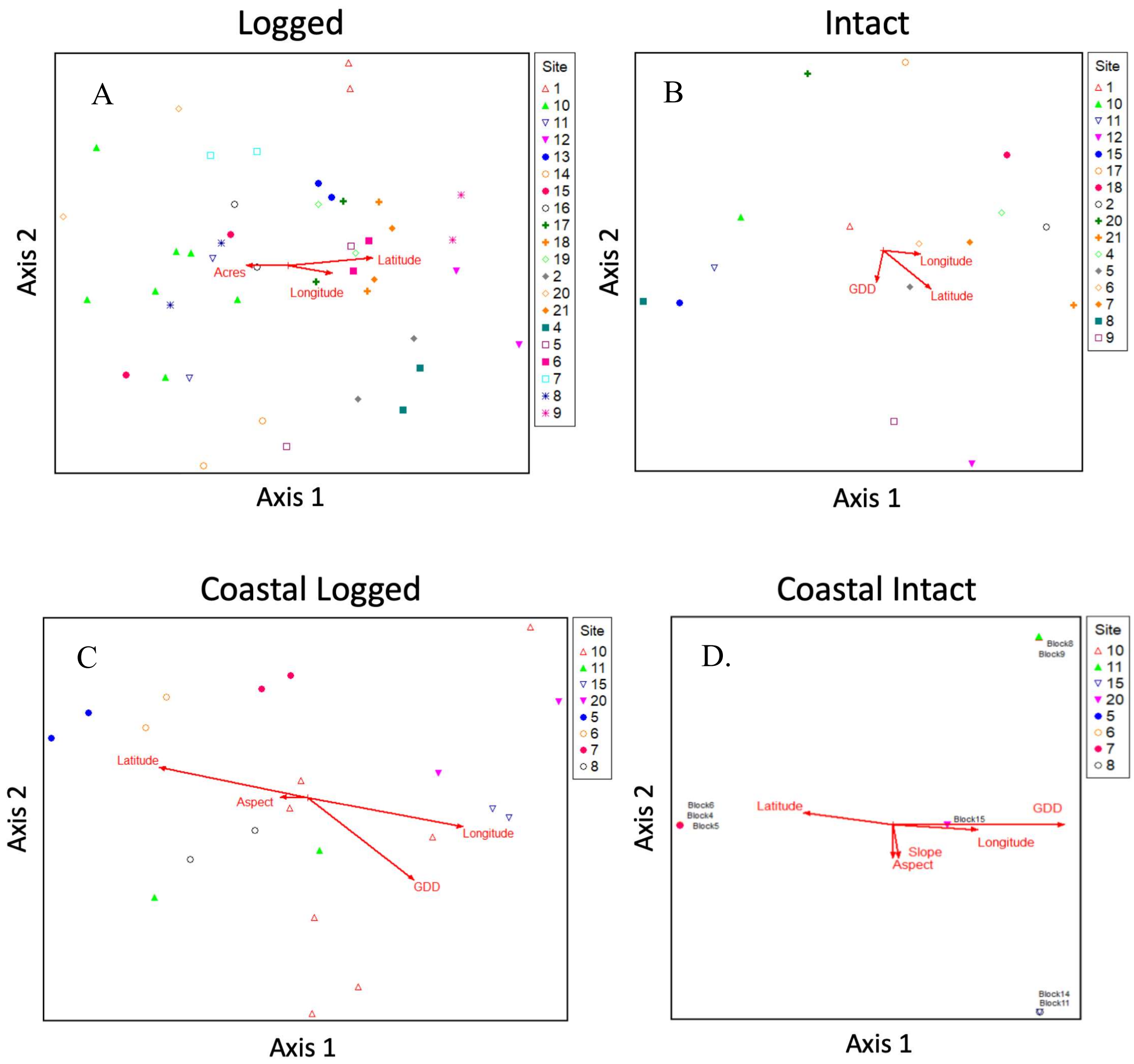

Figure 1.8. Results from non-metric multidimensional scaling (NMDS) analysis for a) logged vs. b) intact plots run in PC-ORD on 'slow-and-thorough' mode with the standard parameters. Pairs of intact and logged plots were surveyed via the Braun-Blanquet method across Northeastern Minnesota; the data from which made up the main matrix in the analysis. Environmental data for each plot was also collected and used as the correlation matrix. A subset of the plots, c) logged and d) intact plots adjacent to Lake Superior, were analyzed separately because they consistently proved to be driven by different types of environmental data. Red arrows show environmental data that significantly influences the spread of plant species in the multi-dimensional space and the direction of that influence. Points located near the arrow end are positively correlated with that variable, while points at the far end are negatively correlated with the environmental variable.

CHAPTER II

Response of herbaceous forest species to simulated climate change

INTRODUCTION

Herbaceous understory species are literally and figuratively overshadowed by trees in forest ecosystems. Even though understory species account for at least two thirds of species diversity in forest ecosystems[88–90], the scientific literature is dominated by studies that exclusively focus on trees. This is an important oversight because of the vital functional role played by this species-rich layer[11,12], which, if unaccounted for, could lead to erroneous conclusions about forest population dynamics[91,92]. The lack of knowledge about herbaceous species is especially concerning in the context of forest restoration[47–49,57]. Forest restorations focus almost exclusively on tree species, with exceedingly few restoration plantings including even a single understory species[48,49] and few studies evaluate the success or diversity of the herbaceous layer after a restoration intervention[93,94]. In fact, herbaceous species are rarely the focus of restoration except in ecosystems where trees are rare or non-existent[1–4]. For example, grassland restoration efforts center on a diverse mix of grasses and forbs, with restoration methods in these systems backed and evaluated by scientific research[95–101]. Moreover, restoration material of herbaceous prairie species is widely available from native prairie plant businesses that also provide guidance to managers for successful projects[102]. There is no equivalent wealth of information or restoration material for forest herbaceous understory species.

The few studies that have tracked the forest herbaceous understory layer show that it is slow to recover after disturbance[49,78,103,104]. For example, Duffy and Meier

(1992) found that the understory community in Appalachian forests had not returned to its pre-disturbance composition even 100 years after logging [5]. In Iowa forests, Brudvig et. al 2011 also found slow recolonization of the understory layer and attributed this to low dispersal, calling into question the idea that the herbaceous layer will quickly return as tree species become established[6]. Although in some systems there may remain a viable seedbank after deforestation, given the impending impacts of climate change, including more frequent and more destructive fires[105,106], as well as other long-term human impacts on forest systems, it is prudent to consider including understory species in restoration efforts to ensure that functional forest ecosystems are reestablished.

The forest herbaceous understory layer provides essential ecosystem services[4,9,10,12,90]. In addition to providing food and shelter for animal species[107], understory species also impact tree recruitment, and therefore the ultimate diversity and make-up of the overstory tree community[15,16,108]. The herbaceous layer plays an integral role in maintaining the hydrology of a region and influences water infiltration, filtration and total evapotranspiration[13]. The roots of understory species hold soil and prevent erosion along streams and steep slopes[14]. Importantly, diverse plant communities are thought to be more resilient in the face of disturbance and the invasion by non-native species[18,19,109]. And diverse communities are more effective at providing essential ecosystem services[110–112]. There is, therefore, ample evidence that more consideration should be given to the herbaceous layer in restoration and conservation efforts.

Maintaining healthy, well-functioning ecosystems that contain a diversity of species and functional groups becomes especially important as we grapple with climate change. In the Midwest, climate change is predicted to cause more-intense rainfall events, separated by periods of longer drought[31–33]. Intense rainfall events may increase the magnitude and frequency of flooding that causes extreme erosion in forest ecosystems. In Minnesota, where this study took place, a large portion of the state has been converted from diverse, natural plant communities to farmland or urban developments[113]. Because diverse plant communities are better buffers against flooding and erosion and are better at providing ecosystem services of all kinds[9,10,14,110,112], it becomes increasingly important to preserve and restore remaining areas of natural habitat to help ameliorate the potential negative impacts of climate change.

Climate change has also increased average temperature in Minnesota by 0.6–1.7°C compared to the early-1900s, and it is predicted that the average temperature will rise another 3-5°C by the end of this century[31–33]. Because some plant species have been shown to have the highest fitness in specific climate envelopes[114,115], increasing average temperatures may put novel stresses on our native plant communities. Accordingly, increasing average temperature has been shown to cause changes in plant community compositions[38,39,78], which may affect an ecosystem's ability to buffer against flooding or provide other important ecosystem services, especially if native species are replaced by monocultures of invasive non-natives[112]. Therefore, not only do we need to consider planting understory species to help restore forested systems, we need to consider how best to do this under increasing temperature. Some thought has gone into this dilemma, with most work restricted to tree or grass species[42–44,46,50,51,116–119]. There is some evidence that we may need to change our plant material sourcing policies, so that we source plants that are best suited to the changing climate of an area. Studies have had mixed results, however, with some studies showing that locally adapted plants are still best suited to planting areas[119–121], while others suggest that plants sourced from drier, warmer areas are already thriving better than locally sourced material[43,44,46,51,122]. However, to our knowledge, no previous work has been done to investigate the effect that climate change will have on the success forest understory restoration.

High latitude areas, such as boreal forests, are predicted to experience the greatest increases in temperature under climate change[31,33], and because these communities are historically adapted to cold conditions, they are also predicted to have the greatest changes in community composition[38,39]. Because of the extreme climate change that has already occurred in the mixed boreal forests of northern MN and the predictions for future change, restorations in northern climates may have a greater probability of persistence if plant material from the southern portion of boreal species' ranges is used for restoration. To address this issue, we studied two common boreal species, Canada mayflower (*Maianthemum canadense* Desf. Greene) and Lindley's aster (*Symphyotrichum ciliolatum* (Lindl.) Á. Löve & D. Löve) that are of sufficient abundance that they may influence the establishment of dominant tree species and total evapotranspiration as documented for other understory species[11,13]. Additionally, *M. canadense* has been designated an indicator species for the sub-boreal and boreal, mixed conifer-hardwood, and conifer forests of the United States and Canada[123]. These species were also chosen because their ranges are limited to northern forests, with the southern extent of their ranges occurring in northern Minnesota, which means they may face extirpation under extreme climate scenarios without human intervention. In this study we test how climate change would impact the growth and success of different sources of herbaceous species native to Minnesota. A southern and northern source of both species were grown in a randomized split-plot design with half the plants exposed to simulated climate change. Plant size and reproductive output were measured and analyzed across treatments. Specifically, we were interested in 1) whether there are trait differences between northern and southern populations of Minnesota native understory species, 2) whether the two populations respond differently to simulated climate change, and 3) specifically whether the northern population has higher or lower fitness under low water availability and/or elevated temperature? We hypothesized that the southern populations of our two species would exhibit traits making them better adapted to withstand warmer, drier conditions; specifically, increased size and growth, thicker leaves, and increased flowering.

MATERIALS AND METHODS

Study Species

This research focuses on two common and wide-spread species in the mixed boreal habitats of northern Minnesota (Chapter 1), *Symphyotrichum ciliolatum* (Lindley's aster) and *Maianthemum canadense* (Canada mayflower). Besides the rationales mentioned in the introduction for choosing these two species, we also found in our survey work from Chapter 1 that these two species' associations with environmental variables, especially latitude, shifted appreciably between intact and logged plots in NMDS analysis, with different site affinity by latitude being more evident in intact plots. In general, *M. canadense* is a low-growing, rhizomatous, understory perennial (2-6m spread)[123,124]. Plants are 3-15cm tall and produce a single leaf until they bolt after which they produce 2-3 leaves and <40 flowers. *M. canadense* is considered a spring ephemeral and flowers early, from May to June, depending on latitude[123]. It is also bird dispersed but has low recruitment from seed. *M. canadense* is known to tolerate low-light levels and is used as an indicator of late-successional forests[123]. Our second study species, *S. ciliolatum,* is a common, perennial, aster[125,126]. Plants are ~1m tall and spread via rhizomes, tending to have a branched caudex. It flowers late in the growing season from August to October. Panicle flowers contain anywhere from 200 to 1000 flowers arranged on 10 to 20 main reproductive branches. Wind-blown seeds facilitate spread and recruitment. *S. ciliolatum* occurs in diverse light conditions but is often found along forest margins and canopy gaps[126].

Simulated Climate Change Experiment

To examine whether population traits and fitness of native species differed under simulated climate change, two populations from each species were grown out-of-doors in a common environment under manipulated temperature and water conditions at the University of Minnesota Duluth Research and Field Studies Center (UMD-RFSC, 46.87˚N, 92.04˚W). However, at the very beginning of the season, the source populations were located approximately 115 miles apart, with the northern populations sourced from Cloquet, MN and initially grown as seedlings in greenhouses by Boreal Natives, Inc., while the southern populations were sourced from near Princeton, MN and grown as seedlings in greenhouses by Prairie Restorations, Inc. Boreal Natives and Prairie Restorations are both part of a larger company with locations throughout Minnesota, which keeps detailed records on the original seed-sourcing locations for all their plant materials.

Seedlings were transplanted in June into tree pots (10.16cm^2 x 30.48cm deep; CP412CH, Stuewe & Sons, Inc., Tangent, Oregon) filled with PROMIX-HP Mycorrhizae (Premiere Tech Horticulture, Quakertown, Pennsylvania) for a total of 1440 plants (2 species x 2 populations x 360 individuals). The tree pots were positioned in 33cm^2 crates (TRAY10, Stuewe & Sons, Inc., Tangent, Oregon) with 9 pots per crate. To achieve a balanced randomized design, one pot per crate was filled with soil but was not planted (Fig. 2.1). We obtained 360 individual *S. ciliolatum* plants from a local native plant nursery (Boreal Natives more info). For *M. canadense*, we obtained 100 plants which divided into three or more clones to obtained 360 experimental units that had 1-5 leaves.

