

The University of Maine
DigitalCommons@UMaine

Electronic Theses and Dissertations

Fogler Library

Summer 8-2019

Understory Response to Gap-based, Multi-aged Silviculture

Maggie R. Mansfield

University of Maine, margaret.mansfield@maine.edu

Follow this and additional works at: <https://digitalcommons.library.umaine.edu/etd>



Part of the [Forest Management Commons](#)

Recommended Citation

Mansfield, Maggie R., "Understory Response to Gap-based, Multi-aged Silviculture" (2019). *Electronic Theses and Dissertations*. 3064.
<https://digitalcommons.library.umaine.edu/etd/3064>

This Open-Access Thesis is brought to you for free and open access by DigitalCommons@UMaine. It has been accepted for inclusion in Electronic Theses and Dissertations by an authorized administrator of DigitalCommons@UMaine. For more information, please contact um.library.technical.services@maine.edu.

UNDERSTORY RESPONSE TO GAP-BASED, MULTI-AGED SILVICULTURE

By

Maggie Mansfield

B.A. College of the Atlantic, 2011

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Forest Resources)

The Graduate School

The University of Maine

August 2019

Advisory Committee:

Robert S. Seymour, Curtis Hutchins Emeritus Professor of Silviculture, Co-advisor

Shawn R. Fraver, Associate Professor of Forest Ecology, Co-advisor

Jacquelyn Gill, Associate Professor of Paleoecology & Plant Ecology

UNDERSTORY RESPONSE TO GAP-BASED, MULTI-AGED SILVICULTURE

By Maggie Mansfield

Thesis Advisors: Dr. Robert S. Seymour & Dr. Shawn R. Fraver

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Degree of Master of Science
(in Forest Resources)
August 2019

The ubiquity of managed forests has created a demand for management practices that simultaneously meet traditional management goals and maintain biodiversity. Ecological forestry, which emulates the outcomes of natural disturbances, is assumed to enhance native species survival by creating conditions similar to those under which species have long survived. We assessed this assumption by exploring the herbaceous plant community response to 20 years of gap-based, multi-aged silviculture treatments. Additionally, we assessed the ability of the treatments to meet silvicultural objectives by exploring trends in tree regeneration. The Acadian Forest Ecosystem Research Project (AFERP) is a replicated study established in 1995 on the Penobscot Experimental Forest, Maine, designed to study the response to two silvicultural treatments which emulate gap dynamics typical of wind disturbance and species-specific insect outbreaks. Results suggest the treatments have not only maintained, but even enhanced understory plant diversity, primarily with native species. Trends in regeneration show certain high-value species increased while components of balsam fir (*Abies balsamea* (L.) Mill) did not. Our findings suggest these ecological forestry treatments could meet traditional management goals while maintaining understory plant diversity.

ACKNOWLEDGEMENTS

Many thanks to Cindy Paschal and the Nutting Hall crew who were there to walk me through the myriad forms of academia. Drs. Shawn Fraver and Robert Seymour provided guidance throughout the program. Dr. Jacquelyn Gill provided much-appreciated advice and feedback as committee member. Dr. Mindy Crandall and the folk involved with SWIFT kept me sane. Friends and family kept me fed and laughing.

Thank you to Garth Holman and the members of Josselyn Botanical Society who welcomed me into their plant-loving community, provided assistance with species ID, taught me the tricks of *Carex* identification, and gave me the confidence to call myself a botanist.

My work was founded on twenty years of science – thanks to all who braved the PEF mosquitos to count Christmas fern and other understory plants. Funding for AFERP and my research was provided by the Maine Agriculture and Forest Experiment Station and the Northeastern States Research Cooperative.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS ii

LIST OF TABLES v

LIST OF FIGURES vi

Chapter 1: HERBACEOUS PLANT RESPONSE TO GAP-BASED, MULTI-AGED SILVICULTURE 1

 Introduction 1

 Methods 2

 Study Area 2

 Field Methods 4

 Statistical Analyses 5

 Richness and Diversity 6

 Community Analysis 7

 Results 8

 Overstory Conditions 8

 Richness and Diversity 8

 Community Analysis 12

 Discussion 13

 Management Implications 16

Chapter 2: REGENERATION RESPONSE TO GAP-BASED, MULTI-AGED SILVICULTURE	17
Introduction	17
Methods.....	19
Study Area.....	19
Field Methods	21
Statistical Analyses.....	21
Results.....	23
Overstory Conditions	23
Regeneration Response	24
Discussion.....	30
Management Implications	33
REFERENCES.....	35
APPENDIX A: SPECIES LIST.....	41
BIOGRAPHY OF THE AUTHOR.....	45

LIST OF TABLES

Table 1: Richness, diversity, and cover	10
Table 2: Species turnover in harvested and unharvested plots	12
Table A.1: Species List	41

LIST OF FIGURES

Figure 1: Site map 3

Figure 2: Understory plant richness..... 9

Figure 3: Species-area curve results. 10

Figure 4: Mean cover per plot of selected species 11

Figure 5: Herbaceous species ordination..... 13

Figure 6: Tree seedling cover by inventory period 25

Figure 7: Mean cover per plot of seedlings and total shrubs after 20 years 27

Figure 8: Seedling cover by harvest gap type 28

Figure 9: Tree seedling ordination. 29

CHAPTER 1

HERBACEOUS PLANT RESPONSE TO GAP-BASED, MULTI-AGED SILVICULTURE

Introduction

A long history of timber harvesting has simplified the structure of managed forests, which may have adverse effects on native biodiversity. The maintenance of forest biodiversity has traditionally been relegated to reserved land; however, the ubiquity of managed forests has created the need for management practices that maintain native biodiversity within these forests as well (Lindenmayer and Franklin 2002). Ecological forestry, which uses silvicultural techniques that emulate processes such as natural disturbance, was designed in response to this need (Seymour and Hunter 1999; Palik et al. 2002; Franklin et al. 2007; Raymond et al. 2009). Because these techniques create conditions similar to those under which species have long survived, managers assume they maintain native species; however, this assumption has rarely been assessed with long-term empirical data. As land managers increasingly adopt ecological forestry techniques, there is a need to evaluate these assumptions.

Understory plant communities within ecological forestry studies remain largely unexplored (but see Roberts et al. 2016; Halpern et al. 2005; Kern et al. 2006, 2014), though the importance of the understory to ecosystem function and diversity is well documented. For example, despite contributing less than 1% of the biomass in temperate forests, an average of 80% of plant species are found in the forest understory (Gilliam 2007). The understory also plays a disproportionately large role in functions such as nutrient cycling (Gilliam, 2007). Diversity in other taxa, such as butterflies, birds, and some mammals, is more closely tied to understory diversity than to overstory diversity (Ricketts et al. 1999). Competition within the understory can determine which tree species become established, thereby controlling the future overstory composition and structure (Royo and Carson 2006; George and Bazzaz 1999).

Forest management practices affect the understory plant community both directly and indirectly (Meier et al. 1995). Changes in the understory can in turn influence the overstory (Gilliam and Roberts 2003), making understory response a valuable metric for assessing management practices, whether intended for production or conservation. The most informative plant community studies span long time periods, tracking changes in communities that often occur on time scales of decades (Halpern and Lutz 2013). When working with the understory, long-term studies ensure capturing the full life cycle of forest herbs, which are often poorly understood (Whigham 2004).

The Acadian Forest Ecosystem Research Project (AFERP) provides an ideal setting to explore the effects of ecological forestry on understory biodiversity. AFERP, designed to study the response to two ecologically based silvicultural systems, is a large-scale, replicated study established in 1995 on the Penobscot Experimental Forest, Maine. The two treatments emulate the process of expanding canopy gaps typical of wind disturbance and species-specific insect outbreaks (Worrall et al. 2005; Bottero et al. 2011). We documented and analyzed the 20-year vegetation response, providing the first study of this temporal scale to examine the understory response to ecological forestry. Our specific objectives were to assess differences in understory species richness and diversity, the abundance of non-native and rare species, and using multivariate analyses, explore community-level changes among the two treatments and an untreated control. Results of this study will allow managers to better meet conservation and production goals by providing insights into the effects of ecological forestry on the understory.

Methods

Study Area

The Acadian Forest Ecosystem Research Project (AFERP) is located on the Penobscot Experimental Forest in central Maine, USA (44°50' N, 68°38' W). The Forest is characterized by a cool moist climate with an average annual temperature of 7.2°C and average annual precipitation of 114 cm, evenly distributed throughout the year. Soils are derived from glacial till, ranging from well drained

loams to poorly drained silty clay loams (Brissette 1996). The terrain is gently rolling, with elevations ranging from 25 to 75 m a.s.l. AFERP is located in the southern part of the Acadian forest region, which is characterized by frequent, small scale disturbances (Seymour et al. 2002). Common tree species, listed in decreasing abundance, include hemlock (*Tsuga canadensis* (L.) Carriere), red maple (*Acer rubrum* L.), white pine (*Pinus strobus* L.), northern white-cedar (*Thuja occidentalis* L.), balsam fir (*Abies balsamea* (L.) Mill.), paper birch (*Betula papyrifera* Marsh.), red spruce (*Picea rubens* Sarg.), trembling and big-toothed aspen (*Populus tremuloides* Michx., *P. grandidentata* Michx.), and red oak (*Quercus rubra* L.).