Temperature and Water Treatments

Plants were organized in a fully randomized split plot design under six rainout shelters, one block per shelter (Fig. 2.1). For each species, two source populations (i.e. north, south) were subjected to a factorial combination of temperature (ambient and +2°C) and water availability treatments (well-watered and -15% soil moisture). To control water availability, the seedlings were planted under 3.7m x 7.9m rainout shelters with open air sides and overlaid with neutral shade cloth (-80% tramsmission; Greenhouse Megastore, 80% Black Knitted Shade Cloth, SC-BL80, Fig. 2.2B) to reduce light damage. Water was delivered to individual plants at two levels by hand-watering. Half of the plants were well-watered, receiving water 1-2 times per week as necessary, while the other half of the plants were only watered after soil moisture reached -15% of the well-watered cohort as measured by volumetric water content via a ThetaProbe (Delta-T Devices, ML3 ThetaProbe Soil Moisture Meter). Tarps on the sides and ends of the shelter were lowered during rainy, windy conditions to maintain the watering treatment. To prevent experimental plants from accessing soil moisture, each pot was lifted ~ bi-weekly. Temperature was elevated with open-top chambers of the ITEX Hexagon Design[127,128]. Chambers were constructed with Sun-Lite® HP fiberglass solar glazing (85-90% transmission, Solar Components Corp, Manchester, New Hampshire, Fig. 2.2A). Previous studies show that these chambers increase temperature by ~1.5°C but do not significantly impact relative humidity[127,129].

Plant measurements

To examine plant response to simulated climate change, we measured plant size (height, stem diameter), leaf specific traits (number of leaves, leaf size, and specific leaf area), and traits related to fitness (survival, date of first flower, number of flowers, buds and reproductive branches, and above-ground biomass), as well as date of senescence. Plant size, as well as leaf number and size, should give us an indication of the ability of plants to provision resources over the course of the growing season, while SLA should give an indication of a plant's ability to endure warmer, drier conditions. Fitness traits should provide an indication of the impacts of the treatments on the longevity and health of the population and its future generations. Finally, phenology occurrences should indicate how changes in the timing of important life cycle events may impact plant responses to the treatments, as well as give indications of any downstream effects on dependent fauna and ecosystem processes.

Plant size*:* Size metrics were recorded in June, July and October with variations from this schedule based on labor capacity or trial runs that showed no significant changes in a metric. Height was measured twice for *S. ciliolatum* but only once for *M. canadense*. Stem diameter was measured at the soil line three times in June, July and October.

***Leaf traits**:* Leaf number was recorded three times for *M. canadense* but only twice for *S. ciliolatum* due to time limitations later in the growing season. Leaf length and width were recorded in July only for *S. ciliolatum.* No significant results were obtained from leaf width and therefore that analysis is not included in the results of this study. Specific leaf area (SLA) was based on leaf disk samples. In August, disks of leaf tissue were obtained from the uppermost fully expanded leaf subtending the reproductive branches with a standard hole punch (6 mm in diameter – 28mm^2). Leaf disks were dried at 70 °C for 72 hours and weighed. SLA was calculated as mm^2 per mg of leaf tissue.

***Fitness**:* Date of first flower was recorded for *S. ciliolatum* when the first petal on any given flower was visible. Flower, bud and reproductive branch number (emanating from the main stem) were measured three weeks after the date of first flower for *S. ciliolatum*. Bud number included flower buds yet to open. *M. canadense* didn't flower during this study, therefore metrics related to flowering were not measured for this species. At the end of the growing season, above-ground biomass was harvested for both species by clipping the plants at the soil line. The biomass was dried at 70 °C for 72 hrs and weighed.

Senescence: Senescence was recorded for *M. canadense* on the date that all leaves had lost their color. Above-ground biomass was collected for *S. ciliolatum* before the plants senesced, as these plants senesce very late in the season.

Data Analysis

Data was analyzed by mixed model ANOVAs (JMP Pro 13, SAS Institute Inc. Cary, NC, 1989-2019). Because the two species are morphologically distinct and preliminary analyses showed different treatment responses, the dataset was divided and species were analyzed separately. Fixed effects included: temperature treatment, water treatment, and population of origin, as well as all two-way interactions and the three-way interactions. Shelter (i.e. blocking factor) was included as a random effect. Data were transformed as necessary to meet analysis assumptions using the natural log or square root transformations. However, figures show untransformed data to facilitate interpretation of the results.

RESULTS

Morphological and phenological differences between northern (i.e. local) and more southern populations were detected for both species in this study. Overall, *S. ciliolatum* was sensitive to both temperature and water manipulations as main effects, but rarely as a two-way interaction between the treatments. However, populations responded to the treatments differently for several traits (i.e. population x temperature x water). In contrast, *M. canadense* was simply less responsive to the environmental treatments, but when they were significant, they were more often manifested as an interaction between temperature and water, rather than as main effects. These results for size traits, leaf traits, and reproductive traits are described in more detail below for each of the two species separately.

Symphiotrichum ciliolatum (Lindley's Aster)

The northern and southern populations of *S. ciliolatum* differed significantly from each other for almost half of the traits measured in this experiment (Table 2.1). The temperature treatment generally had strong effects on plant phenotype, significantly affecting 80% of the traits. The watering treatment generally had weaker effects, especially early in the summer, but the cumulative effects of water shortage became more pronounced as the season progressed. For some traits, populations responded to the environmental treatments in different ways (i.e. significant population x treatment interactions).

Size traits: Plant height different between populations in June (Table 2.1). At this time, plants from the northern population were on average 45% taller than plants from the southern population (Fig. 2.3A). Although the temperature and watering treatment did not have significant main effects or two-way interactions that affected plant height, the three-way interaction between population, temperature, and water treatment was significant. After only two weeks in the environmental treatments, there were particularly striking differences in population response to the elevated temperature/low water treatment compared to the other treatment combinations. Under the elevated temperature/low water treatment, northern plants were 11% shorter relative to the ambient/low water, while southern plants were 10% taller in elevated/low water relative to all the other treatment combinations. Interestingly, the northern population also did poorly under ambient temperature while being well-watered and had about the same average height as northern plants exposed to low water/elevated temperature. Height growth rate from June to July, in contrast, was more strongly influenced by the main effects of the temperature and watering treatment, although the three-way interaction between population, temperature, and water was still marginally significant (Table 2.1). On average, plants exposed to elevated temperature grew 5% faster than those in the ambient temperature treatment; plants that were well watered 7% faster than those that were subjected to the low water treatment.

The diameter of stems in June did not differ between northern and southern populations but was significantly affected by the temperature treatment (Table 2.1). Plants in the elevated temperature treatment had 7% wider stems than plants grown in ambient temperature (Fig. 2.3B). In addition, although the main effect of the watering treatment was not significant for this trait, the populations responded water availability in different ways (i.e. significant population x watering treatment interaction). Specifically, plants from the northern population had 3% wider stems than the southern population when well-watered but 8% narrower stems under water shortage.

Leaf traits: Leaf traits included leaf number in June, as well as length of the upper-most fully expanded leaf, and specific leaf area (SLA) measured in July. In June, leaf number differed between populations with the southern population having 2% more leaves than the northern population (Table 2.1). There were no other significant effects that influenced leaf production. Leaves of the northern population were 26% longer than leaves of the southern population. Leaf length was also significantly affected by the temperature treatments; leaves were 3% longer under elevated temperature compared to ambient temperature. In addition, there was a significant three-way interaction for this trait between population, temperature, and water treatments (Fig. 2.3C). Leaf length of the southern population was greater in elevated and the longest under elevated temperature/high-water availability. In contrast, the northern population's leaf length responded uniquely to the water treatment depending upon the temperature treatment. In ambient conditions leaf length was greatest with high water availability, while in elevated temperature leaf length was greatest with low water availability.

Populations did not differ with respect to specific leaf area (SLA) on average. However, this trait exhibited plastic responses to both the temperature and water treatments (Table 2.1). Plants grown in elevated temperature had 4% lower SLAs (i.e. thicker leaves) than those in ambient conditions (Fig. 2.3D). Plants grown in the low-water treatment had 14% lower SLA than plants grow high in the well-watered treatment. However, the interaction between temperature and water also had significant effects on SLA with the lowest values in the elevated temperature/low water treatment combination. Finally, although not quite significant (p=0.07, Table 2.1) the northern and southern populations tended to have different responses to the combination of temperature and water treatments. First, both populations had low and equivalent SLA values in the low water treatment regardless of the temperature treatment. In contrast, populations responded differently to temperature when well-watered. SLA of the southern population dropped 13% under elevated compared to ambient temperature when well-watered, while the SLA of the northern population was generally higher and did not change in response to temperature.

Reproductive traits and biomass: To assess aspects of seasonal reproduction and fitness, we recorded the date of first flower and, three weeks later, the number of flowers and buds per plant as well as end-of-the-growing-season above-ground biomass. There were highly significant differences for flowering phenology between the northern and southern populations (Table 2.1). The northern population started flowering at the beginning of August, 26 days earlier than the southern population which began flowering in early September. The watering treatment had a marginally significant effect on flowering phenology ($p = 0.07$) with plants in the low-water treatment tending to flower about two days later relative to their well-watered counterparts (Fig. 2.3E).

To capture flower production at the same phenological stage, the number of open flowers and unopened buds were measured 21 days after the first flower opened for each individual plant in the experiment. The number of flowers that had already opened three-weeks after the date of first flowering differed significantly between populations (Table 2.1) with the southern plants having already produced three times as many flowers as northern plants at this phenological stage (Fig. 2.3F). Although flower production was 22% higher in the elevated temperature treatment on average (main effect), this was largely due to the positive response of the southern population to warmer temperature (population x temperature treatment). Specifically, southern plants produced 26% more flowers in the elevated vs. ambient treatment, whereas the northern population has a negligible response to temperature.

The potential for continued reproduction to the end of the growing season, as measured by the number of unopened buds, did not differ between populations on average (Table 2.1). Bud number was, however, strongly affected by the temperature treatment with plants exposed to elevated temperature producing 13% more buds compared to plants in exposed to ambient temperature (Fig. 2.3G). Moreover, the northern and southern populations responded to both the temperature and water treatments in different ways as indicated by a significant population x water treatment interaction and a significant population x temperature x water treatment interaction. When exposed to ambient temperature the southern population produced 3-4% more buds than the northern population regardless of water availability. However, when exposed to elevated temperature, the populations responded to water availability in opposite ways. Under well-watered conditions, the northern population produced 13% more buds than the southern population, whereas under low-water conditions, the southern population produced 11% more buds than the northern population.

Seasonal growth, as measured by above-ground biomass, also showed strong effects of the environmental treatments but no differences between populations either as a main effect or as an interaction temperature or water (Table 2.1, Fig. 2.3H). Compared to the ambient temperature treatment, plants grown in the elevated temperature treatment produced 20% more above-ground biomass by the end of the growing season. In addition, there was a significant effect of the watering treatment with well-watered plants producing 14% more above-ground biomass than those with limited water availability.

Maianthemum canadense **(Canada Mayflower)**

The northern and southern populations of *M. canadense* differed significantly from each other for more than half of the traits reported here (Table 2.2). However, the temperature and watering treatments only had a significant effect on one of these traits as detailed below.

Size traits*:* The northern and southern population of *M. canadense* differed significantly for height in June (Table 2.2). The southern population was 6% taller than the northern population (Fig. 2.4A). Plant height, however, did not differ between the environmental treatments as main effects or as interactions with temperature and water. Similarly, stem diameter differed between populations but not in response to the temperature and water treatments (Fig. 2.4B). Stems of the southern population were 11% wider than the stems of the northern population. These populations differences were retained to the end of the growing season (data not shown).

Leaf traits: The number of leaves per plant differed significantly between the northern and southern population during the middle of the growing season in July (Table 2.2). At this time, the northern population had 69% more leaves than the southern population (Fig. 2.4C). There was also a marginally significant interaction between population, water, and temperature treatments for this trait ($P = 0.08$) with the northern population tending to show greater plasticity in response to treatment combinations compared to the southern population.

Specific leaf area (SLA) did not differ between the northern and southern population of *M. canadense*. However, it was the only trait measured on this species that responded to the environmental treatments in a statistically significant way (Table 2.2). Water availability has a statistically significant effect on SLA with plants grown in low water conditions having 2% lower SLA (thicker leaves) compared to plants with ample water (Fig. 2.4D). Temperature also had a marginally significant effect on SLA ($P = 0.08$). The SLA of plants in this experiment responded most dramatically to the combination of the elevated temperature and well-watered treatment where plants produced leaves with~4% lower SLA than in any other treatment combination.

***Phenology and biomass**:* In their first year of growth under these experimental conditions, *M. canadense* plants did not flower and, by early August, the plants began to senesce. Although there were no significant population or treatment effects on the timing of senescence, there was a trend toward later senescence for plants exposed to elevated temperature and low water availability (Fig. 2.4E, water x temperature interaction, P = 0.08). Generally, plants exposed to ambient temperature and well-watered conditions senesced 3 to 5 days earlier than plants exposed to low water and/or elevated temperature conditions, although this was only a marginally significant pattern. At the end of the growing season, above-ground biomass differed significantly between populations (Table 2.2) with the northern population having produced 12% more vegetative material compared to the southern population (Fig. 2.4F). This trait, however, did not respond to either the temperature or water treatment.

DISCUSSION

Herbaceous understory species are overshadowed by trees in forest ecosystems. Even though understory species account for two thirds of species diversity in these systems,[88–90] the scientific literature is dominated by studies that focus on trees. This is an important oversight because of the vital functional role played by this species-rich layer[11,12]. The forest understory layer provides essential ecosystem services[4,9,10,12,90]. In addition to providing food and shelter for animal species[107], understory species also impact tree recruitment, and therefore the ultimate diversity and make-up of the overstory tree community[15,16,108]. The herbaceous layer also plays an integral role in maintaining the hydrology of a region and influences water infiltration, filtration and total evapotranspiration[13]. The roots of understory species hold soil and prevent erosion along streams and steep slopes[14]. Importantly, diverse plant communities are thought to be more resilient in the face of disturbance and the invasion by non-native species[18,19,109]. And Isbell et al. 2011, among others, argue that diverse communities are more effective at providing essential ecosystem services across diverse eocsystems[110–112]. There is, therefore, ample justification for deeper investigation into all aspects of the herbaceous layer, including population differences.

However, to our knowledge, although some work has been done on temperature forest species in general, no previous work has been done to investigate trait differences between populations of temperate herbaceous forest species and their climate responses. This foundational knowledge is an essential first step in considering the best methods for forest restoration under climate change, where the lack of knowledge about herbaceous species is especially concerning[47–49,57]. Exceedingly few forest restoration plantings include even a single understory species[48,49]. Fewer yet evaluate the success or diversity of the herbaceous layer after a restoration intervention[93,94]. This is in striking contrast to grassland restoration efforts that center on a diverse mix of grasses and forbs. Moreover, seed sourcing decisions in these systems are more often based on scientific research that guides decisions about both species composition and source populations within species[95–101]. This lack of information on the best species and populations for forest restoration is especially important in that the forest herbaceous understory layer has been shown to recover slowly after disturbance[49,78,103,104]. For example, Duffy and Meier (1992) found that the understory in Appalachian forests failed to return to its pre-disturbance composition even 100 years after logging [5]. Similarly, Brudvig et. al 2011 found slow recolonization of the understory layer in Iowa forests. They attributed this to low dispersal of these species and called into question the idea that the herbaceous layer will easily return as tree species become reestablished[6]. Although in some systems there may remain a viable seedbank after deforestation, given the impending impacts of climate change, including more frequent and more destructive fires[105,106], as well as other long-term human impacts on forest systems, it is prudent to consider including understory species in restoration efforts to enhance restored forest ecosystem function.

To improve our knowledge of herbaceous species and their responses to a changing climate, this experiment examined traits associated with the growth and fitness of a northern (ie. local) population and a southern population of two native herbaceous species planted under experimentally imposed elevated temperature and low water availability conditions. Given the lack of information on population differentiation in forest understory species, a fundamental question was whether populations sampled from a northern and more southern MN DNR seed zone differed for traits that might be relevant for climate response. We found strong evidence of population differentiate for both of these morphologically distinct species, *Maianthemum canadense* (Canada Mayflower) and *Symphiotrichum ciliolatum* (Lindley's Aster). For *M. canadense,* the southern population had fewer, bigger leaves, wider stems, and lower above ground biomass, while for *S. ciliolatum*, the southern population was smaller statured early in the growing season, had more and shorter leaves, as well as having substantially more flowers which arrived later in the season. These population differences may be related to distinct selective pressures in the contrasting environments from which these populations originated. Although there is a lack of studies on forest understory species and their populations to which we can compare our results, population differentiation has been widely documented for herbaceous species in other systems. In some of these studies, for example work on a grassland species, *Ambrosia artemisiifolia*[130], trait differentiation was hypothesized to be driven by adaptation to different abiotic environmental conditions at the growing sites of distinct populations[131].

A second major goal for this research was to determine whether the northern and southern populations of these two species responded differently to experimental treatments that mimic climate change. Climate change has increased the average temperature in Minnesota by 0.6–1.7°C compared to the early-1900s, and it is predicted to increase another 3-5°C by the end of this century[31–33]. In the Midwest, climate change is also predicted to alter rainfall patterns, potentially causing more intense rainfall events separated by periods of longer drought[31–33]. This study clearly showed that temperature and water availability impacts traits associated with growth and fitness. Confirming our hypothesis, the most striking result of the treatments was a uniquely detrimental effect of low water availability and elevated temperature on the northern population of both species. We saw a clear indication that the northern population was disadvantaged for *S. ciliolatum* across four separate metrics: height, stem diameter, leaf length and SLA, while for *M. canadense* this effect was only obvious in leaf number. Overall however, the southern populations had increased size and fitness under elevated temperature and low water availability, while the northern populations occasionally benefitted in size and fitness under elevated temperature, but this benefit was negated under the combination of elevated temperature and low water availability. For some *S. ciliolatum* metrics (eg. bud number, June stem diameter) the northern population grew larger than the southern population under elevated temperature/high water availability, but its size plummeted when low water availability was combined with elevated temperature. Of particular interest, the northern and southern populations of *S. ciliolatum* had different SLA responses to the combination of temperature and water treatments. Both populations had low SLA (thicker leaves) under low water availability across temperature treatments. However, under well-watered conditions, the southern population had reduced SLA when in elevated temperature, while the northern population's SLA was uniformly high. This suggests that the southern population has a more plastic and adaptive SLA response to elevated temperature, which could better guard it against potential water stress associated with higher temperatures[132–134]. Overall, these trends suggest that the northern populations of both species are negatively affected by the combination of low water availability and elevated temperature, while the southern populations do not suffer from the same negative effects and have more plastic and adaptive responses to these climatic changes. Although to our knowledge no work has approached this subject with native understory species, many studies have been conducted on the combined effects of low water availability and elevated temperature on crop species[135–145]. These studies also found that the impacts of low water and elevated temperature were not simply additive but had uniquely detrimental effects on plant size and physiology. In these studies, there was also evidence that certain plant lineages had better tolerance to this combination of treatments. Many of these studies conclude that planting heat or low-water resistant cultivars will maintain the healthiest, most robust plants as climate change progresses, suggesting that plantings of native species could also benefit from this proactive approach given the evidence of differential success under simulated climate change.

The response of *S. ciliolatum's* flowering to the treatments also indicates an adaptive advantage of the southern population. First, to begin with the southern *S. ciliolatum*s had three times as many flowers as the northern population. This stark difference was then increased under elevated temperature. The northern population had the same number of flowers regardless of the treatments, but the southern population's flower number increased substantially under elevated temperature. The advantage of the southern population was also evident in bud number. Although under well-watered/elevated temperature conditions the northern population had more unopened flower buds than the southern population, under low water/elevated temperature this advantage was lost, and the southern population had significantly more buds. These results have important implications for fitness and survival under climate change. The reproductive fitness of the southern population of *S. ciliolatum* was significantly higher to begin with and it was then able to increase this advantage under elevated temperature. Although to our knowledge no studies have addressed differences in flowering characteristics of temperature forest herb populations under climate change, these results are consistent with broader trends. Research has shown that warming can increase flower number, although the effects seems to be very species- and site-specific[146–148]. However, one study, Michalski et al. 2017, found that the northern population of the grassland species *Arrhenatherum elatius* had a lower flowering probability than southern population when grown in a common environment[149]. Similarly, the results of our experiment suggest that the southern population has multiple advantages over the northern population under climate change.

More broadly, at the species level treatment responses revealed striking differences in trait plasticity between *M. canadense* and *S. ciliolatum*. Specifically, *S. ciliolatum* exhibited strong plastic responses to the treatments overall, with more than half of the measured traits responding to the treatments, while *M. canadense* was largely unresponsive to the treatments, maintaining population differences throughout the season for most measured traits. For *S. ciliolatum,* elevated temperature and well-watered conditions had positive impacts on plant size and fitness. In contrast, for *M. canadense* the only significant response to the treatments occurred in SLA, where well-watered plants in elevated temperature had higher SLA. These differences suggest that these species react to climatic change in different ways. Based the results of this study, *M. canadense* appears to be more resilient to contrasting climate conditions as evidenced by the fact that population differences generally were not altered by the treatments. Importantly, when *M. canadense* did respond, the direction could be seen as mal-adaptive, as high SLA (thin leaves) under elevated temperature could expose this species to water stress. Alternatively, this species' stable size metrics even under low water availability and elevated temperature could mean that it might have the ability to persist and adapt in-situ under climate change. However, since we tracked the size and fitness of the population for only one growing season, this conclusion would be bolstered by tracking this species exposed to these treatments over multiple years. *M. canadense* also didn't flower during this first growing season, and data related to flowering would help elucidate fitness impacts. In contrast, *S. ciliolatum,* responded strongly to climatic changes and appeared to take advantage of elevated temperature and high-water availability by growing larger and, most significantly, producing many more flowers.

This ability of *S. ciliolatum* to respond to changing environmental conditions with increased plant size and flowering could ultimately give this species a competitive advantage in a changing climate. Accordingly, other studies have documented differences in plasticity to environmental changes and associated trade-offs. Prock et al. 1996 showed that reciprocally transplanted herbs across a range of elevations and latitudes had markedly different plasticity to climatic changes. In particular, species of the genus *Guem* were able to take advantage of warming temperatures and increase their biomass and reproductive capacities, while species from the genus *Ranunculus* were constrained by photoperiod responses[150]. Similar results have been found for temperate grasses by Crick and Grime 1987, where they show that different grass species had different amounts of plasticity related to root system development. Interestingly, the two major strategies appeared to be beneficial in different types of climatic scenarios. High plasticity was favored in nutrient-rich, competitive environments, while low plasticity was favored in nutrient-poor environments[151]. Similarly, our findings suggest that the strategies employed by *S. ciliolatum* may confer a competitive advantage as temperatures warm and temperate forests become more productive.

Increases in the size and fitness of *S. ciliolatum* under well-watered conditions are unsurprising, however, it is somewhat surprising that elevated temperature also resulted in increased growth. Elevated temperature generally increases evaporation[152], which can lead to water stress in plants. However, these results suggest that a 2°C increase in temperature is not sufficient to cause water stress when these plants have ample soil moisture. It could also be that *S. ciliolatum* is demonstrating a tradeoff between cold tolerance and competitive ability, suggesting that it has a lower cold tolerance but the ability to capitalize on elevated temperature to increase growth and fitness. In contrast, the stable size metrics of *M. canadense* could suggest that this species falls on the opposite end of the spectrum, having higher cold tolerance but lower ability to capitalize on elevated temperature. This type of trade-off has been documented for other species, although studies of this type have been mainly restricted to tree species[153–155].

Finally, the effects of low water availability and elevated temperature may also change the timing of critical phenological events in a plant's life cycle. *S. ciliolatum* plants tended to flower later in the season by a few days if exposed to low water availability. Interestingly, the flowering results run counter to the prevailing findings, which show that both elevated temperature and low water availability tend to favor earlier flowering[3,156–163]. However, since these results do not meet the standard p-value threshold of <0.05, another trial run should be conducted to see the exact effect of low water availability on the flowering of *S. ciliolatum.* Similarly, *M. canadense* plants tended to senesce later in the season by a few days if exposed to low water availability and/or elevated temperature. In contrast, the findings for senescence align with the majority of studies that find senescence is delayed with rising temperatures[164–166]. Specifically, Rice et al. 2018 found delayed senescence for understory herbs in the boreal-temperate ecotone under elevated temperature[3]. Interestingly, Keenan and Richardson 2015 suggest that fall senescence may be restricted by the timing of spring phenology, and that well documented advances in spring phenology could also advance the timing of critical fall events[167,168]. Regardless of the direction, changes in the timing of flowering or senescence could impact important components and processes in an ecosystem such as herbivores, pollinators, the length of the growing season, nutrient cycling and total evapotranspiration[167].

This experiment was designed to assess trait differences between populations of herbaceous boreal forest species and how these traits relate to fitness under simulated climate change. Temperate boreal forests are facing multiple human-driven challenges; climate change coupled with extensive logging threaten to reduce the biodiversity and functionality of these forests[31,38,39,110]. In northern Minnesota, the logging industry has heavily impacted the northern half of the state for 200 years[21,22], which has resulted in a somewhat homogenous cover of young to mid-aged forests[7,23,169]. These stands lack the full range of herbaceous species representative of old-growth areas[7,8]. The lack of refugia for late-successional species is then compounded by warmer and drier conditions under climate change which may put additional stresses on these species that are adapted to cool, moist conditions. This combination of factors highlights the need to help boreal forests maintain diversity and functionality by active restoration of the herbaceous layer. Although trees are often planted after logging efforts, herbaceous species are rarely included, under the assumption that they will emerge naturally once the canopy is established. Studies in high-elevation Appalachian forests have shown that the understory had not fully recovered 100 years after logging[5]. Although simply including herbaceous species in forest restoration plantings is a needed first step, we should also develop and employ seed transfer guidelines that will establish successful communities under the new stressors of climate change. Our work suggests that sourcing material from southern populations of herbaceous species could result in more successful restoration plantings in a changing climate. Again, we suggest that research be done over many growing seasons to elucidate the long-term impacts of these climatic changes, as these long-term responses will ultimately determine the success of this restoration technique.

CONCLUSION

The reactions of these two morphologically distinct species to simulated climate change suggest that northern, cold-adapted populations of native boreal herbaceous species may be at a competitive disadvantage to their southern relatives as temperature warms and precipitation patterns shift. And the negative impacts of low water availability and elevated temperature on the northern populations of these native Minnesota flora suggest that restoration efforts could benefit from climate-informed plantings. Other research has found that southern sources of *Quercus macrocarpa* already have higher survival in restoration sites across northern Minnesota than local sources of plant material[51]. More broadly, there have been several studies testing the assisted migration of tree species that have found plant material sourced from historically warmer, drier sites are already surviving better than local seed sources in restoration plantings. The authors of these studies conclude that climate-informed plantings of species or ecotypes is a viable option for preserving the productivity and diversity of forest systems[43,44,46,116,118,122,170,171]. Some work on herbaceous species has been done with graminoids, and although the results are more limited, there is also some indication that genotypes better adapted to changing climate conditions could outcompete local seed sources[119,172]. Accordingly, our work also suggests that southern seed sources could improve the success of forest restoration plantings in a changing climate. We also urge further research into the impacts of climate change on herbaceous species, on differential effects across populations, and across many growing seasons so that we may better judge the outcomes of these potential restoration methods.