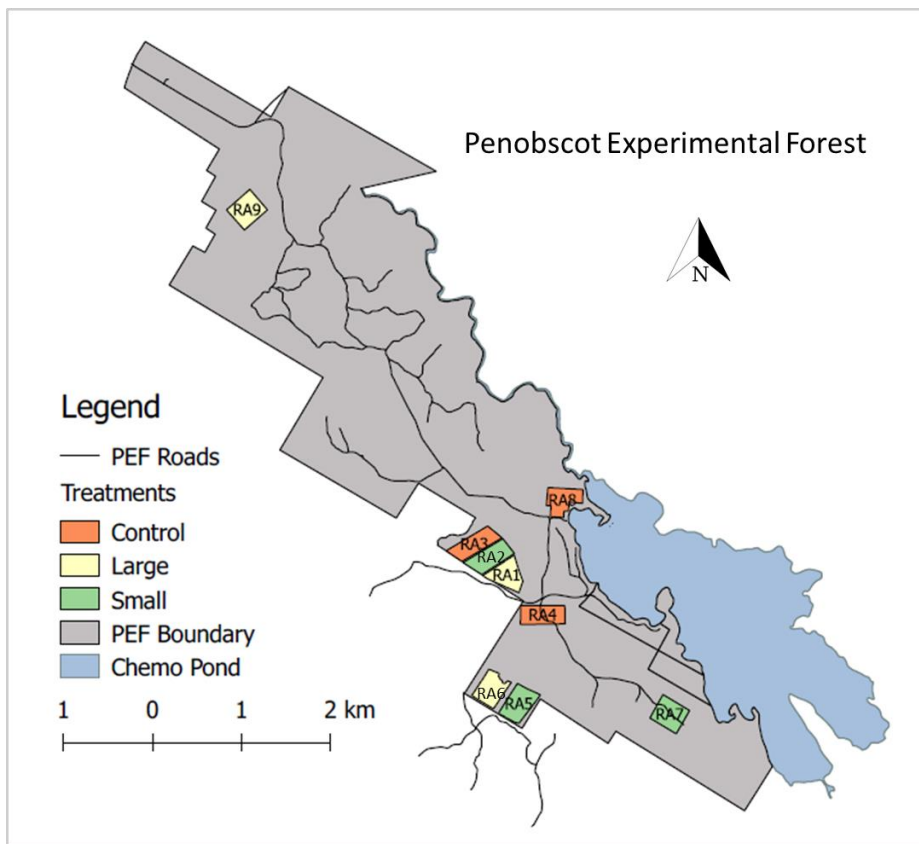


Figure 1: Site map. Penobscot Experimental Forest showing the nine AFERP research areas (RA).

AFERP is composed of three treatments, each replicated three times (treatment blocks) thus occupying nine research areas (RAs), which range from 8.9 to 11.3 ha. Upon establishment in 1995, RAs were randomly assigned a treatment of small gap, large gap, or untreated control within each block (Figure 1). Prior to treatments, the RAs did not differ with respect to tree volume, basal area, or density

(Arsenault et al. 2011), and non-metric multidimensional scaling (NMS) ordinations of pre-treatment tree species composition did not reveal groupings among RAs that might confound interpretation of understory responses (data not shown).

Both small and large gap treatments are area-based approaches loosely based on the Bavarian variant of the Femelschlag system (Troup 1928), characterized by distinct harvest gaps that are expanded on a regular cutting cycle. Treatments are harvested every 10 years, treat an average of 1% per year of the RA, and leave 10% basal area in gaps as permanent reserve trees. These trees were selected for high quality wildlife habitat, locally uncommon tree species, relatively large size, or potential for high timber value under a long rotation. Small gap treatments are a group-selection system in which 10% of the area is harvested at each harvest entry; initial gaps of approximately 0.1 ha were established in the first and second harvest entry; gaps are expanded in alternating entries (every 20 years) until the total area of each RA has been treated after 100 years. Large gap treatments are an irregular group shelterwood system (Raymond et al. 2009) in which 20% of the area is regenerated at each harvest entry; initial gaps of approximately 0.2 ha were established with the first harvest; gaps are expanded with each subsequent harvest until the full area has been treated after 50 years; these RAs will then be left for 50 years with no additional harvesting. Further details on the AFERP design and inventory protocols can be found in Seymour (2005) and Saunders and Wagner (2005).

Field Methods

A 50m × 50m grid was overlaid on each RA, and 20 permanent plot locations were established on randomly selected grid intersects. Sampling occurred every 5 years, beginning in 1995, before the first harvest, which occurred in the winter of 1995-1996. Overstory data were collected on 0.05 ha, circular plots on trees over 9.5 cm diameter at breast height (DBH; 1.3 m). Understory plots are defined by four, 1 m × 1 m quadrats placed 8 meters from plot center, at 90° angles from each other. All vascular plant species were inventoried, with the exception of tree seedlings, which were assessed separately.

Visual estimates of percent cover were recorded for each species including graminoids. Taxonomy, nomenclature, and residency follow Haines et al. (2011). Cover data collected on quadrats were averaged to represent each plot. Plot data were then averaged to represent the treatment response of each RA.

Statistical Analyses

We created two datasets to assess understory plant response to the silvicultural treatments. The first is composed of both the initial inventory (1995-1997) and the most recent inventory (2017-2018), referred to as the combined dataset. To account for taxonomic resolution that differed between the initial and most recent inventory, taxa in the combined dataset were lumped to the finest resolution identified for both inventories. For example, because the initial inventory identified graminoids only to genus or family level, graminoids in the combined dataset were lumped to family level. We used this dataset for all analyses that explicitly compare pre- and post-treatment. The second dataset is composed of only the most recent inventory and uses the full taxonomic resolution, referred to as the full dataset. We excluded shrubs, or herbs that were not identified to at least family level in both datasets (seven in the initial inventory, one in the most recent).

For most analyses, research area is treated as the experimental unit. However, we also wanted to specifically test the community response within gaps. To this end, plot locations within treated research areas were assigned to either gap or untreated matrix. For the most recent, 20-year samples, treatment response for the small gap treatment represents the weighted average of 31% of plots located in harvest gaps of various ages versus 69% of plots in the matrix that have yet to be treated. Comparable values for the large gap treatment are 62% in harvest gaps, 38% in matrix.

Richness and Diversity

We used the combined dataset to generate species-area curves, allowing us to explore changes in richness resulting from each treatment. Species-area curves were generated using the 'vegan' package in R (Oksanen et al 2018). We tested for differences between the initial and the most recent species-area curves in each treatment using a generalized linear model based on the points of each generated RA curve (six curves total for each treatment, three for each inventory period), specifically testing the inventory period \times richness interaction (R 1.0.153; R Core Team 2017). A significant interaction would indicate that the species-area curves differed pre- to post-treatment. However, for simplicity in graphical presentation, we averaged the initial (pre-treatment) data for the three RAs representing each treatment to generate a single curve, which we compared to individual RA curves from the most recent inventory.

The plot network in one research area was compromised, post-establishment, by road construction, which eliminated five of the 20 plots, thereby reducing sampling area (relative to other RAs) and confounding calculations of richness and diversity. To overcome this limitation, we ran a series of simulations to estimate richness and Shannon's diversity index (H') for this RA, had 20 plots been surveyed. We randomly selected 15 plots from each fully sampled RA and calculated richness and H' from these plots. We then created a regression model for each metric, regressing values of the full 20 plots against those from the randomly selected 15 plots, repeating this process 100 times. These simulations allowed us to predict mean richness and H' had this RA been fully sampled (richness = 42, sd = 1.53; H' = 2.56, sd = 0.06). These estimates were used in all analyses of richness and diversity based on the full dataset.

We ran one-way ANOVAs on the full dataset to test for differences among treatments regarding richness, H' , mean total cover per plot, and mean total cover per plot for individual species. Because

analyses were performed at RA level, power was limited by the small sample size ($n = 9$ RAs); therefore, we were unable to incorporate plot and treatment block as random effects or plot-specific covariates into the model. P-values were adjusted using the 'Holm' method to account for family wise error in individual species ANOVAs. Post-hoc comparisons of mean total cover per plot among treatments for individual species that showed significant difference in ANOVAs ($p < 0.1$) were performed using Tukey's honest significant difference test. ANOVAs and Tukey's tests were performed in R 1.0.153 (R Core Team 2017).

To isolate direct effects of harvesting on species turnover (gains vs losses) between the two inventories, we post-stratified plot data according to its location during the most recent inventory. Instead of using RA as the experimental unit, plots in the combined dataset were categorized as either small or large harvest gap, the intervening matrix of mature forest, or control area. We then calculated Whittaker's beta diversity and tallied any species gained or lost between inventories for each strata.

Community Analysis

We explored community composition among treatments using non-metric multidimensional scaling (NMS) ordination. The community matrix was arranged with RAs as rows ($n = 9$) and species as columns ($n = 93$) using the most recent, full dataset containing percent cover values. To reduce noise in the data set, we excluded species found on only one plot. We used the Bray-Curtis similarity metric based on untransformed cover data to create a distance matrix and ran the ordination with 50 random starts. Statistical separation among treatments was tested with distance-based multivariate analysis of variance (PERMANOVA). To determine which species were driving community separation, we calculated Kendall's rank correlation coefficients between species' abundance and their NMS scores. We then tested for indicator species associated with only one treatment. The multivariate analyses were

performed using the 'vegan' package, and indicator species analysis was performed using the 'indicspecies' package in R 1.0.153 (Oksanen et al. 2018; De Caceres and Legendre 2009).

Results

Overstory Conditions

As of 2017, the overstory in all RAs was dominated by hemlock, white pine, and red maple. The treated RAs have been harvested three times since the study began. All sets of gaps have been initiated; the first set of small gaps have been expanded once, and the large gaps have been expanded twice. Control treatments averaged 43.8 m²/ha (sd = 10.9) basal area (BA), of which 5% was in the sapling class (1.5 cm – 9.5 cm DBH) and 2,452 trees per ha (sd = 1,615) of which 67% were saplings. Small gap treatments averaged 40.9 m²/ha (sd = 10.7) BA, of which 6% was in the sapling class and 2,492 trees per ha (sd = 1,767), of which 64% were saplings. Large gap treatments averaged 31.6 m²/ha (sd = 12.9) BA, of which 14% was in the sapling class with 3,909 trees per hectare (sd = 2,785), of which 84% were saplings.