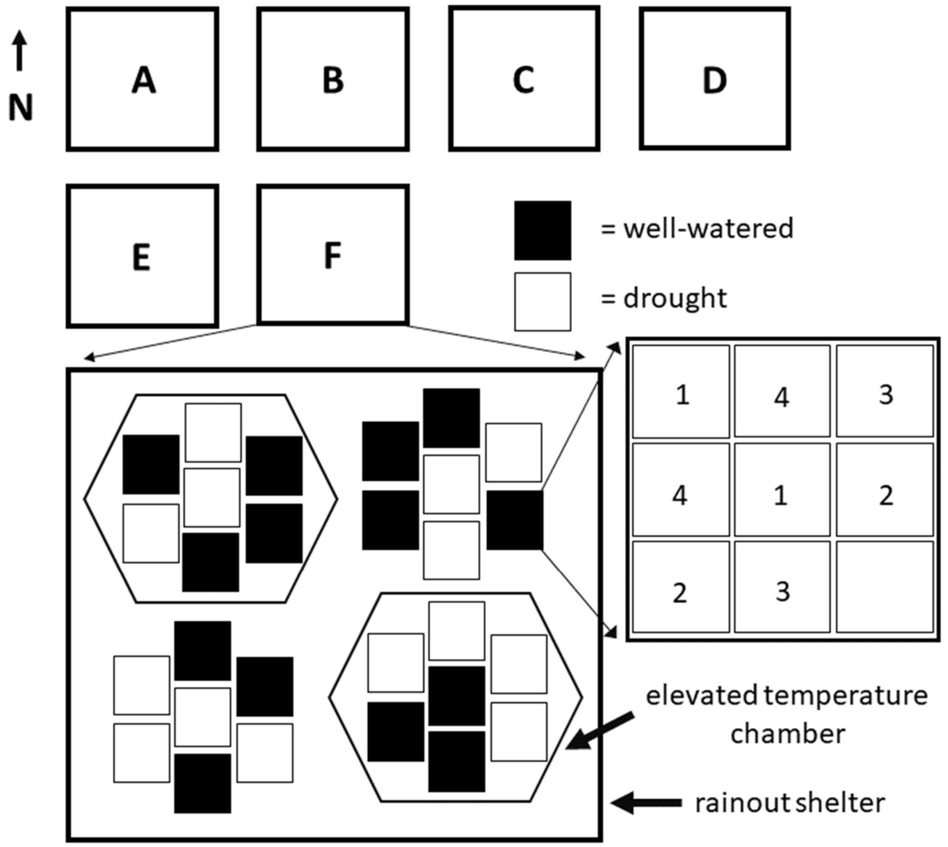

Figure 2.1. Randomized block experimental design. One block was contained under each of 6 rainout shelters (90% transmissible clear roofs with retractable tarps to block out rain). Each block contained 14 crates within open-top elevated temperature chambers (ITEX design) and 14 crates in ambient temperature conditions. Each crate house nine individual plant pots. Each crate of nine pots contained two of each population for each species (1- southern *Symphyotrichum ciliolatum*, 2 – northern *S. ciliolatum*, 3 – southern *Maianthemum canadense*, 4 – northern *M. canadense)*, with one pot in the crate filled only with soil and all randomly assigned within each crate. Plants were placed under the rainout shelters at least 50cm from the edges, and tarps were lowered during rain events. Plants were lifted monthly to avoid root growth out of containers. The watering treatment was randomized by crate within each temperature treatment and water was hand delivered so that droughted plants reached -15% soil moisture before they were watered, while well-watered plants were watered approximately weekly.

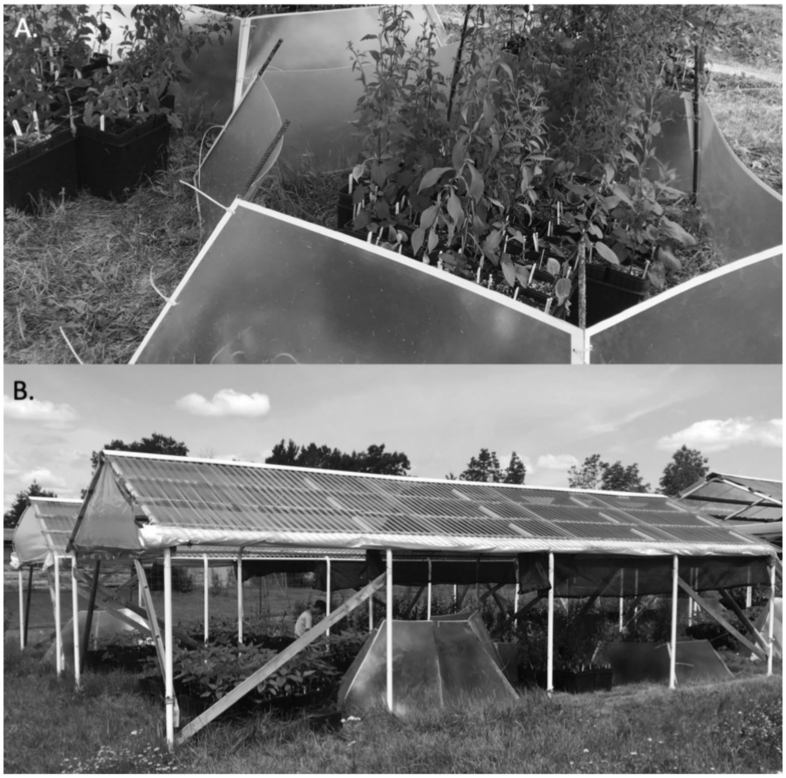

Figure 2.2. Photos of the A) elevated temperature chambers and B) rainout shelters, used to impose/control the temperature and water treatments in this study.

Table 2.1. Results of a mixed model analysis of variance (ANOVA) for traits measured on two populations of *Symphyotrichum ciliolatum* (Lindley's Aster). The populations were grown in a common garden and exposed to a factorial combination of elevated (+2°C) or ambient temperatures and low water availability (-15% soil moisture) or well-watered conditions.

	Pop (P)		Temp (T)		Water (W)		T*W		P*T		P*W		P*T*W	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Height – June[1]	59.03	**<0.0001**	0.17	0.68	0.01	0.91	1.15	0.28	0.03	0.86	0.16	0.69	4.24	**0.04**
Height- early growth rate[2]	0.40	0.53	3.81	**0.05**	6.48	**0.01**	0.11	0.74	0.06	0.80	0.05	0.82	3.61	0.06
Stem Diameter – June[3]	0.74	0.39	5.98	**0.01**	1.08	0.30	0.002	0.97	0.14	0.71	4.28	**0.04**	0.67	0.41
Leaf # – June[4]	4.60	**0.03**	0.74	0.39	0.39	0.53	0.33	0.57	0.02	0.89	0.77	0.38	1.32	0.25
Leaf Length[5]	183.80	**0.0001**	4.10	**0.04**	0.10	0.76	0.52	0.47	1.68	0.19	0.46	0.50	5.18	**0.02**
SLA[6]	1.04	0.31	5.03	**0.03**	56.27	**<0.0001**	3.82	**0.05**	0.69	0.41	0.14	0.71	3.39	0.07
Date of First Flower[7]	582.30	**<0.0001**	0.26	0.61	3.40	0.07	0.02	0.89	1.16	0.28	0.85	0.36	0.06	0.81
Flower Number[8]	460.39	**<0.0001**	13.85	**0.0002**	0.67	0.41	0.0004	0.98	5.36	**0.02**	0.12	0.73	0.96	0.33
Bud Number[9]	0.15	0.70	18.47	<**0.0001**	1.02	0.31	0.05	0.83	0.55	0.46	4.55	**0.03**	4.21	**0.04**
Above Ground Biomass[10]	0.57	0.45	33.19	**<0.0001**	15.20	**0.0001**	0.09	0.77	0.14	0.70	0.04	0.84	1.53	0.22

df for P, T, W and interactions: [1, 3, 4, 6, 10] 1,659; [2] 1,658; [5] 1,657; [7] 1,649, [8] 1,642, [9] 1,639

Wald-p significance values for blocking factor (1 block/ rainout shelter): [1] **0.01**, [2] **0.01**, [3] 0.20, [4] 0.60, [5] 0.66, [6] 0.09, [7] 0.44, [8] 0.22, [9] 0.46, [10] 0.44. *df* = 1 for [1-10].

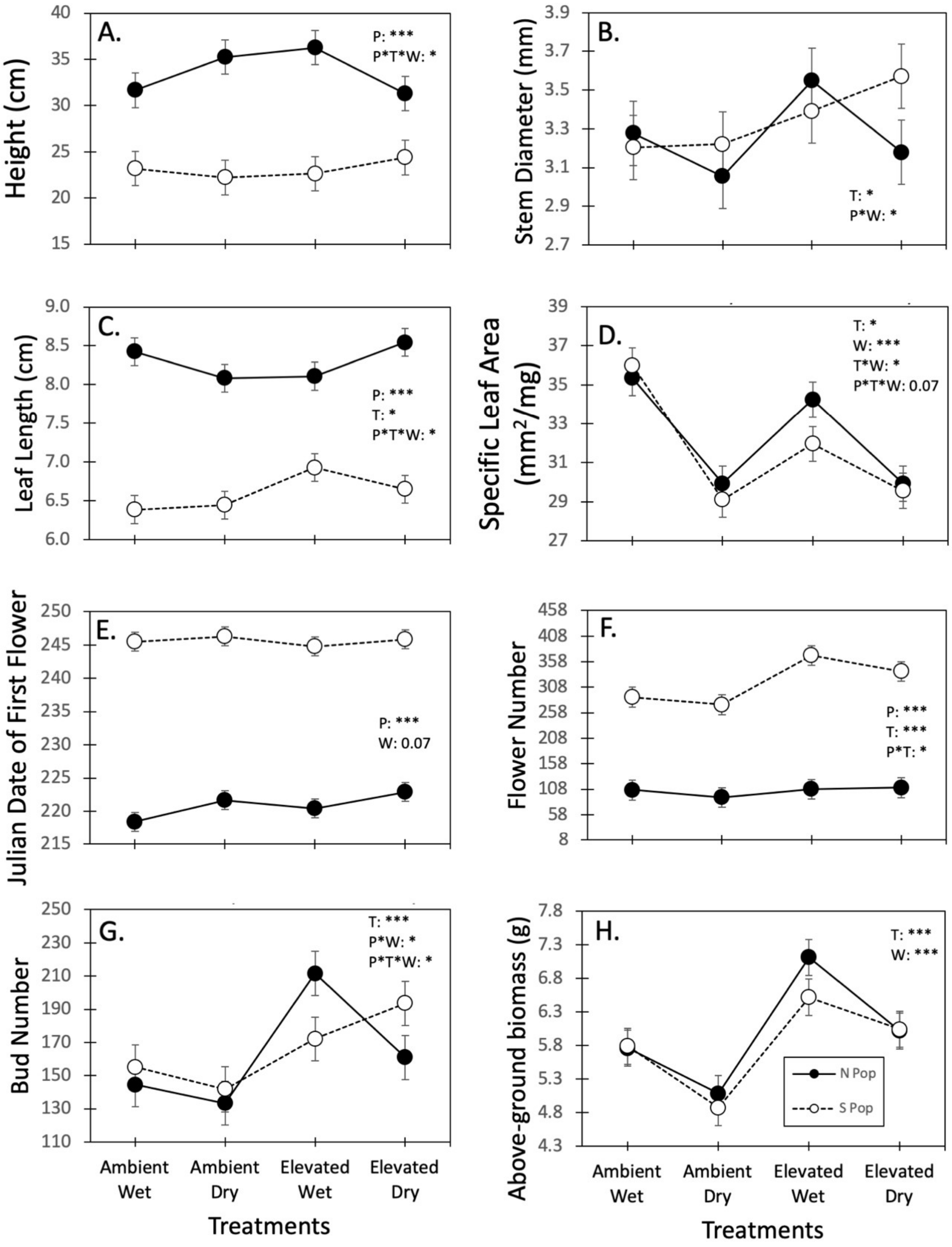

Figure 2.3. Trait responses of two populations of *Symphyotrichum ciliolatum* to simulated climate change. Northern (closed circles, dotted lines) and southern (open circles, solid lines) populations were grown in a common garden and exposed to a factorial combination of elevated (+2°C) or ambient temperatures and low water availability (-

15% soil moisture) or well-watered conditions. Important trait responses between populations or treatments as follows: A) Height (cm) of plants measured in June. B) Stem diameter(mm) measured in June. C) Leaf length(cm) measured in July. D) Specific leaf area(mm^2/mg). E) Julian date of first flower. F) Number of open flowers counted 3 weeks after the date of first flowering. G) Unopened flower buds recorded 3 weeks after the date of first flowering. H) Above ground biomass(g) at the end of the season. Values reported are least square means with standard error. Significant effects for population (P), temperature treatment (T), water treatment (W) and their interactions are reported as: * $p<0.05$, ** $p<0.01$ and ***$p<0.001$.

Table 2.2. Results of a mixed model analysis of variance (ANOVA) for traits measured on two populations of *Maianthemum canadense* (Canada mayflower). The populations were grown in a common garden and exposed to a factorial combination of elevated (+2°C) or ambient temperatures and low water availability (-15% soil moisture) or well-watered conditions.

	Pop (P)		Temp (T)		Water (W)		T*W		P*T		P*W		P*T*W	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Height – June[1]	26.52	**<0.0001**	0.21	0.65	0.004	0.95	0.01	0.93	0.29	0.59	0.52	0.47	0.07	0.79
Stem Diameter – June[2]	152.60	**<0.0001**	1.47	0.23	0.08	0.77	0.07	0.79	0.44	0.51	2.31	0.13	1.48	0.22
Leaf Number – July[3]	156.46	**<0.0001**	0.01	0.97	0.18	0.67	2.34	0.13	1.54	0.22	0.02	0.89	3.04	0.08
SLA[4]	0.11	0.74	3.36	0.07	8.45	**0.004**	5.71	**0.02**	0.96	0.33	0.38	0.54	0.30	0.58
Date Senesced[5]	0.30	0.58	0.94	0.33	1.21	0.27	3.17	0.08	0.01	0.93	1.14	0.29	0.54	0.46
Above Ground Biomass[6]	14.38	**0.0002**	1.69	0.19	1.11	0.29	0.003	0.96	0.35	0.56	0.02	0.88	1.02	0.31

df for P, T, W and interactions: [1-2, 4, 6] 1,659; [3] 1,650; [5] 1,658.

Wald-p significance values for blocking factor (1 block/ rainout shelter): [1] 0.26, [2] 0.14, [3] 0.45, [4] **0.01**, [5] 0.63, [6] 0.47. *df* = 1 for [1-6].

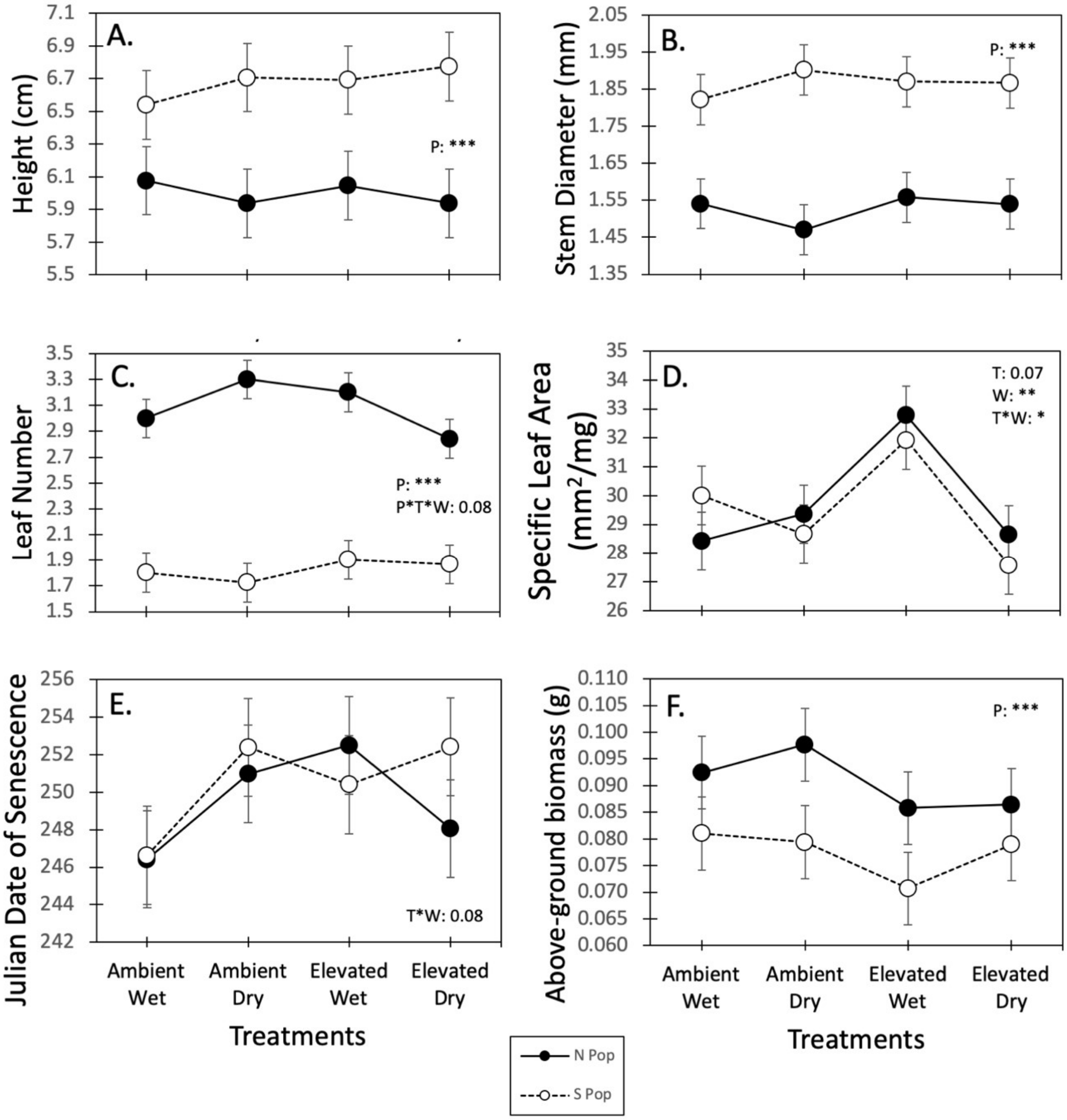

Figure 2.4. Trait responses of two populations of *Maianthemum canadense* to simulated climate change. Northern (closed circles, dotted lines) and southern (open circles, solid lines) populations were grown in a common garden and exposed to a factorial combination of elevated (+2°C) or ambient temperatures and low water availability (-15% soil moisture) or well-watered conditions. Important trait responses between populations or treatments as follows: A) Height(cm) of plants measured in June. B) Stem(mm) diameter measured in June. C) Leaf number measured in July. D) Specific leaf area(mm^2/mg). E) Julian date of senesce. F) Above ground biomass at the end of the season(g). Values reported are least square means with standard error. Significant effects for population (P), temperature treatment (T), water treatment (W) and their interactions are reported as: * $p<0.05$, ** $p<0.01$ and ***$p<0.001$.

BIBLIOGRAPHY

1. Roberts, M. R. Response of the herbaceous layer to natural disturbance in North American forests. *Can. J. Bot.* **82**, 1273–1283 (2004).
2. Jochum, G. M., Mudge, K. W. & Thomas, R. B. Elevated temperatures increase leaf senescence and root secondary metabolite concentrations in the understory herb Panax quinquefolius (Araliaceae). *Am. J. Bot.* **94**, 819–826 (2007).
3. Rice, K. E., Montgomery, R. A., Stefanski, A., Rich, R. L. & Reich, P. B. Experimental warming advances phenology of groundlayer plants at the boreal-temperate forest ecotone. *Am. J. Bot.* **105**, 851–861 (2018).
4. Cook, J. E. Structural effects on understory attributes in second-growth forests of northern Wisconsin, USA. *For. Ecol. Manag.* **347**, 188–199 (2015).
5. Duffy, D. C. & Meier, A. J. Do Appalachian Herbaceous Understories Ever Recover from Clearcutting? *Conserv. Biol.* **6**, 196–201 (1992).
6. Brudvig, L. A., Mabry, C. M. & Mottl, L. M. Dispersal, not Understory Light Competition, Limits Restoration of Iowa Woodland Understory Herbs. *Restor. Ecol.* **19**, 24–31 (2011).
7. Moola, F. M. & Vasseur, L. The maintenance of understory residual flora with even-aged forest management: A review of temperate forests in northeastern North America. *Environ. Rev.* **16**, 141–155 (2008).
8. Meier, A. J., Bratton, S. P. & Duffy, D. C. Possible Ecological Mechanisms for Loss of Vernal-Herb Diversity in Logged Eastern Deciduous Forests. *Ecol. Appl.* **5**, 935–946 (1995).

9. Hart, S. A. & Chen, H. Y. H. Understory Vegetation Dynamics of North American Boreal Forests. *Crit. Rev. Plant Sci.* **25**, 381–397 (2006).

10. Costanza, R. *et al.* The value of the world's ecosystem services and natural capital. *Nature* **387**, 253–260 (1997).

11. Gilliam, F. S. The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems. *BioScience* **57**, 845–858 (2007).

12. Elliott, K. J., Vose, J. M., Knoepp, J. D., Clinton, B. D. & Kloeppel, B. D. Functional Role of the Herbaceous Layer in Eastern Deciduous Forest Ecosystems. *Ecosystems* **18**, 221–236 (2015).

13. Yepez, E. A., Williams, D. G., Scott, R. L. & Lin, G. Partitioning overstory and understory evapotranspiration in a semiarid savanna woodland from the isotopic composition of water vapor. *Agric. For. Meteorol.* **119**, 53–68 (2003).

14. Soil Erosion, Forest Health Issues. https://www.fs.fed.us/foresthealth/fhm/pubs/96seros.htm.

15. Franklin, J. A., Zipper, C. E., Burger, J. A., Skousen, J. G. & Jacobs, D. F. Influence of herbaceous ground cover on forest restoration of eastern US coal surface mines. *New For.* **43**, 905–924 (2012).

16. Gómez-Aparicio, L. The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *J. Ecol.* **97**, 1202–1214 (2009).

17. Walker, M. D. *et al.* Plant community responses to experimental warming across the tundra biome. *Proc. Natl. Acad. Sci. U. S. A.* **103**, 1342–1346 (2006).

18. Elmqvist, T. *et al.* Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* **1**, 488–494 (2003).
19. Tilman, D. Community Invasibility, Recruitment Limitation, and Grassland Biodiversity. *Ecology* **78**, 81–92 (1997).
20. Miles, P. D. *et al.* USDA Forest Service Forest Inventory and Analysis Program Northern Research Station, St. Paul, MN. 96.
21. Timeline. *Minnesota Historical Society* https://www.mnhs.org/foresthistory/learn/timeline.
22. MPR: A History of Timbering in Minnesota. http://news.minnesota.publicradio.org/features/199811/16_engerl_history-m/.
23. Hupperts, S. F., Dickinson, Y. L., Webster, C. R. & Kern, C. C. Promoting structural and species diversity in Great Lakes northern hardwoods: a conceptual model and its application. *For. Int. J. For. Res.* **92**, 16–25 (2019).
24. How Aspens Grow. https://www.fs.fed.us/wildflowers/beauty/aspen/grow.shtml.
25. Betula papyrifera. https://www.fs.fed.us/database/feis/plants/tree/betpap/all.html.
26. Superior National Forest: North Shore Forest Restoration Project | Climate Change Response Framework. https://forestadaptation.org/adapt/demonstration-projects/superior-national-forest-north-shore-forest-restoration-project.
27. Lozon, J. D. & MacIsaac, H. J. Biological invasions: are they dependent on disturbance? *Environ. Rev.* **5**, 131–144 (1997).
28. Stuble, K. L. & Souza, L. Priority effects: natives, but not exotics, pay to arrive late. *J. Ecol.* **104**, 987–993 (2016).

29. Wilsey, B. J., Barber, K. & Martin, L. M. Exotic grassland species have stronger priority effects than natives regardless of whether they are cultivated or wild genotypes. *New Phytol.* **205**, 928–937 (2015).
30. Allen, C. D. *et al.* A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.* **259**, 660–684 (2010).
31. Collins, M. *et al. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. (Cambridge University Press, 2013).
32. Galatowitsch, S., Frelich, L. & Phillips-Mao, L. Regional climate change adaptation strategies for biodiversity conservation in a midcontinental region of North America. *Biol. Conserv.* **142**, 2012–2022 (2009).
33. Pryor, S. C. *et al. Ch. 18: Midwest. Climate Change Impacts in the United States: The Third National Climate Assessment*. https://nca2014.globalchange.gov/downloads (2014) doi:10.7930/J0J1012N.
34. Dukes, J. S. *et al.* Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict?This article is one of a selection of papers from NE Forests 2100: A Synthesis of Climate Change Impacts on Forests of the Northeastern US and Eastern Canada. *Can. J. For. Res.* **39**, 231–248 (2009).
35. Duveneck, M. J., Scheller, R. M. & White, M. A. Effects of alternative forest management on biomass and species diversity in the face of climate change in the northern Great Lakes region (USA). *Can. J. For. Res.* **44**, 700–710 (2014).

36. Prasad, A. M., Iverson, L. R., Matthews, S. & Peters, M. *A Climate Change Atlas for 134 Forest Tree Species of the Eastern United States [database].* https://www.nrs.fs.fed.us/atlas/tree (2007).

37. Stevens, J. T., Safford, H. D., Harrison, S. & Latimer, A. M. Forest disturbance accelerates thermophilization of understory plant communities. *J. Ecol.* **103**, 1253–1263 (2015).

38. Skov, F. & Svenning, J.-C. Potential impact of climatic change on the distribution of forest herbs in Europe. *Ecography* **27**, 366–380 (2004).

39. Pastor, J. & Post, W. M. Response of northern forests to CO2-induced climate change. *Nature* **334**, 55–58 (1988).

40. Keddy, P. A. & Drummond, C. G. Ecological Properties for the Evaluation, Management, and Restoration of Temperate Deciduous Forest Ecosystems. *Ecol. Appl.* **6**, 748–762 (1996).

41. Burkett, V. R. *et al.* Nonlinear dynamics in ecosystem response to climatic change: Case studies and policy implications. *Ecol. Complex.* **2**, 357–394 (2005).

42. McKenney, D., Pedlar, J. & O'Neill, G. Climate change and forest seed zones: Past trends, future prospects and challenges to ponder. *For. Chron.* **85**, 258–266 (2009).

43. Isaac-Renton, M. G., Roberts, D. R., Hamann, A. & Spiecker, H. Douglas-fir plantations in Europe: a retrospective test of assisted migration to address climate change. *Glob. Change Biol.* **20**, 2607–2617 (2014).

44. McLane, S. C. & Aitken, S. N. Whitebark pine (Pinus albicaulis) assisted migration potential: testing establishment north of the species range. *Ecol. Appl.* **22**, 142–153 (2012).