Richness and Diversity

We found 128 vascular plant species representing 45 families in the most recent survey. Sixty-four species were found in the controls, 71 in the small gap treatments, and 101 in the large gap (Figure 2). Six species are not native to the region, one of which was found in the control RAs, two in small gap RAs, and all six of which were found in the large gap RAs. We found one known non-native, invasive species in the small and large gap areas (glossy buckthorn; *Frangula alnus* Mill.), and one non-native, potentially invasive species in control and large gap areas (broad-leaved helleborine; *Epipactis helleborine* (L.) Crantz). Because both were in low abundance, we were unable to attribute their presence to treatment effects.

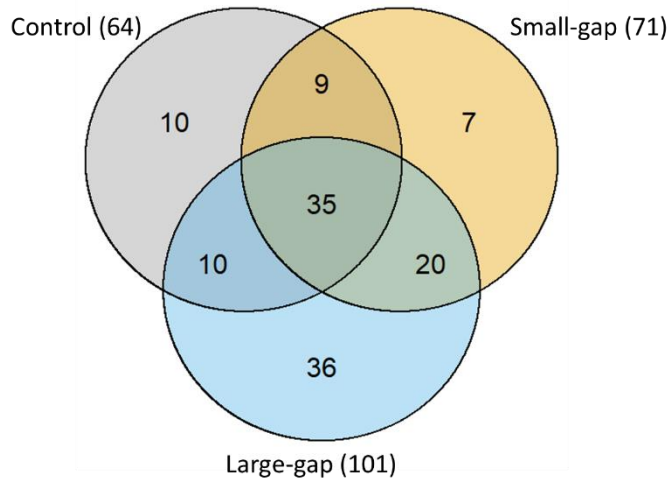


Figure 2: Understory plant richness. Number of understory species found within various treatments shows that species were generally gained in treated areas.

Species-area curves for the most recent data show no change from the initial conditions in the control treatments, as expected. The same contrast showed a slight increase of richness in the small gap treatments, and a near doubling in the large gap treatments (Figure 3). The inventory \times richness interaction of the generalized linear models confirmed that curves did not differ significantly in control areas ($p = 0.33$), differed marginally in small gap areas ($p = 0.12$), and differed significantly in the large gap treatment ($p < 0.001$). Richness from the most recent, full dataset corroborated this pattern with an average of 56 species in the large gap RAs compared to 38 in small gaps and 33 in controls. However, owing to small sample size ($n = 3$) and high variability, these richness differences were not statistically significant.

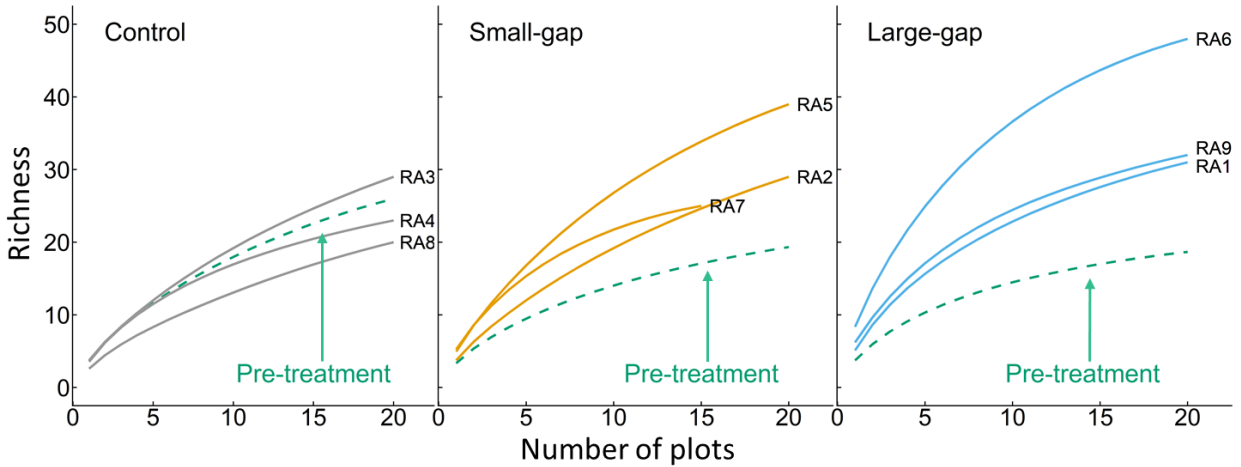


Figure 3: Species-area curve results. Species accumulation of individual research areas during the most recent inventory compared to their pretreatment average (dashed line) show richness did not change in control (a), increased moderately in small gap (b), and nearly doubled in large gap (c) treatments.

Our results suggest both small and large gap treatments increased Shannon’s diversity index (H') when compared to untreated control areas (Table 1). H' averaged 2.7 in control RAs, 3.0 in small gap RAs, and 3.3 in large gap RAs. Average total cover per plot showed similar patterns, increasing from 3.4% in control RAs to 3.6% in small gap and 6.7% in large gap RAs. However, differences were not statistically significant regarding either H' or cover.

Table 1: Richness, diversity, and cover. Total richness, Shannon’s diversity index (H'), and mean percent cover per plot by control, small gap, and large gap treatment using the full taxonomic resolution of the most recent inventory.

	Richness	H'	Percent cover
Control	64	2.7	3.4%
Small gap	71	3.0	3.6%
Large gap	101	3.3	6.7%

We examined differences among treatments in the mean cover per plot for individual species, presenting those most common to the region or of particular interest to managers (Figure 4). Raspberry (*Rubus idaeus* L.) and bracken fern (*Pteridium aquilinum* (L.) Kuhn), both disturbance dependent species, were found only in treated areas. Common species such as bunchberry (*Chamaepericlymenum canadense* (L.) Aschers. & Graebn.), Canada mayflower (*Maianthemum canadense* Desf.), starflower (*Lysimachia borealis* (Raf.) U. Manns & A. Anderb.), and wild sarsaparilla (*Aralia nudicaulis* L.) increased moderately in small gap treatments and greatly in large gap treatments over controls (Figure 4). After adjusting p-values for family wise error, ANOVAs were significant only for starflower. Tukey's honest significant difference test showed significant differences between control and large gap treatments for starflower ($p = 0.01$). No patterns were discernable in shade tolerant non-woody species, due to their general rarity.

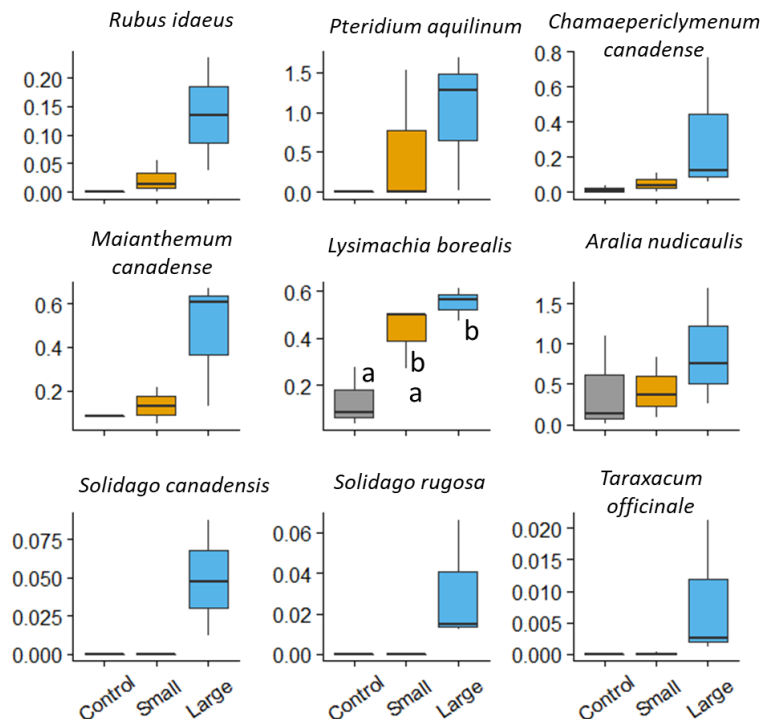


Figure 4: Mean cover per plot of selected species. Letters indicate significant difference between treatments from Tukey's honest significant difference tests.

Plots stratified by location in small or large harvest gap, matrix, or control showed increased turnover in harvest gaps and matrix plots, though most turnover was attributed to species gained rather than species lost (Table 1). Beta diversity was 0.20 in the control plots, 0.30 in the matrix plots, 0.32 in small gap plots and 0.35 in the large gap plots. Interestingly, control plots lost the most species from the initial to the most recent inventory, while large gap plots lost the fewest species (Table 2).

Table 2: Species turnover in harvested and unharvested plots. Number of species gained or lost between pre- and post- treatment inventories and Whittaker’s *beta* diversity by control, matrix (unharvested plots within the treated areas), small gap, and large gap plots suggest harvests are not causing species loss after 20 years of treatment.