45. Operations, M. of F. L. and N. R. Assisted Migration Adaptation Trial - Province of British Columbia. https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/tree-seed/forest-genetics/seed-transfer-climate-change/assisted-migration-adaptation-trial (2018).
46. Schreiber, S. G. *et al.* Frost hardiness vs. growth performance in trembling aspen: an experimental test of assisted migration. *J. Appl. Ecol.* **50**, 939–949 (2013).
47. Mabry, C. M. Regional Genetic Differences in Forest Herbaceous Species. *Ecol. Restor.* **35**, 291–296 (2017).
48. Mottl, L. M., Mabry, C. M. & Farrar, D. R. Seven-Year Survival of Perennial Herbaceous Transplants in Temperate Woodland Restoration. *Restor. Ecol.* **14**, 330–338 (2006).
49. Harris, C. J., Leishman, M. R., Fryirs, K. & Kyle, G. How Does Restoration of Native Canopy Affect Understory Vegetation Composition? Evidence from Riparian Communities of the Hunter Valley Australia. *Restor. Ecol.* **20**, 584–592 (2012).
50. Mead, J. Climate-informed restoration of white pine: Impacts of seed source, planting site, and earthworms. (2016).
51. Kavajecz, L. Assisted Migration Of Quercus Rubra And Quercus Macrocarpa From Two Seed Zones Into Four Forest Types In Northeastern Minnesota. (2016).
52. Van Der Maarel, E. The Braun-Blanquet approach in perspective. *Vegetatio* **30**, 213–219 (1975).
53. McCune, B. & Mefford, M. J. *PC-ORD. Multivariate Analysis of Ecological Data.* (MjM Software Design, 2016).

54. Niejenhuis, A. van & Parker, W. H. Adaptive variation in jack pine from north central Ontario determined by short-term common garden tests. *Can. J. For. Res.* **26**, 2006–2014 (1996).

55. MN DNR. Nursery Seed Source Control. 9 (2016).

56. *JMP Pro®*. (SAS Institute Inc, 2019).

57. Altrichter, E. A., Thompson, J. R. & Mabry, C. M. Stakeholders' Perceptions of Native Plants and Local Ecotypes in Ecological Restoration. *Ecol. Restor.* **35**, 218–227 (2017).

58. Newaz, Md. S., Mallik, A. U. & Mackereth, R. W. Riparian vegetation recovery in a 23 year chronosequence of clear-cuts along boreal headwater streams. *For. Ecol. Manag.* **443**, 69–83 (2019).

59. Venier, L. A. *et al.* Effects of natural resource development on the terrestrial biodiversity of Canadian boreal forests. *Environ. Rev.* **22**, 457–490 (2014).

60. Roberts, M. W., D'Amato, A. W., Kern, C. C. & Palik, B. J. Long-term impacts of variable retention harvesting on ground-layer plant communities in Pinus resinosa forests. *J. Appl. Ecol.* **53**, 1106–1116 (2016).

61. Abella, S. R. & Springer, J. D. Effects of tree cutting and fire on understory vegetation in mixed conifer forests. *For. Ecol. Manag.* **335**, 281–299 (2015).

62. Fenton, N. J., Frego, K. A. & Sims, M. R. Changes in forest floor bryophyte (moss and liverwort) communities 4 years after forest harvest. *Can. J. Bot.* **81**, 714–731 (2003).

63. Ecological Classification System (ECS) - Minnesota DNR. https://www.dnr.state.mn.us/ecs/index.html.

64. Agricultural Research Service. USDA Plant Hardiness Zone Map, 2012.

65. Thomas, S. C., Halpern, C. B., Falk, D. A., Liguori, D. A. & Austin, K. A. Plant Diversity in Managed Forests: Understory Responses to Thinning and Fertilization. *Ecol. Appl.* **9**, 864–879 (1999).

66. Why do we harvest trees in the winter? – MyMinnesotaWoods. http://www.myminnesotawoods.umn.edu/2018/01/why-do-we-harvest-trees-in-the-winter/.

67. Rydgren, K., Hestmark, G. & Økland, R. H. Revegetation following experimental disturbance in a boreal old-growth Picea abies forest. *J. Veg. Sci.* **9**, 763–776 (1998).

68. Hart, S. A. & Chen, H. Y. H. Fire, Logging, and Overstory Affect Understory Abundance, Diversity, and Composition in Boreal Forest. *Ecol. Monogr.* **78**, 123–140 (2008).

69. Haughian, S. R. & Frego, K. A. Short-term effects of three commercial thinning treatments on diversity of understory vascular plants in white spruce plantations of northern New Brunswick. *For. Ecol. Manag.* **370**, 45–55 (2016).

70. Belote, R. T., Jones, R. H. & Wieboldt, T. F. Compositional stability and diversity of vascular plant communities following logging disturbance in Appalachian forests. *Ecol. Appl.* **22**, 502–516 (2012).

71. Kembel, S. W., Waters, I. & Shay, J. M. Short-term effects of cut-to-length versus full-tree harvesting on understorey plant communities and understorey-regeneration associations in Manitoba boreal forests. *For. Ecol. Manag.* **255**, 1848–1858 (2008).

72. Boch, S. *et al.* High plant species richness indicates management-related disturbances rather than the conservation status of forests. *Basic Appl. Ecol.* **14**, 496–505 (2013).

73. Weldon, J. & Grandin, U. Major disturbances test resilience at a long-term boreal forest monitoring site. *Ecol. Evol.* **9**, 4275–4288 (2019).

74. Mabry, C. M. & Fraterrigo, J. M. Species traits as generalized predictors of forest community response to human disturbance. *For. Ecol. Manag.* **257**, 723–730 (2009).

75. Pinno, B. D. & Errington, R. C. Burn Severity Dominates Understory Plant Community Response to Fire in Xeric Jack Pine Forests. *Forests* **7**, 83 (2016).

76. Frenne, P. D. *et al.* Microclimate moderates plant responses to macroclimate warming. *Proc. Natl. Acad. Sci.* **110**, 18561–18565 (2013).

77. Harrison, S., Damschen, E. I. & Grace, J. B. Ecological contingency in the effects of climatic warming on forest herb communities. *Proc. Natl. Acad. Sci.* **107**, 19362–19367 (2010).

78. Gottfried, M. *et al.* Continent-wide response of mountain vegetation to climate change. *Nat. Clim. Change* **2**, 111–115 (2012).

79. Haeussler, S., Bedford, L., Leduc, A., Bergeron, Y. & Kranabetter, J. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. *Silva Fenn.* **36**, (2002).

80. Frelich Lee E. *et al.* Trophic cascades, invasive species and body-size hierarchies interactively modulate climate change responses of ecotonal temperate–boreal forest. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 2955–2961 (2012).

81. Beckage, B. *et al.* A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proc. Natl. Acad. Sci.* **105**, 4197–4202 (2008).

82. McClain, C. D., Holl, K. D. & Wood, D. M. Successional Models as Guides for Restoration of Riparian Forest Understory. *Restor. Ecol.* **19**, 280–289 (2011).
83. Scheller, R. M. & Mladenoff, D. J. Understory Species Patterns and Diversity in Old-Growth and Managed Northern Hardwood Forests. *Ecol. Appl.* **12**, 1329–1343 (2002).
84. Augspurger, C. K. & Buck, S. Decline in herb species diversity over two decades in a temperate deciduous forest in Illinois1. *J. Torrey Bot. Soc.* **144**, 392–405 (2017).
85. Chapin, F. S. *et al.* Global Change and the Boreal Forest: Thresholds, Shifting States or Gradual Change? *AMBIO J. Hum. Environ.* **33**, 361–365 (2004).
86. Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z. & Schepaschenko, D. G. Boreal forest health and global change. *Science* **349**, 819–822 (2015).
87. Chapin, F. S. *et al.* Resilience of Alaska's boreal forest to climatic changeThis article is one of a selection of papers from The Dynamics of Change in Alaska's Boreal Forests: Resilience and Vulnerability in Response to Climate Warming. *Can. J. For. Res.* **40**, 1360–1370 (2010).
88. Gentry, A. H. & Dodson, C. Contribution of Nontrees to Species Richness of a Tropical Rain Forest. *Biotropica* **19**, 149–156 (1987).
89. Ricketts, T. H., Dinerstein, E., Olson, D. M. & Loucks, C. Who's Where in North America?Patterns of species richness and the utility of indicator taxa for conservation. *BioScience* **49**, 369–381 (1999).
90. Gilliam, F. S. & Roberts, M. R. *The Herbaceous Layer in Forests of Eastern North America*. (Oxford University Press, 2003).

91. Schnitzer, S. A. & Carson, W. P. Have we forgotten the forest because of the trees? *Trends Ecol. Evol.* **15**, 375–376 (2000).

92. Schnitzer, S. A. & Carson, W. P. Treefall Gaps and the Maintenance of Species Diversity in a Tropical Forest. *Ecology* **82**, 913–919 (2001).

93. Stanturf, J. A. & Madsen, P. Restoration concepts for temperate and boreal forests of North America and Western Europe. *Plant Biosyst. - Int. J. Deal. Asp. Plant Biol.* **136**, 143–158 (2002).

94. Dellasala, D. *et al.* A Citizen's Call for Ecological Forest Restoration: Forest Restoration Principles and Criteria. *Ecol. Restor.* **21**, 14–23 (2003).

95. Barr, S., Jonas, J. L. & Paschke, M. W. Optimizing seed mixture diversity and seeding rates for grassland restoration. *Restor. Ecol.* **25**, 396–404 (2017).

96. Martin, L. M., Moloney, K. A. & Wilsey, B. J. An assessment of grassland restoration success using species diversity components. *J. Appl. Ecol.* **42**, 327–336 (2005).

97. Martin, L. M. & Wilsey, B. J. Assessing grassland restoration success: relative roles of seed additions and native ungulate activities. *J. Appl. Ecol.* **43**, 1098–1109 (2006).

98. Polley, H. W., Derner, J. D. & Wilsey, B. J. Patterns of Plant Species Diversity in Remnant and Restored Tallgrass Prairies. *Restor. Ecol.* **13**, 480–487 (2005).

99. McCain, K. N. S., Baer, S. G., Blair, J. M. & Wilson, G. W. T. Dominant Grasses Suppress Local Diversity in Restored Tallgrass Prairie. *Restor. Ecol.* **18**, 40–49 (2010).

100. Török, P., Vida, E., Deák, B., Lengyel, S. & Tóthmérész, B. Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. *Biodivers. Conserv.* **20**, 2311–2332 (2011).

101. Lawson, C. S., Ford, M. A. & Mitchley, J. The influence of seed addition and cutting regime on the success of grassland restoration on former arable land. *Appl. Veg. Sci.* **7**, 259–266 (2004).

102. Prairie Restoration Guides. https://www.nature.org/en-us/about-us/where-we-work/united-states/minnesota/stories-in-minnesota/prairie-restoration-guides/.

103. Godefroid, S., Rucquoij, S. & Koedam, N. To what extent do forest herbs recover after clearcutting in beech forest? *For. Ecol. Manag.* **210**, 39–53 (2005).

104. Verheyen, K., Honnay, O., Motzkin, G., Hermy, M. & Foster, D. R. Response of forest plant species to land-use change: a life-history trait-based approach. *J. Ecol.* **91**, 563–577 (2003).

105. Flannigan, M. D., Stocks, B. J. & Wotton, B. M. Climate change and forest fires. *Sci. Total Environ.* **262**, 221–229 (2000).

106. Wotton, B. M., Nock, C. A. & Flannigan, M. D. Forest fire occurrence and climate change in Canada. *Int. J. Wildland Fire* **19**, 253–271 (2010).

107. Plant and Animal Habitats. http://www.missouribotanicalgarden.org/visit/family-of-attractions/shaw-nature-reserve/conservation-at-shaw-nature-reserve/plants-animals-habitats.aspx.

108. George, L. & Bazzaz, F. The Herbaceous Layer as a Filter Determining Spatial Pattern in Forest Tree Regeneration. in *The Herbacesous Layer in Forest of Eastern North America* 340–355 (2014). doi:10.1093/acprof:osobl/9780199837656.003.0014.

109. Walker, B., Kinzig, A. & Langridge, J. Original Articles: Plant Attribute Diversity, Resilience, and Ecosystem Function: The Nature and Significance of Dominant and Minor Species. *Ecosystems* **2**, 95–113 (1999).

110. Turner, M. G., Donato, D. C. & Romme, W. H. Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research. *Landsc. Ecol.* **28**, 1081–1097 (2013).

111. Benayas, J. M. R., Newton, A. C., Diaz, A. & Bullock, J. M. Enhancement of Biodiversity and Ecosystem Services by Ecological Restoration: A Meta-Analysis. *Science* **325**, 1121–1124 (2009).

112. Isbell, F. *et al.* High plant diversity is needed to maintain ecosystem services. *Nature* **477**, 199–202 (2011).

113. Loveland, T. *et al. National climate assessment technical report on the impacts of climate and land use and land cover change.* (2012).

114. Pearson, R. G. & Dawson, T. P. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* **12**, 361–371 (2003).

115. Hijmans, R. J. & Graham, C. H. The ability of climate envelope models to predict the effect of climate change on species distributions. *Glob. Change Biol.* **12**, 2272–2281 (2006).

116. O'neill, G. A. *et al. 048 Assisted Migration to Address Climate Change in British Columbia Recommendations for Interim Seed Transfer Standards*.

117. Ukrainetz, N. K., O'Neill, G. A. & Jaquish, B. Comparison of fixed and focal point seed transfer systems for reforestation and assisted migration: a case study for interior spruce in British Columbia. *Can. J. For. Res.* **41**, 1452–1464 (2011).

118. Wadgymar, S. M., Cumming, M. N. & Weis, A. E. The success of assisted colonization and assisted gene flow depends on phenology. *Glob. Change Biol.* **21**, 3786–3799 (2015).

119. Beierkuhnlein, C., Thiel, D., Jentsch, A., Willner, E. & Kreyling, J. Ecotypes of European grass species respond differently to warming and extreme drought. *J. Ecol.* **99**, 703–713 (2011).