	Gained	Lost	<i>Beta</i> diversity
Control	8	10	0.20
Matrix	23	4	0.30
Small gap	15	4	0.32
Large gap	29	2	0.35

Community Analysis

The NMS ordination converged with lowest stress using three axes (stress = 0.03). Results were somewhat ambiguous due to the high number of zeros in the community matrix; however, the large gap RAs were separated from control RAs in ordination space, while the small gap RAs bridged the large gap and control RAs (Figure 5). PERMANOVA results were marginally significant ($p = 0.08$), indicating weak separation among treatments. The first axis was correlated with abundance of Canada mayflower and velvet-leaved blueberry (*Vaccinium myrtilloides* Michx.); the second axis was correlated with bunchberry; and the third axis was correlated with evergreen wood fern (*Dryopteris intermedia* (Mulh.

ex Willd.) A. Gray). Indicator species analysis found Canada goldenrod (*Solidago canadensis* L.), wrinkle-leaved goldenrod (*Solidago rugosa* Mill.), and common dandelion (*Taraxacum officinale* F. H. Wigg.) associated with large gap treatments (Figure 4). No species were associated with control or small gap treatments.

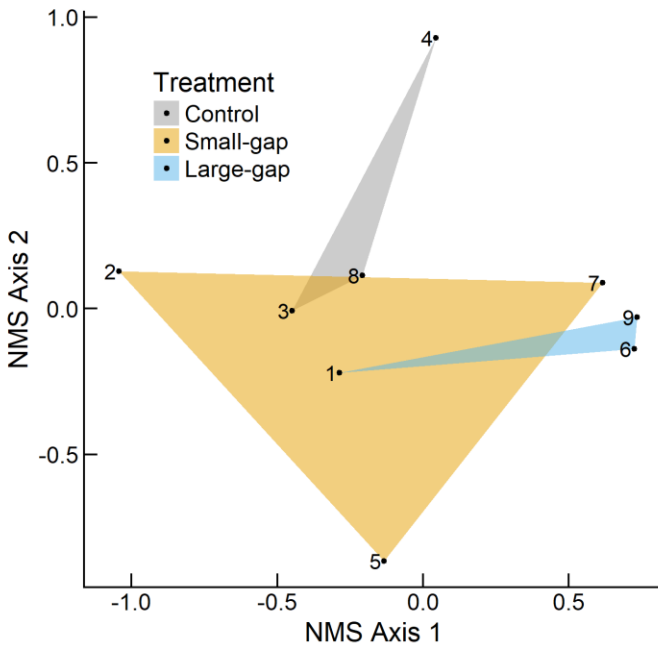


Figure 5: Herbaceous species ordination. Results of research areas (RA) 1-9 by control (gray), small gap (yellow), and large gap (blue) treatments show separation among control and large gap treatments.

Discussion

Our results suggest that 20 years of expanding gap silviculture has not only maintained, but enhanced richness and diversity of the understory plant community. Species-area curves show an increase in richness from the initial inventory in treated areas, and the most recent inventory shows higher richness and Shannon’s diversity index (H') in treated areas when compared to untreated controls. Ordinations, though limited by the number of zeros in the matrix, indicate community

separation among treatments, with greatest separation between the large gap and control treatments (Figure 5).

Some of our comparisons among treatments were not statistically significant, although this was somewhat expected given the realities of large-scale silvicultural experiments, which require treatment areas of 10 ha each, thus limiting the feasibility of extensive replication (Seymour et al. 2006).

Furthermore, the sparse, patchy nature of understory vegetation of the Acadian forest provides additional challenges to capture the diversity of a site.

Both the small and large gap treatments are intended to open growing space for seedlings and saplings of desirable tree species (Seymour 2005). Understory herbaceous species also respond to increased resources and changes in microclimate, such as increased light and access to mineral soil, with response often increasing with increased harvest intensity (Haeussler et al. 2002; Raymond et al. 2018). Accordingly, the small gap treatments show a moderate increase, while large gap treatments show a larger increase in herbaceous richness, diversity, and cover.

Increases in richness following harvest can be undesirable if it results in colonization by undesirable species, including non-native, disturbance-dependent and non-native, invasive species (Oswalt and Oswalt 2007). We found a limited increase of non-native species in the treated RAs, only two of which are considered invasive or potentially invasive in the region, though none were abundant enough to analyze. All species whose cover correlated with ordination axes are native to the region, as are two of the three indicator species, suggesting that composition changes among treatments are driven primarily by native species.

In a study on the surrounding Penobscot Experimental Forest, Olson et al. (2011) found that invasive plants were abundant in forested sites that had been previously cleared for agriculture. While invasions were limited in stands more closely resembling those of the AFERP study, Olson et al. (2011)

suggested such sites are susceptible to future invasion. Invasive species colonization is a factor of disturbance, propagule pressure, and resource availability (D'Antonio 1993; Richardson and Pysek 2006; Davis et al. 2000), all of which may increase with timber harvest. Additionally, timber harvest and other human caused disturbances can create conditions to which native species are not adapted, thus giving non-native species a competitive advantage (Byers 2002). Silvicultural practices that aim to create conditions similar to those of natural forests may therefore limit invasion, though this theory has not been explicitly tested. Glossy buckthorn, the most widespread invasive plant in the surrounding forest, was found for the first time in the most recent inventory on three of 175 AFERP plots and may be worth monitoring as the study progresses.

Late-successional forests are increasingly rare in the Acadian region, causing widespread concern over the loss of shade-dependent species (Mosseler et al. 2003). These species are often particularly sparse and patchily distributed, making it especially difficult to capture them in studies of larger areas (Stohlgren 2007). While this study was not designed to assess the success of individual species, more species were lost from control and matrix plots than from harvest gaps, indicating that gap treatments have not led to species loss. Indian-pipe (*Monotropa uniflora* L.) and blue-bead lily (*Clintonia borealis* (Ait.) Raf.), the only species lost from large gap plots between the pre- and post-treatment inventories, are both shade-dependent species, though not listed as species of concern in the state of Maine (Maine Natural Areas Program 2015).

Species loss following harvest can come from both direct and indirect causes, including crushing from equipment or changes in habitat conditions (Meier et al. 1995). The limited species loss observed on AFERP sites could be the result of minimal damage during harvest or moderated environmental conditions from reserve trees. The expanding gap system allows for efficient allocation of trails (well under 10% of area, less than half that of a typical commercial operation), thus minimizing the area of

heaviest impact (Berger et al. 2004). All harvests occurred in winter when frozen soils and snow-pack further protect understory species (Wolf et al. 2008). Reserve trees are known to alter understory conditions post-harvest, though the minimum level of retention required to ameliorate harsh conditions following harvest varies (Halpern et al. 2012; Lilles et al. 2018; Craig and Macdonald 2009).

Management Implications

Ecological forestry provides an alternative to strictly economically driven silviculture systems, prioritizing biodiversity and other ecological values within managed forests. Our results suggest the silvicultural treatments tested on AFERP, one of the longest running research trials of ecological forestry, could maintain, and even enhance, species richness and diversity within managed forests. Importantly, this enhancement is not the result of gaining unwanted (non-native, invasive) species, as has occurred in many traditional harvesting studies (Oswalt and Oswalt 2007). AFERP treatments consist of both harvest gaps and structural retention that emulate the outcomes of natural disturbances, the combination of which may contribute to our results. While the study design does not allow us to parse out individual effects of the treatments – including effects of canopy gaps, gap expansion, time since harvest, or retention of reserve trees – the most recent inventory captures the cumulative effects of 20 years of ecological forestry. Species were maintained within all treatments as well as within harvest gaps, and treatments appear to enhance richness and diversity, primarily with native species.

CHAPTER 2

REGENERATION RESPONSE TO GAP-BASED, MULTI-AGED SILVICULTURE

Introduction

Years of forest harvesting with little attention to forest renewal has led to undesirable species composition and simplified structure in many managed forests. Ecological forestry, which uses silvicultural techniques to emulate processes such as natural disturbance, has been suggested as a method to reverse these trends (Seymour and Hunter 1999; Palik et al. 2002; Franklin et al. 2007; Raymond et al. 2009). Many studies have demonstrated that ecological forestry prescriptions enhance structural complexity, creating stands with attributes similar to those of old growth forests which can support higher levels of biodiversity (Franklin et al. 2007; Bauhus et al. 2009; Keeton 2006). However, far fewer studies of ecological forestry have focused on forest regeneration (but see Bolton and D'Amato 2011; Roberts et al. 2017; Olson and Wagner 2011; Urgenson et al. 2013), despite the fact that regeneration is often the focus of traditional silvicultural treatments.

Tree regeneration is critical to sustainable forests, determining in part a stand's future structure, composition, and productivity. Natural regeneration requires favorable conditions for seed production, seed dissemination, seedling germination, seedling establishment, and seedling growth (Grubb 1977). Favorable conditions are species specific, and often the same species will have different requirements depending on its development stage (Kneeshaw et al. 2006). Forest managers utilize these differences in regeneration requirements to control tree species composition through light and other resource gradients in the understory.

Gap-based ecological forestry creates harvest gaps to control these resource gradients, altering their size, shape, and frequency within the bounds found in natural canopy gaps, to create conditions appropriate for regeneration of target species. The gradient of light and other resources within a gap

lead to an array of microclimates (Prevost and Raymond 2012; Gálhidy et al. 2006; Gray and Spies 1997). In theory, these microclimates allow space for shade tolerant species to establish on the shaded edges and less tolerant species to establish in the center and edges that receive more light (Runkle 1982; Gálhidy et al. 2006; Gray and Spies 1996; Van Couwenberghe et al. 2010). This theory of gap partitioning has been used to promote gap-based silviculture for increasing tree species diversity; however, tree regeneration does not always respond to gaps as expected, leading to regeneration failures or regeneration of non-target species (Forrester et al. 2014; Reuling et al. 2019).

Canopy gaps interact with a number of confounding environmental factors, and previous studies have shown that emulating gap size and frequency alone may not be sufficient to regenerate stands of the desired tree species (Bolton and D'Amato 2011; Kern et al. 2017). For example, studies have shown regeneration to respond more to substrate conditions (Prevost 2008; Gray and Spies 1997), browse pressure (Forrester et al. 2014; Walters et al. 2016), and interfering understory vegetation (Roberts et al. 2017; George and Bazzaz 1999) than to gap characteristics *per se*. In addition to the complexities of predicting tree regeneration, natural regeneration is facing increased ecological, social, and economic pressures throughout the United States (Dey et al. 2019). These challenges highlight the need for a clear understanding of long-term regeneration responses to ecological forestry. Despite decades of detailed studies of natural gap dynamics and gap-based silviculture, much remains unknown regarding the application of these findings to ecological forestry prescriptions that incorporate attributes of natural disturbance in addition to gap characteristics.

The Acadian Forest Ecosystem Research Project (AFERP), established in 1995, provides an ideal opportunity to explore natural tree regeneration following twenty years of ecological forestry. Two silvicultural treatments emulate the process of expanding canopy gaps typical of wind disturbance and species-specific insect outbreaks (Worrall et al., 2005; Bottero et al. 2007), incorporating permanent

tree retention to closer emulate the outcomes of natural disturbance (Carter et al. 2017; Gustafsson et al. 2012). The expanding gap system allows managers to capitalize on advance regeneration, a critical component of natural regeneration in the Acadian forest region, and essential to promoting shade tolerant species that are often out-competed by faster growing intolerant species (Seymour 1992). One AFERP treatment is designed to accelerate managed forests to old-growth conditions, while the other aims to increase the stocking of valuable species while maintaining some component of less valuable species.

Using 20 years of longitudinal data, we examined changes in tree regeneration, cover, and composition. Our specific objectives were to explore trends in tree seedling cover or composition attributable to treatments, specifically looking at the response of target species. Additionally, we examined changes in seedling cover between harvest gaps and the unharvested matrix and explored the potential of an interfering shrub layer. Results of this study will allow managers to better meet production and conservation goals by providing insights into the regeneration response to twenty years of ecological forestry.

Methods

Study Area

The Acadian Forest Ecosystem Research Project (AFERP) is located on the Penobscot Experimental Forest in central Maine, USA (44°50' N, 68°38' W). The Forest is characterized by a cool moist climate with an average annual temperature of 7.2°C and average annual precipitation of 114 cm, evenly distributed throughout the year. Soils are derived from glacial till, ranging from well drained loams to poorly drained silty clay loams (Brissette 1996). Elevations at the AFERP sites range from 25 to 75 m above sea level. AFERP is located in the southern part of the Acadian forest region, which is characterized by frequent, small scale disturbances (Seymour et al. 2002). Common tree species, listed

in decreasing abundance, include hemlock (*Tsuga canadensis* (L.) Carriere), red maple (*Acer rubrum* L.), white pine (*Pinus strobus* L.), northern white-cedar (*Thuja occidentalis* L.), balsam fir (*Abies balsamea* (L.) Mill.), paper birch (*Betula papyrifera* Marsh.), red spruce (*Picea rubens* Sarg.), trembling and big-toothed aspen (*Populus tremuloides* Michx., *P. grandidentata* Michx.), and red oak (*Quercus rubra* L.).

AFERP is composed of three treatments, each replicated three times thus occupying nine research areas (RAs), which range from 8.9 to 11.3 ha (Figure 1). Upon establishment in 1995, RAs were randomly assigned a treatment of small gap, large gap, or untreated control within each replicate. Prior to treatments, the RAs did not differ with respect to tree volume, basal area, or density (Arsenault et al. 2011), and non-metric multidimensional scaling (NMS) ordinations of initial tree species composition did not reveal groupings among RAs that might confound interpretation of tree seedling responses (data not shown).

Both small and large gap treatments are area-based approaches loosely following the Bavarian variant of the Femelschlag system (Troup 1928) characterized by distinct harvest gaps that are expanded on a regular cutting cycle. Treatments are harvested every 10 years, treat an average of 1% per year of the RA, and leave 10% living tree basal area in gaps as permanent legacy retention. Reserve trees are selected for high quality wildlife habitat, locally uncommon tree species, relatively large size, or potential for high timber value under a long rotation. Small-gap treatments are a group-selection system in which 10% of the area is harvested at each harvest entry; initial gaps of approximately 0.1 ha were established in the first and second harvest entry; gaps are expanded in alternating entries (every 20 years) until the total area of each RA has been treated after 100 years. Large-gap treatments are an irregular group shelterwood system (Raymond et al. 2009) in which 20% of the area is regenerated at each harvest entry; initial gaps of approximately 0.2 ha were established with the first harvest; gaps are expanded with each subsequent harvest until the full area has been treated after 50 years; these RAs

will then be left for 50 years with no additional regeneration harvesting. The primary objective of the small gap treatment is to accelerate stands to late successional structure and composition; the primary objective of the large gap treatment is to shift species composition to a more valuable mixture while maintaining components of less valuable species. Further details on the AFERP design and inventory protocols can be found in Seymour (2005) and Saunders and Wagner (2005).

Field Methods

A 50m × 50m grid was overlaid on each RA, and 20 permanent plot locations were established on randomly selected grid intersects. Sampling occurred every 5 years, beginning in 1995, before the first harvest, which occurred in the winter of 1995-1996. Overstory data were collected on 0.05 ha, circular plots on trees over 9.5 cm diameter at breast height (DBH; 1.30 m). Regeneration plots are defined by four 1 m × 1 m quadrats placed 8 meters from plot center, at 90° angles from each other. Visual estimates of seedling percent cover for each tree species were recorded for all tree stems < 1.5 cm diameter at breast height. Cover data collected on quadrats were averaged to represent each plot. Plot data were then averaged to represent the treatment response of each RA.

Statistical Analyses

For most analyses, research area is treated as the experimental unit. However, we also wanted to specifically explore species' response within harvest gaps. To this end, plot locations within treated RAs were assigned to either gap or untreated matrix based. For the most recent, 20-year samples, treatment response for the small gap treatment represents the weighted average of 31% of plots located in harvest gaps of various ages versus 69% of plots in the matrix that have yet to be treated, very close to the expected values of 30% and 70%. Comparable values for the large gap treatment are 62% in harvest gaps, 38% in matrix, again close to expected values of 60% and 40%. We assess longitudinal trends using a dataset composed of all five inventories and explore current conditions using data from

the most recent inventory. We used seedling cover for all analyses, as both new germinants and established seedlings were recorded. Percent cover provides a reliable estimate of established seedling success, as germinants will inherently cover smaller areas.

We evaluated to what extent seedling cover (by species) varied in response to the ecological forestry treatments using repeated-measures analyses of variance (ANOVA), which tested if seedling cover varied among treatments (between-subjects main effect), among inventory periods (within-subjects main effect), as well as treatment \times inventory interaction. The interaction specifically tested if temporal patterns (cover through time) varied by treatment (von Ende 1993). We included an error term for RAs (within-subjects error) to account for autocorrelation caused by repeated measures. Thus, ANOVAs included five inventory periods and nine RAs grouped into three treatments. ANOVAs were run separately for the most common species (red maple, balsam fir, hemlock, and white pine) or species of particular interest (red spruce). Less common species were grouped according to shade tolerance. Birches (with the exception of yellow birch (*Betula alleghaniensis* Britton)), poplars, and pin cherry (*Prunus virginiana* L.) were grouped as 'intolerant' species; yellow birch, red oak, and ash species (*Fraxinus sp.* L.) were grouped as 'intermediate' species. Remaining species were not analyzed. P-values were adjusted using the 'Holm' method to account for family-wise error rate (Quinn and Keough 2002).

To assess the success of the treatments (after 20 years) in favoring target species, we ran one-way ANOVAs using seedling cover data from the most recent inventory, testing for differences among mean cover per plot for individual tree species. We examined shrub response to treatment by testing for differences in mean total shrub cover among treatments. Data are presented according the silvics categories of 'long-lived, intermediate to tolerant' (LIT) species or non-LIT species, as defined by McGrath (2017). As above, tree species were analyzed as red maple, balsam fir, hemlock, white pine, red spruce, intolerant, or intermediate species. P-values were again adjusted using the 'Holm' method

(Quinn and Keough 2002). To further examine species' responses to harvest gaps, we post-stratified plot data according to their location during the most recent inventory (as above). For these analyses, instead of using RA as the experimental unit, plots in the most recent inventory were categorized by the location of plot center in either small or large harvest gap, the intervening matrix of mature forest, or control area. These data were used to further explore patterns revealed in RA-level analyses. All ANOVAs were performed in R 1.0.153 (R Core Team, 2017).

We explored changes in community composition of tree seedlings using non-metric multidimensional scaling (NMS) ordinations of seedling cover data. The community matrix was arranged with site as rows ($n = 15$) and species as columns ($n = 25$). We averaged RA means to represent treatments for clearer presentation. We included all species in the matrix because infrequent observations did not seem to confound results. Percent covers were relativized by site total before creating a distance matrix using Bray-Curtis metric. Ordinations were run with 50 random starts. We tested for significant differences among treatments, inventories, and the treatment \times inventory interaction with distance-based multivariate analysis of variance (PERMANOVA). We calculated Kendall's rank correlation coefficient between species abundances and their NMS scores to determine which, if any, species were driving ordination axes. Ordinations and PERMANOVAs were run using the 'vegan' package and correlation coefficients using the 'psych' package in R (Oksanen et al. 2018; Revelle 2017).