120. Durka, W. *et al.* Genetic differentiation within multiple common grassland plants supports seed transfer zones for ecological restoration. *J. Appl. Ecol.* **54**, 116–126 (2017).

121. Leimu, R. & Fischer, M. A Meta-Analysis of Local Adaptation in Plants. *PLOS ONE* **3**, e4010 (2008).

122. Castellanos-Acuña, D., Lindig-Cisneros, R. & Sáenz-Romero, C. Altitudinal assisted migration of Mexican pines as an adaptation to climate change. *Ecosphere* **6**, 1–16 (2015).

123. Pavek, D. Maianthemum canadense. *Fire Effects Information System* https://www.fs.fed.us/database/feis/plants/forb/maican/all.html (1993).

124. Maianthemum canadense (Canada Mayflower): Minnesota Wildflowers. https://www.minnesotawildflowers.info/flower/canada-mayflower.

125. Minnesota Seasons - Lindley's aster. http://minnesotaseasons.com/Plants/Lindleys_aster.html.

126. Symphyotrichum ciliolatum (Lindley's Aster): Minnesota Wildflowers. https://www.minnesotawildflowers.info/flower/lindleys-aster.

127. Marion, G. m. *et al.* Open-top designs for manipulating field temperature in high-latitude ecosystems. *Glob. Change Biol.* **3**, 20–32 (1997).

128. Molau, U. & Mølgaard, P. *ITEX Manual*. (Danish Polar Center, 1996).

129. Winkler, K. J. Plasticity, genetic diversity, natural selection, and physiology of polyploid Solidago altissima (Asteraceae) under simulated climate change. (2013).

130. Chun, Y. J., Le Corre, V. & Bretagnolle, F. Adaptive divergence for a fitness-related trait among invasive Ambrosia artemisiifolia populations in France. *Mol. Ecol.* **20**, 1378–1388 (2011).

131. Waser, N. M. & Price, M. V. Reciprocal Transplant Experiments with Delphinium Nelsonii (ranunculaceae): Evidence for Local Adaptation. *Am. J. Bot.* **72**, 1726–1732 (1985).

132. Ramírez-Valiente, J. A., Sánchez-Gómez, D., Aranda, I. & Valladares, F. Phenotypic plasticity and local adaptation in leaf ecophysiological traits of 13 contrasting cork oak populations under different water availabilities. *Tree Physiol.* **30**, 618–627 (2010).

133. Knight, C. A. & Ackerly, D. D. Evolution and plasticity of photosynthetic thermal tolerance, specific leaf area and leaf size: congeneric species from desert and coastal environments. *New Phytol.* **160**, 337–347 (2003).

134. Liu, F. & Stützel, H. Biomass partitioning, specific leaf area, and water use efficiency of vegetable amaranth (Amaranthus spp.) in response to drought stress. *Sci. Hortic.* **102**, 15–27 (2004).

135. Correia, B. *et al.* Combined Drought and Heat Activates Protective Responses in Eucalyptus globulus That Are Not Activated When Subjected to Drought or Heat Stress Alone. *Front. Plant Sci.* **9**, (2018).

136. Siddique, K. Individual and combined effects of transient drought and heat stress on carbon assimilation and seed filling in chickpea. *Funct. Plant Biol.* **41**, (2014).

137. Machado, S. & Paulsen, G. M. Combined effects of drought and high temperature on water relations of wheat and sorghum. *Plant Soil* **233**, 179–187 (2001).

138. Qaseem, M. F., Qureshi, R. & Shaheen, H. Effects of Pre-Anthesis Drought, Heat and Their Combination on the Growth, Yield and Physiology of diverse Wheat (Triticum aestivum L.) Genotypes Varying in Sensitivity to Heat and drought stress. *Sci. Rep.* **9**, 1–12 (2019).

139. Hussain, H. A. *et al.* Interactive effects of drought and heat stresses on morpho-physiological attributes, yield, nutrient uptake and oxidative status in maize hybrids. *Sci. Rep.* **9**, 1–12 (2019).

140. Rizhsky, L., Liang, H. & Mittler, R. The Combined Effect of Drought Stress and Heat Shock on Gene Expression in Tobacco. *Plant Physiol.* **130**, 1143–1151 (2002).

141. Duan, H. *et al.* Individual and interactive effects of drought and heat on leaf physiology of seedlings in an economically important crop. *AoB Plants* **9**, (2016).

142. Orians, C. M., Schweiger, R., Dukes, J. S., Scott, E. R. & Müller, C. Combined impacts of prolonged drought and warming on plant size and foliar chemistry. *Ann. Bot.* **124**, 41–52 (2019).

143. Urban, M. C. *et al.* Improving the forecast for biodiversity under climate change. *Science* **353**, aad8466 (2016).

144. Jin, R., Wang, Y., Liu, R., Gou, J. & Chan, Z. Physiological and Metabolic Changes of Purslane (Portulaca oleracea L.) in Response to Drought, Heat, and Combined Stresses. *Front. Plant Sci.* **6**, (2016).

145. Silva, E. N. *et al.* Photosynthetic changes and protective mechanisms against oxidative damage subjected to isolated and combined drought and heat stresses in Jatropha curcas plants. *J. Plant Physiol.* **167**, 1157–1164 (2010).

146. Aerts, R., Cornelissen, J. H. C., Dorrepaal, E., Logtestijn, R. S. P. V. & Callaghan, T. V. Effects of experimentally imposed climate scenarios on flowering phenology and flower production of subarctic bog species. *Glob. Change Biol.* **10**, 1599–1609 (2004).

147. Liancourt, P. *et al.* Vulnerability of the northern Mongolian steppe to climate change: insights from flower production and phenology. *Ecology* **93**, 815–824 (2012).

148. Klanderud, K. Climate change effects on species interactions in an alpine plant community. *J. Ecol.* **93**, 127–137 (2005).

149. Michalski, S. G., Malyshev, A. V. & Kreyling, J. Trait variation in response to varying winter temperatures, diversity patterns and signatures of selection along the latitudinal distribution of the widespread grassland plant Arrhenatherum elatius. *Ecol. Evol.* **7**, 3268–3280 (2017).

150. Prock, S. & Körner, C. A Cross-Continental Comparison of Phenology, Leaf Dynamics and Dry Matter Allocation in Arctic and Temperate Zone Herbaceous Plants from Contrasting Altitudes. *Ecol. Bull.* 93–103 (1996).

151. Crick, J. C. & Grime, J. P. Morphological Plasticity and Mineral Nutrient Capture in Two Herbaceous Species of Contrasted Ecology. *New Phytol.* **107**, 403–414 (1987).

152. Snyder, R. L. *et al.* EVAPOTRANSPIRATION RESPONSE TO CLIMATE CHANGE. *Acta Hortic.* 91–98 (2011) doi:10.17660/ActaHortic.2011.922.11.

153. Koehler, K., Center, A. & Cavender-Bares, J. Evidence for a freezing tolerance–growth rate trade-off in the live oaks (Quercus series Virentes) across the tropical–temperate divide. *New Phytol.* **193**, 730–744 (2012).

154. Lubbe, F. C. & Henry, H. A. L. The cost of depth: frost avoidance trade-offs in herbaceous plants. *Plant Soil* (2019) doi:10.1007/s11104-019-04266-9.

155. Savage, J. A. & Cavender-Bares, J. Phenological cues drive an apparent trade-off between freezing tolerance and growth in the family Salicaceae. *Ecology* **94**, 1708–1717 (2013).

156. Frenne, P. D. *et al.* Temperature effects on forest herbs assessed by warming and transplant experiments along a latitudinal gradient. *Glob. Change Biol.* **17**, 3240–3253 (2011).

157. Suzuki, S. & Kudo, G. Short-term effects of simulated environmental change on phenology, leaf traits, and shoot growth of alpine plants on a temperate mountain, northern Japan. *Glob. Change Biol.* **3**, 108–115 (1997).

158. Arft, A. M. *et al.* Responses of Tundra Plants to Experimental Warming:meta-Analysis of the International Tundra Experiment. *Ecol. Monogr.* **69**, 491–511 (1999).

159. Theobald, E. J., Breckheimer, I. & HilleRisLambers, J. Climate drives phenological reassembly of a mountain wildflower meadow community. *Ecology* **98**, 2799–2812 (2017).

160. Anderson, J. T., Inouye, D. W., McKinney, A. M., Colautti, R. I. & Mitchell-Olds, T. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proc. R. Soc. Lond. B Biol. Sci.* rspb20121051 (2012) doi:10.1098/rspb.2012.1051.

161. Franks, S. J. Plasticity and evolution in drought avoidance and escape in the annual plant Brassica rapa. *New Phytol.* **190**, 249–257 (2011).

162. Kenney, A. M., McKay, J. K., Richards, J. H. & Juenger, T. E. Direct and indirect selection on flowering time, water-use efficiency (WUE, δ (13)C), and WUE plasticity to drought in Arabidopsis thaliana. *Ecol. Evol.* **4**, 4505–4521 (2014).

163. Franks, S. J. & Weis, A. E. A change in climate causes rapid evolution of multiple life-history traits and their interactions in an annual plant. *J. Evol. Biol.* **21**, 1321–1334 (2008).

164. Marchand, F. L. *et al.* Climate Warming Postpones Senescence in High Arctic Tundra. *Arct. Antarct. Alp. Res.* **36**, 390–394 (2004).

165. Estiarte, M. & Peñuelas, J. Alteration of the phenology of leaf senescence and fall in winter deciduous species by climate change: effects on nutrient proficiency. *Glob. Change Biol.* **21**, 1005–1017 (2015).

166. Gill, A. L. *et al.* Changes in autumn senescence in northern hemisphere deciduous trees: a meta-analysis of autumn phenology studies. *Ann. Bot.* **116**, 875–888 (2015).

167. Keenan, T. F. & Richardson, A. D. The timing of autumn senescence is affected by the timing of spring phenology: implications for predictive models. *Glob. Change Biol.* **21**, 2634–2641 (2015).

168. Office, A. of B. Leaf senescence varies widely across species and sites « Botany One. *Botany One* https://www.botany.one/2015/11/leaf-senescence-varies-widely-across-species-and-sites/ (2015).

169. Neuendorff, J. K., Nagel, L. M., Webster, C. R. & Janowiak, M. K. Stand Structure and Composition in a Northern Hardwood Forest after 40 Years of Single-Tree Selection. *North. J. Appl. For.* **24**, 197–202 (2007).

170. Grady, K. C. *et al.* Genetic variation in productivity of foundation riparian species at the edge of their distribution: implications for restoration and assisted migration in a warming climate. *Glob. Change Biol.* **17**, 3724–3735 (2011).

171. Winder, R., Nelson, E. & Beardmore, T. Ecological implications for assisted migration in Canadian forests. *For. Chron.* **87**, 731–744 (2011).

172. Bucharova, A. *et al.* Genetic differentiation and regional adaptation among seed origins used for grassland restoration: lessons from a multispecies transplant experiment. *J. Appl. Ecol.* **54**, 127–136 (2017).

APPENDIX

Table 1.2. Environmental characteristics of the survey plots in Chapter 1. Data on logged plots was obtained from the Adaptation Forestry Project, a joint effort between the Nature Conservancy and the Etterson Lab at the University of Minnesota Duluth and was collected in 2014 and 2015. Data in intact plots was collected in 2017, except for soil characteristics and growing degree days which were defined to be the same value as those of the closest logged plot. Topography values are as follows: 1=flat, 2=lower slope, 3=mid-slope, 4=shoulder, 5=summit. Microtopography values are defined as follows: 0=smooth/no mounds, 1= small mounds (0.3m high, any number), 2= few medium mounds (0.3-1m high, 7+m apart), 3=several medium mounds (0.3-1m high, 3-7m apart), 4=many medium mounds (0.3-1m high, 1-3m apart), 5=very many medium mounds (0.3-1m high, <1m apart), 6=several large mounds (1+m high, 3+m apart), and 7=many large mounds (1+m high, <3m apart). Soil family values are as follows: 1=Aeric Glossaqualfs, 2=Histic Humaquepts, 3=Typic Borohemists, 4=Typic Dystrochrepts, 5=Typic Haplumbrepts. And soil texture values are as follows: 1=coarse-loamy, 2=coarse-loamy over sandy or sandy-skeletal, 3=dysic, and 4=fine-loamy.