Results

Overstory Conditions

As of 2017, all treatments were dominated by hemlock, white pine, and red maple. The treated RAs have been harvested three times since the study began. All sets of gaps have been initiated; the first set of small gaps have been expanded once, and the large gaps have been expanded twice. Control treatments averaged 43.8 m²/ha (sd = 10.9) basal area (BA), of which 5% was in the sapling class (1.5 cm

– 9.5 cm DBH) and 2,452 trees per ha (sd = 1,615) of which 67% were saplings. Small gap treatments averaged 40.9 m²/ha (sd = 10.7) BA, of which 6% was in the sapling class and 2,492 trees per ha (sd = 1,767), of which 64% were saplings. Large gap treatments averaged 31.6 m²/ha (sd = 12.9) BA, of which 14% was in the sapling class with 3,909 trees per hectare (sd = 2,785), of which 84% were saplings.

Regeneration Response

Seedlings of twenty-five tree species were found on the AFERP sites over the course of the study. Most seedling species were found in all treatment areas in all inventories, with only a few uncommon species found. Plots on all treatments were dominated by hemlock and balsam fir seedlings. Mean seedling cover per plot increased from the initial inventory to the most recent inventory in all treatment areas, increasing from 16% to 18% in control areas, 14% to 22% in small gap areas, and 19% to 24% in large gap areas (Figure 6).

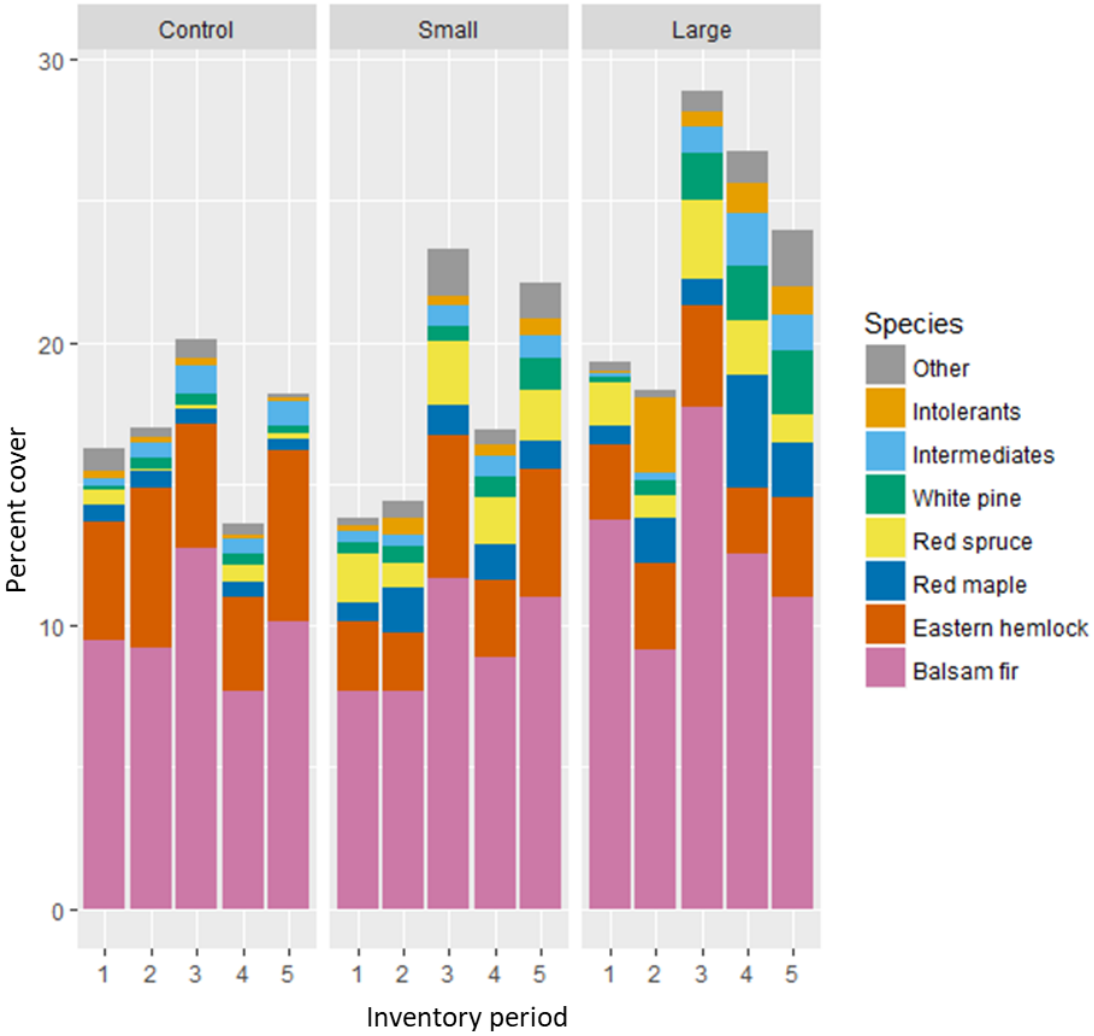


Figure 6: Tree seedling cover by inventory period. Mean percent cover per plot of seedling species and groups of species, shown for each inventory period, beginning in 1995 and ending in 2017. ‘Intolerant’ species include birch species (with the exception of yellow birch), poplar species, and pin cherry. ‘Intermediate’ species include ash species, red oak, and yellow birch. Remaining species are included as ‘Other’.

Repeated-measures ANOVAs run on the longitudinal data of species and tolerance groups showed significant effects for treatment, inventory and the treatment × inventory interaction for red maple (‘Holm’ adjusted p-value < 0.1); treatment effect was significant for white pine, red spruce, and

shade-intolerant species; inventory effect was significant for white pine; no effects were significant for hemlock, balsam fir or intermediate species.

Seedling cover response in the most recent inventory varied by shade tolerance. Shade intolerant species generally had higher cover in treated areas than control areas (Figure 7). Cover of red maple and white pine, both intermediate shade tolerant species, increased from control, to small gap, to large gap areas, though other intermediate species showed no difference among treatments. Balsam fir, hemlock, and red spruce, all shade tolerant species, showed a full range of responses from increased cover in treated areas to decreased cover to minimal change. Shrubs showed little difference among treatments (Figure 7). Differences were not statistically significant, though this is not surprising given the small sample size ($n = 9$ RAs). Post-stratification of plots by harvest gap type suggests that cover changes seen in cover of individual species are occurring in matrix, small gap, and large gap plots, but not the control (Figure 8).

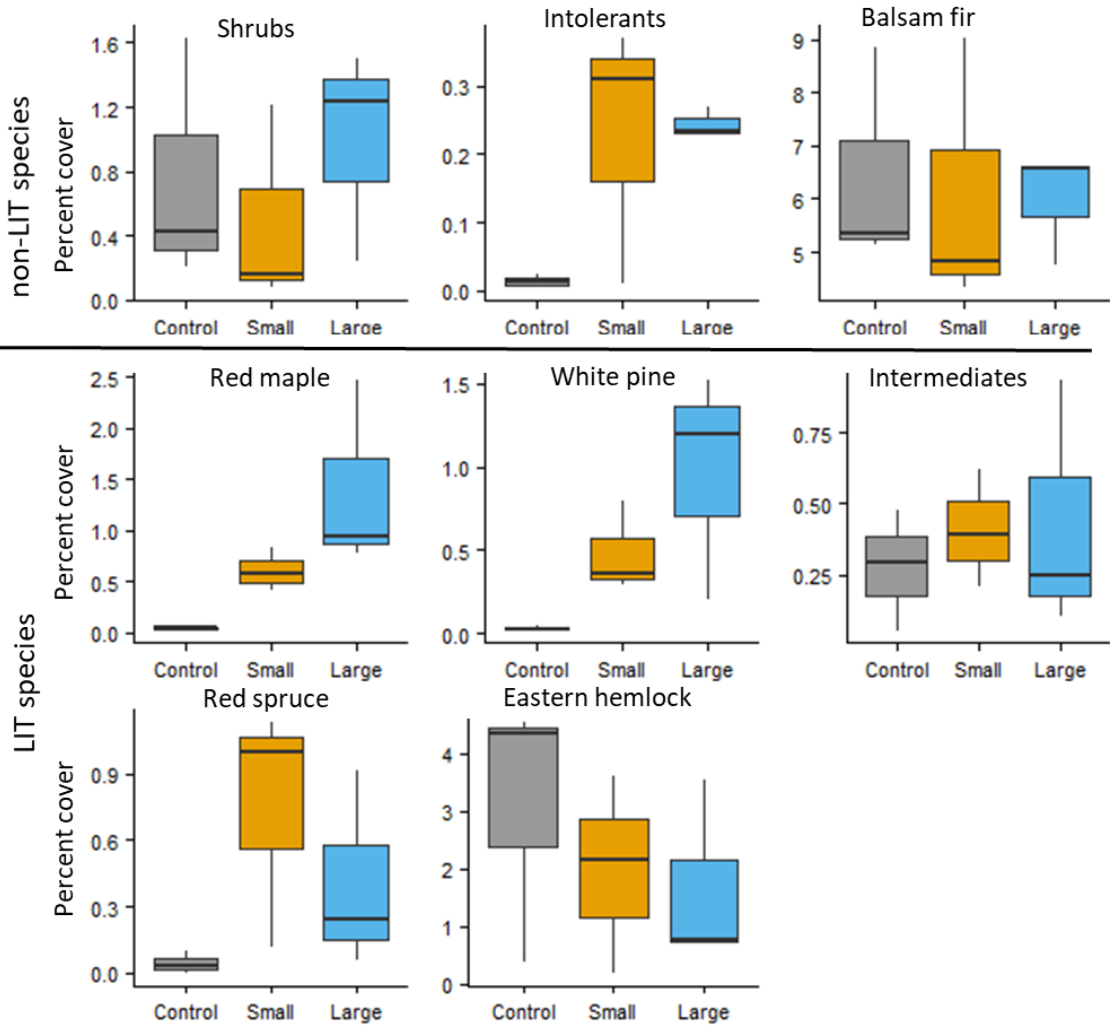


Figure 7: Mean cover per plot of seedlings and total shrubs after 20 years. The bottom two rows show 'long-lived, intermediate to tolerant' (LIT) species; top row shows shrubs and non-LIT tree species.