Site	Treatment	Aspect (°)	Slope (°)	Topo-graphy	Micro-topography	Soil Family	Soil Texture	Latitude	Longitude	MN DNR Seed Zone	Growing Degree Days (2016)	Thickness of the B Horizon (inch)	Thickness of the O Horizon (inch)
1	Logged	268	5	3	3	4	2	47.79794	90.8124	102	2469	34	6
1	Logged	35	3	3	3	4	2	47.79883	90.81408	102	2469	34	6
1	Intact	220	5	4	3	4	2	47.80028	90.81231	102	2469	34	6
2	Logged	343	12	4	2	3	3	47.50986	91.87412	104	2529	30	4
2	Logged	180	8	5	2	4	1	47.50855	91.86675	104	2529	33	3
2	Intact	268	2	4	2	3	3	47.51314	91.86873	104	2529	31.5	3.5
4	Logged	350	6	4	3	4	1	47.94125	91.79932	102	3168	27	6
4	Logged	332	6	3	2	4	1	47.94348	91.79877	102	3168	23	0
4	Intact	5	13	4	2	4	1	47.94053	91.80224	102	3168	25	3
5	Logged	118	4	5	2	5	1	47.75621	90.71444	102	2469	40	0
5	Logged	270	1	1	0	5	1	47.75661	90.69884	102	2469	30	10
5	Intact	110	1	1	1	5	1	47.75886	90.70792	102	2469	35	5

6	Logged	240	3	4	3	5	1	47.76059	90.73589	102	2469	35	0
6	Logged	210	1	1	2	5	1	47.75679	90.73175	102	2469	25	2
6	Intact	216	10	4	2	5	1	47.76443	90.74062	102	2469	30	1
7	Logged	332	2	3	1	5	1	47.76409	90.75328	102	2469	32	5
7	Logged	4	5	4	2	5	1	47.76348	90.74757	102	2469	40	0
7	Intact	144	4	3	2	5	1	47.76121	90.75106	102	2469	36	2.5
8	Logged	300	8	3	2	1	4	47.62683	90.84651	102	2998	31	0
8	Logged	232	6	3	2	1	4	47.62856	90.84178	102	2998	33	5
8	Intact	279	8	3	1	1	4	47.62628	90.84618	102	2998	32	2.5
9	Logged	280	6	3	2	4	1	48.07398	91.96938	102	3168	34	1
9	Logged	106	4	3	2	4	1	48.07289	91.96846	102	3168	24	3
9	Intact	274	3	4	2	4	1	48.07941	91.9681	102	3168	29	2
10	Logged	130	3	3	1	4	1	47.47634	91.15156	104	2998	46	4
10	Logged	140	2	2	1	4	1	47.4778	91.15045	104	2998	30	0
10	Logged	70	8	0	0	4	1	47.47651	91.1508	104	2998	28	4
10	Logged	132	1	2	1	4	1	47.47829	91.15136	104	2998	19	4
10	Logged	160	14	3	1	4	1	47.47773	91.1525	104	2998	36	2
10	Logged	185	10	2	1	4	1	47.47916	91.15151	104	2998	1	6
10	Logged	210	7	2	1	4	1	47.47897	91.14969	104	2998	36	2
10	Intact	25	8	4	2	4	1	47.47664	91.15196	104	2998	28	3.1
11	Logged	265	4	2	1	5	1	47.58952	91.05097	104	2998	26	0
11	Logged	150	4	3	1	5	1	47.58872	91.05136	104	2998	33	0
11	Intact	213	4	3	2	5	1	47.58718	91.05198	104	2998	29.5	0
12	Logged	231	1	3	2	4	1	47.81475	91.72443	102	3168	32	2
12	Logged	85	3	3	2	4	1	47.8143	91.72687	102	3168	34	6

12	Intact	269	4	4	2	4	1	47.81764	91.72174	102	3168	33	4
13	Logged	218	2	5	3	4	1	47.4378	91.77017	104	2905	46	10
13	Logged	250	1	5	2	4	1	47.43893	91.76659	104	2905	49	6
14	Logged	72	4	3	2	2	4	47.18924	91.54916	104	3067	38	2
14	Logged	100	7	3	1	2	4	47.19341	91.54943	104	3067	37	3
15	Logged	240	5	2	1	4	1	47.1165	91.68859	104	3067	29	2
15	Logged	208	6	3	2	4	1	47.11521	91.68678	104	3067	27	5
15	Intact	146	10	3	1	4	1	47.11674	91.68777	104	3067	28	3.5
16	Logged	295	10	3	1	4	1	47.39698	91.93458	104	2905	21	0
16	Logged	88	3	3	1	4	1	47.39846	91.92836	104	2905	28	0
17	Logged	320	1	1	2	4	1	47.54892	91.65207	104	2542	31	1
17	Logged	204	1	1	2	4	1	47.54632	91.65248	104	2542	28	1
17	Intact	98	1	1	2	4	1	47.54915	91.64948	104	2542	29.5	1
18	Logged	40	2	3	2	4	1	47.4697	91.83046	104	2905	32	10
18	Logged	138	3	4	2	4	1	47.47346	91.82957	104	2905	27	13
18	Intact	356	1	1	2	4	1	47.46483	91.82866	104	2905	29.5	11.5
19	Logged	356	2	4	2	4	1	47.51311	91.8854	104	2529	36	4
19	Logged	295	1	5	1	4	1	47.51279	91.88358	104	2529	30	7
20	Logged	75	2	3	2	5	1	47.47099	91.18	104	2998		
20	Logged	62	3	3	2	5	1	47.46865	91.18686	104	2998		
20	Intact	145	1	1	2	5	1	47.47099	91.17904	104	2998		
21	Logged	108	1	5	2	4	1	47.83833	91.78725	102	3168	26	7
21	Logged	342	6	3	3	4	1	47.83795	91.78489	102	3168	33	3
21	Intact	159	4	4	2	4	1	47.83663	91.78403	102	3168	29.5	5

Table 1.3. Species list of understory species identified during the plot surveys in Chapter 1.

Scientific name	**Common name**
Achillea millefolium	Yarrow
Actaea pachypoda	White baneberry
Actaea rubra	Red baneberry
Actaea species	Baneberries
Agrostis gigantea	Redtop
Agrostis scabra	Rough bentgrass
Amelanchier species	Juneberry
Anaphalis margaritacea	Western pearly everlasting
Anemone quinquefolia	Wood anemone
Apocynum androsaemifolium	Spreading dogbane
Aquilegia canadensis	Wild columbine
Aralia nudicaulis	Wild sarsaparilla
Aralia hispida	Bristly sarsaparilla
Arisaema triphyllum	Jack-in-the-pulpit
Aster species	Asters
Athyrium filix-femina	Common ladyfern
Botrychium virginianum	Rattlesnake fern
Bromus ciliatus	Fringed brome
Bromus species	Brome grasses
Calamagrostis canadensis	Bluejoint
Calystegia spithamaea	Low bindweed
Calamagrostis stricta	Narrow-leaved reedgrass
Capnoides sempervirens	Pink corydalis
Carex adusta	Lesser brown sedge
Carex arctata	Northern cluster sedge
Carex backii	Back's sedge
Carex brunnescens	Brownish sedge
Carex crawfordii	Crawford's sedge
Carex deflexa	Northern sedge
Carex deweyana	Dewey sedge
Carex foenea	Dryspike sedge
Carex houghtoniana	Houghton's sedge
Carex intumescens	Bladder sedge

Carex leptonervia	Nerveless woodland sedge
Carex penduncolata	Long-stalked sedge
Carex pensylvanica	Pennsylvania sedge
Carex species	Sedges
Carex spicata	Prickly sedge
Carex stipata	Awlfruit sedge
Carex trichocarpa	Hairyfruit sedge
Carex umbellata	Parasol sedge
Cerastium fontanum	Mouse-eared chickweed
Chamerion angustifolium	Fireweed
Chenopodium album	Lamb's-quarters
Chenopodium simplex	Maple-leaved goosefoot
Chenopodium species	Goosefoots
Chimaphila umbellata	Pipsissewa
Cinna latifolia	Wood reedgrass
Circaea alpina	Small enchanter's nightshade
Cirsium arvense	Canada thistle
Cirsium species	Thistle
Cirsium vulgare	Bull thistle
Clematis occidentalis	Purple clematis
Clintonia borealis	Blue-bead Lily
Comptonia peregrina	Sweetfern
Conyza canadensis	Horseweed
Coptis trifolia	Threeleaf goldthread
Cornus alternifolia	Alternate-leaved dogwood
Cornus canadensis	Bunchberry dogwood
Cornus sericea	Red osier dogwood
Corylus cornuta	Beaked hazelnut
Corallorhiza maculata	Spotted coralroot
Cornus rugosa	Round-leaved dogwood
Cyperacea species	Sedge family
Danthonia spicata	poverty oats grass
Dendrolycopodium species	Ground pines
Dendrolycopodium dendroideum	Tree clubmoss
Dichanthelium species	Panic grasses
Dichanthelium implicatum	Panic grass
Dichanthelium xanthophysum	Slender rosette grass
Diervilla lonicera	Bush honeysuckle
Diphasiastrum complanatum	Groundcedar

Doellingeria umbellata	Flat-topped white aster
Dracocephalum parviflorum	Dragonhead
Dryopteris carthusiana	Spinulose woodfern
Dryopteris cristata	Crested shield fern
Dryopteris species	Woodferns
Epigaea repens	Trailing-arbutus
Epilobium ciliatum	Willow-herb
Epilobium leptophyllum	Fen willow-herb
Equisetum sylvaticum	Woodland horsetail
Eurybia macrophylla	Large-leaved aster
Euthamia graminifolia	Grass-leaved goldenrod
Fallopia cilinodis	Fringed false-buckwheat
Fallopia scandens	False buckwheat
Fragaria virginiana	Virginia strawberry
Galeopsis tetrahit	Hemp nettle
Galium triflorum	Sweet scented bedstraw
Gaultheria procumbens	Wintergreen
Geranium bicknellii	Northern crane's-bill
Geum aleppicum	Yellow avens
Geum species	Avens
Goodyera species	Rattlesnake plantains
Gymnocarpium dryopteris	Common oak fern
Hepatica americana	Round-lobed hepatica
Hieracium aurantiacum	Orange hawkweed
Hieracium piloselloides	Yellow hawkweed
Hieracium species	Hawkweeds
Huperzia lucidula	Shining club-moss
Hypericum species	St. John's worts
Impatiens capensis	Spotted touch-me-not
Juncus tenuis	Path rush
Lactuca biennis	Tall blue lettuce
Lactuca canadensis	Wild lettuce
Lactuca species	Wild lettuces
Lamiaceae species	Mints
Lathyrus ochroleucus	Pale vetchling
Lathyrus palustris	Marsh vetchling
Lathyrus venosus	Veiny pea
Leucanthemum vulgare	Ox-eye daisy

Leucophysalis grandiflora	White-flowered ground-cherry
Linnaea borealis	Twinflower
Lonicera canadensis	Northern fly honeysuckle
Lonicera dioica	Glaucous honeysuckle
Lonicera hirsuta	Hairy honeysuckle
Lonicera species	Honeysuckles
Luzula acuminata	Hairy woodrush
Luzula acuminata	Hairy woodrush
Lycopodium clavatum	Running clubmoss
Lycopus americanus	Common water horehound
Lycopus species	Bugleweeds
Lycopus uniflorus	Northern bugleweed
Maianthemum canadense	Canada mayflower
Maianthemum racemosum	False spikenard
Matteuccia struthiopteris	Ostrich fern
Melampyrum lineare	Cow-wheat
Mertensia paniculata	Bluebells
Milium effusum	Wood millet
Mitella nuda	Naked miterwort
Monotropa uniflora	Indian pipe
Oryzopsis asperifolia	Mountain rice grass
Osmorhiza claytonii	Sweet cicely
Osmunda claytoniana	Interrupted fern
Ostrya virginiana	Ironwood
Oxalis stricta	Yellow wood-sorrel
Persicaria sagittata	Arrow-leaved tear-thumb
Petasites frigidus	Sweet-coltsfoot
Phalaris arundinacea	Reed canary grass
Phegopteris connectilis	Long beech fern
Piptatherum pungens	Rice-grass
Plantago major	Common plantain
Poa compressa	Canada bluegrass
Poaceae species	Grasses
Poa pratensis	Kentucky bluegrass
Polygonatum pubescens	Hairy solomon's seal
Potentilla norvegica	Rough cinquefoil
Prenanthes alba	Rattlesnake-root
Prunella vulgaris	Self-heal

Prunus pensylvanica	Pin cherry
Prunus virginiana	Choke cherry
Pteridium aquilinum	Western brackenfern
Pyrola elliptica	Waxflower shinleaf
Pyrola species	Pyrolas
Ranunculus acris	Common buttercup
Rhamnus alnifolia	Alder-leaved buckthorn
Rhododendron groenlandicum	Labrador tea
Ribes species	Currants
Ribes glandulosum	Skunk currant
Ribes hirtellum	Swamp currant
Ribes triste	Swamp red currant
Rosa acicularis	Wild rose
Rosa species	Roses
Rubus occidentalis	Black raspberry
Rubus parviflorus	Thimbleberry
Rubus pubescens	Dwarf red blackberry
Rubus species	Raspberries
Rubus strigosus	Wild red raspberry
Rumex acetosella	Red sorrel
Sambucus racemosa	Red elderberry
Schizachne purpurascens	False melic grass
Scirpus atrovirens	Bullrush
Scirpus cyperinus	Wool-grass
Scirpus species	Scirpus
Scrophularia lanceolata	Early figwort
Scutellaria lateriflora	Mad-dog skullcap
Scutellaria galericulata	Marsh skullcap
Maianthemum racemosum	False spikenard
Sium suave	Water-parsnip
Silene latifolia	White campion
Solidago canadensis	Canada goldenrod
Solidago flexicaulis	Zigzag goldenrod
Solidago gigantea	Late goldenrod
Solidago species	Goldenrods
Sonchus arvensis	Field sow-thistle
Sonchus oleraceus	Common sow-thistle
Sonchus species	Sow-thistles
Sorbus decora	Northern mountain ash

Spinulum annotinum	Stiff clubmoss
Streptopus lanceolatus	Rose twisted-stalk
Symphyotrichum ciliolatum	Northern heart-leaved aster
Symphyotrichum lanceolatum	Panicled aster
Tanacetum vulgare	Common tansy
Taraxacum officinale	Common dandelion
Thelypteris phegopteris	Northern beech fern
Trientalis borealis	Star flower
Trillium cernuum	Nodding trillium
Trifolium aureum	Hop clover
Trifolium hybridum	Alsike colver
Trifolium pratense	Red clover
Trifolium repens	White clover
Trifolium species	Clovers
Trillium cernuum	Nodding trillium
Trillium species	Trilliums
Uvularia sessilifolia	Sessile bellwort
Vaccinium angustifolium	Lowbush blueberry
Vaccinium myrtilloides	Velvetleaf huckleberry
Verbascum thapsus	Mullein
Veronica officinalis	Common speedwell
Viburnum rafinesqueanum	Downy arrowwood
Vicia americana	American vetch
Viola adunca	Sand violet
Viola pubescens	Downy yellow violet
Viola species	Violets