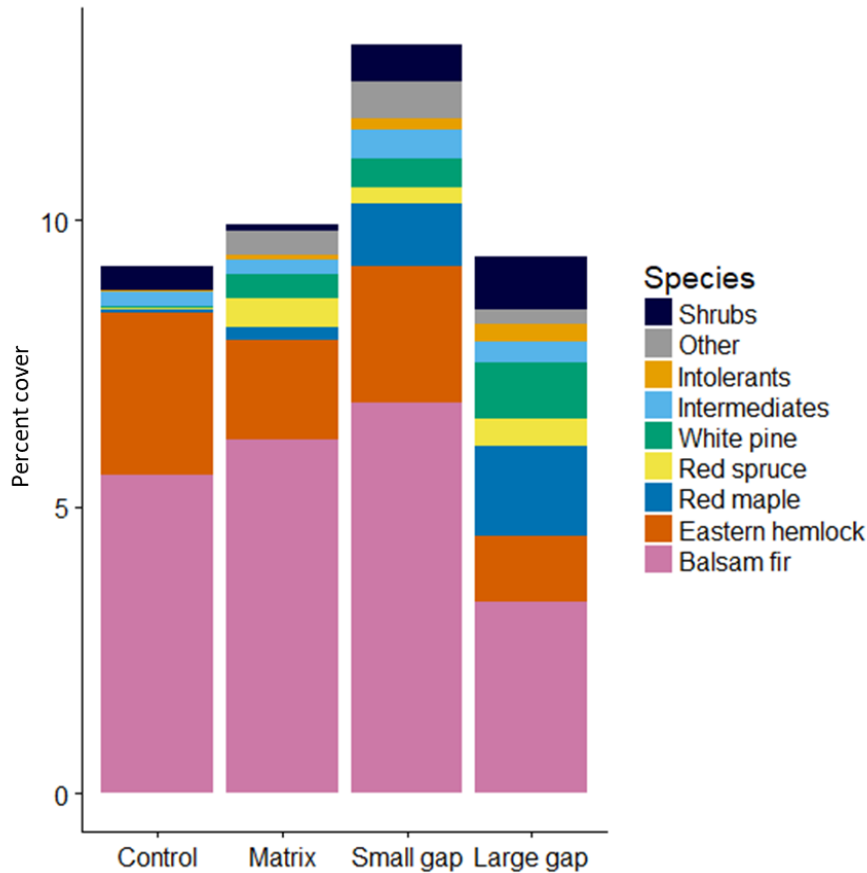


Figure 8: Seedling cover by harvest gap type. Mean percent cover per plot for each harvest gap type in which individual plots were located. Matrix refers to unharvested plots within treated research areas. ‘Intolerant’ species include birch species (with the exception of yellow birch), poplar species, and pin cherry. ‘Intermediate’ species include ash species, red oak, and yellow birch. Remaining tree species are included as ‘Other’.

Ordinations of seedling cover data by treatment and inventory converged with lowest stress using three axes (stress = 0.045). PERMANOVA results indicated separation among treatments ($p = 0.002$) but no separation by inventory period ($p = 0.15$) or treatment \times inventory interaction ($p = 0.32$). Vectors representing each treatment’s shift through time in ordination space show that control and small gap treatments largely remained in similar areas of composition, while large gap treatments moved substantially through ordination space (Figure 9). Changes in the large gap treatment were not

uniformly directional, which could be the result of increased shade as conditions return to the stem exclusion development stage between harvests. Red maple was the only species with significant correlation between cover and NMS scores of the first axis (Kendall's rank correlation $p < 0.001$).

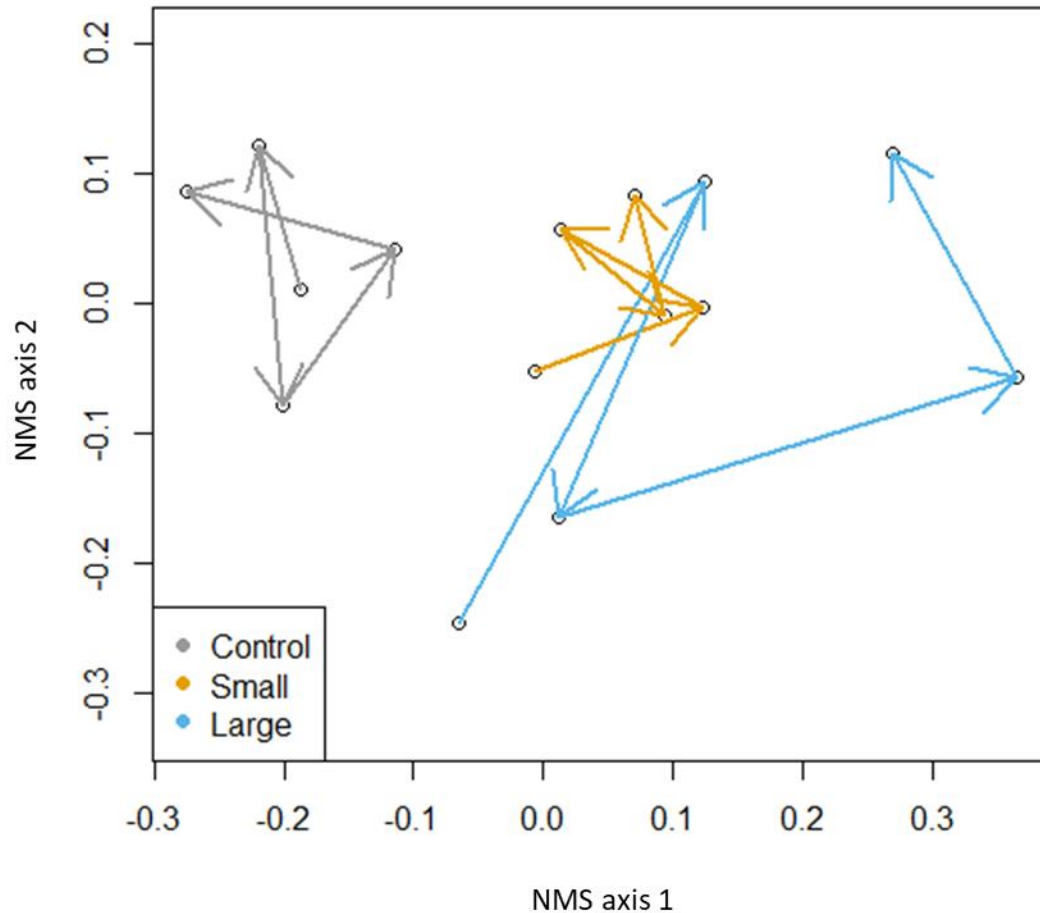


Figure 9: Tree seedling ordination. NMS ordination of tree seedling covers at each of five sequential inventory periods. Large gap treatments have larger shifts in ordination space than control or small gap treatments. Each point represents control, small gap, or large gap treatments at a sample period.

Discussion

Our study represents one of the longest-running examinations of tree regeneration response to ecological forestry treatments. Results indicate that twenty years of such treatments has increased tree seedling cover of target species, while maintaining lesser components of other species. Few of these trends in seedling cover were statistically significant, though this is unsurprising given the limited replication of the AFERP treatments, a result of the large areas required for multi-aged silvicultural studies (Seymour et al. 2006).

Three harvests on AFERP sites have left harvest gaps in various stages of development. We were unable to examine harvest effects in individual plots due to high inter-plot variability and concerns over pseudo-replication. Thus, samples represent the cumulative effects of treatments, including potential moderating effects of reserve trees and development status post-harvest. Development is evident in ordination results that show the temporal shifts in community composition between inventory periods for each treatment (Figure 9). As expected, shifts between inventories are much greater for the large gap treatment than for the control or small gap treatments. Red maple cover is correlated with axis 1, indicating higher cover in treated areas.

All inventory periods and treatment areas were dominated by balsam fir and hemlock seedlings, though our results suggest some increase in seedling cover of high value species in treated areas (Figure 6). White pine seedling cover increased marginally over time in treated areas, showing the greatest increase in large gap treatments. Though not statistically significant, our results suggest increases of red spruce in treated areas (Figure 7). Red maple also increased significantly over time in treated areas, similarly showing greatest increase in large gap treatments. Red maple is a generalist species of lower value that often benefits from silvicultural treatments (Abrams 1998). It is therefore unsurprising that seedling cover has increased with treatment; however, actual cover values are still low (Figure 7).

Shade intolerant species, which were low in all inventory periods and treatments, showed no statistical differences among treatments or trends over time, though seedling cover on plots stratified by harvest gap suggests intolerant species may be increasing in response to increased light availability within gaps (Figure 8). In an initial examination of AFERP's expanding gap treatments, Arsenault et al. (2011) found ten years of treatment had increased stocking of intolerant and tolerant species equally, suggesting intervening treatments may be needed to shift species composition of the stands. Our results support this finding, though this could shift as treatment continues and gaps are further expanded, highlighting the importance of long-term studies examining the cumulative effects of ecological forestry treatments.

Given its susceptibility to spruce budworm (*Choristoneura fumiferana* Clemens), relative lower value, and historically low abundance in old-growth forests of the region (Fraver and White 2005), both AFERP treatments aimed to reduce balsam fir seedling cover. In a previous study on the AFERP sites, Olson and Wagner (2011) found abundance of balsam fir regeneration reduced tree seedling richness. However, because of its prolific regeneration and ability to compete with other tree species in this region, it can be difficult to achieve lower components of fir without some form of thinning (Seymour 1992; Moores et al. 2007). While balsam fir seedlings have not decreased in any areas, neither have they increased in response to treatments (Figure 7).

Both AFERP treatments aimed to increase red spruce, a species well adapted to persist as advance regeneration before release. Harvest gaps are assumed to create light conditions favorable to shade-intermediate or shade-tolerant seedlings on gap edges (Van Couwenberge et al. 2010). The overstory can then be removed as gaps are expanded, thus releasing the seedlings previously established near the edge. Temporal trends in red spruce cover were not significant when looking at the cumulative treatment effects; however, we were unable to account for individual plot locations within

matrix or harvest gaps with this analysis. Post-stratification of plots by their location within harvest gaps suggest red spruce has increased equally in matrix and harvest gap plots (Figure 8). This finding could be the result of how we categorized gap or matrix plots, which does not account for plot distance from or position within gaps. Thus, advance regeneration establishing on gap edges may be contributing to cover within matrix plots.

Forest operations require careful planning and implementation to protect seedlings in systems that depend on advance regeneration. Accordingly, all AFERP harvests took place in winter when frozen soils and snow-pack protect seedlings (Wolf et al. 2008). The expanding gap system further protects advance regeneration through efficient trail allocation (well under 10% of area) and by limiting equipment travel over already harvested areas.

While our results suggest that seedlings on the treated AFERP sites may be responding to light increases as predicted by theories of gap partitioning (Van Couwenberghe et al. 2010; Gray and Spies 1997), the regeneration process is known to be highly complex and stochastic (Bataineh et al. 2013; Paluch 2005). Many environmental factors can interact with or override light effects, including seed source, regeneration substrate, understory dynamics, and browsing pressure. In a regeneration study on the surrounding Penobscot Experimental Forest, Bataineh et al. (2013) found overstory and understory vegetation were the best predictor of regeneration composition. While this finding is not new or surprising, it highlights the importance of controlling surrounding vegetation. Understory plant layers that might out-compete or interfere with tree seedling growth and survival are especially influential in regeneration success.

Dense layers of understory plants can sometimes form after canopy removal, acting as a filter or barrier to tree regeneration (George and Bazzaz 1999; Royo and Carson 2006). Several species found on AFERP sites known to form these dense layers include raspberry (*Rubus sp. L.*), blueberry (*Vaccinium sp.*

L.), hazelnut (*Corylus sp. L.*), and hay-scented fern (*Dennstaedtia punctilobula* (Michx.) T. Moore). Widen et al. (2018) found that raspberry, which regularly forms such dense layers in this region, have greater effects on germinating seedlings than on advance regeneration. AFERP's reliance on advance regeneration in combination with reserve trees, which moderate light conditions within harvest gaps, could limit the formation of impermeable raspberry or other shrub layers. Importantly, the regional concern that harvest gaps, particularly large gaps, will lead to the establishment of dense shrub layers was not borne out in this study; in fact, current shrub cover is low on all AFERP treatments (Figure 8).

Reserve trees are a critical component of the AFERP treatments, as natural disturbances in this system rarely kill all individuals within a gap (Worrall et al. 2005). While reserve trees can slow seedling growth (Urgenson et al. 2013; Peck et al. 2012), they may also enhance survival by moderating light conditions and maintaining communities of mycorrhizal fungi and soil fauna (Cline et al. 2007; Outerbridge and Trofymow 2009; Siira-Pietikäinen and Haimi 2009). Our study design does not allow for explicit testing of reserve tree influence on regeneration; however, given the complex interactions documented in other studies (Urgenson et al. 2013, Roberts et al. 2017) and the unprecedented rate of reserve tree survival on the AFERP sites (Carter et al. 2017), further studies could provide valuable insight into effects of retention on regeneration.

Management Implications

Our results suggest the expanding gap treatments tested on the AFERP sites could be effective at promoting regeneration of desired species, providing a sustainable alternative to strictly economically driven silviculture. The large gap treatment, aimed to increase components of high-value species, shows higher seedling cover of white pine and red spruce. The small gap treatment, aimed to accelerate stands to old-growth conditions, shows minimally higher seedling cover of red spruce. Intolerant and intermediate species showed varied to little response to the treatments. These trends are in line with

those found by Arsenault et al. (2011) after ten years of treatment, though their assessment of sapling data suggests pre-commercial thinning may be necessary to attain desired levels of shade intolerant species.

The sites on AFERP are currently free from a number of pressures that can interfere with natural regeneration such as dense layers of understory vegetation and high browse pressure. Our results suggest that in the absence of these pressures the two silvicultural treatments tested on AFERP could be effective at promoting target species, with gap size and reserve trees allowing for some control over composition. Some intervening treatments such as pre-commercial thinning may be needed to attain desired levels of shade-intolerant and intermediate species.

REFERENCES

- Abrams, M.D., 1998. The red maple paradox. *Bioscience*, 48 (5), 355-364.
- Arseneault, J.E., Saunders, M.R., Seymour, R.S., Wagner, R.G., 2011. First Decadal Response to Treatment in a Disturbance-Based Silviculture Experiment in Maine. *For. Ecol. Manag.* 262 (3), 404-412.
- Bataineh, M., Kenefic, L., Weiskittel, A., Wagner, R., Brissette, J., 2013. Influence of partial harvesting and site factors on the abundance and composition of natural regeneration in the Acadian forest of Maine, USA. *For. Ecol. Manag.* 306, 96-106.
- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes *For. Ecol. Manag.* 258 (4), 525-537.
- Berger, A. L., Puettman, K. J., & Host, G. E., 2004. Harvesting impacts on soil and understory vegetation: the influence of season of harvest and within-site disturbance patterns on clear-cut aspen stands in Minnesota. *Can. J. For. Res.* 34 (10), 2159–2168.
- Bolton, N. W., & D'Amato, A. W. 2011. Regeneration responses to gap size and coarse woody debris within natural disturbance-based silvicultural systems in northeastern Minnesota, USA. *For. Ecol. Manag.* 262(7), 1215-1222.
- Bottero, A., Garbarino, M., Dukic, V., Govedar, Z., Lingua, E., Nagel, T.A., Motta, R., 2011. Gap-phase dynamics in the old-growth forest of Lom (Bosnia-Herzegovina). *Silva Fenn.* 45, 875-887.
- Brissette, J.C. 1996. Effects of intensity and frequency of harvesting on abundance, stocking, and composition of natural regeneration in the Acadian forest of eastern North America. *Silva Fenn.* 30, 301–314.
- Byers, J.E., 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos* 97 (3), 449-458.
- Carter, D.R., Seymour, R.S., Fraver, S., Weiskittel, A., 2017. Reserve tree mortality in two expanding-gap silvicultural systems 20 years after establishment in the Acadian forest of Maine, USA. *For. Ecol. Manag.* 389, 149-157.
- Craig, A., Macdonald, S.E., 2009. Threshold effects of variable retention harvesting on understory plant communities in the boreal mixedwood forest. *For. Ecol. Manag.* 258 (12), 2619-2627.
- Cline, E., Vinyard, B., Edmonds, R., 2007. Spatial effects of retention trees on mycorrhizas and biomass of douglas-fir seedlings. *Can. J. For. Res.* 37 (2), 430-438.
- D'Antonio, C., 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. *Ecology* 74 (1), 83-95
- Davis, M., Grime, J., Thompson, K., 2000. Fluctuating resources in plant communities: A general theory of invasibility. *J. Ecol.* 88 (3), 528-534.

- De Caceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology*, URL <http://sites.google.com/site/miqueldecaceres/>
- Dey, D.C., Knapp, B.O., Battaglia, M.A.; Deal, R.L., Hart, J.L., O'Hara, K.L., Schweitzer, C.J., Schuler, T.M., 2019. Barriers to natural regeneration in temperate forests across the USA. *New For.* 50, 11-40.
- Forrester, J.A., Lorimer, C.G., Dyer, J.H., Gower, S.T., Mladenoff, D.J., 2014. Response of tree regeneration to experimental gap creation and deer herbivory in north temperate forests *For. Ecol. Manag.* 329, 137-147.
- Franklin, J.F., Mitchell, R.J., Palik, B.J., 2007. Natural disturbance and stand development principles for ecological forestry. Gen. Tech. Rep. NRS-19. Newtown Square, PA: US Department of Agriculture, Forest Service, Northern Research Station. 44, 19.
- Fraver, S., White, A.S., 2005. Disturbance dynamics of old-growth picea rubens forests of northern maine. *J. of Veg. Sci.* 16 (5), 597-610.
- Gálhidy, L., Mihók, B., Hagyó, A., Rajkai, K., Standovár, T., 2006. Effects of gap size and associated changes in light and soil moisture on the understory vegetation of a Hungarian beech forest. *Plant Ecol.* 183 (1), 133-145.
- George, L.O. and Bazzaz, F.A., 1999. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. *Ecology* 80 (3), 833-845.
- Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience* 57 (10), 845-858.
- Gilliam, F.S., Roberts, M. R., 2003. The herbaceous layer in forests of eastern north America. GB: Oxford University Press.
- Gray, A.N., Spies, T.A., 1996. Gap size, within-gap position, and canopy structure effects on conifer seedling establishment. *J. Ecol.* 84, 635-645.
- Gray, A.N., Spies, T.A., 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. *Ecology* 78 (8), 2458-2473.
- Grubb, P.J., 1977. The Maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52, 107-145.
- Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Löhmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., W. Jan A. Volney, Wayne, A., Franklin, J.F., & Sveriges, L., 2012. Retention forestry to maintain multifunctional forests: A world perspective. *Bioscience* 62 (7), 633-645.
- Haeussler, S., Bedford, L., Leduc, A., Bergeron, Y., Kranabetter, J., 2002. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. *Silva Fenn.* 36 (1).

- Haines, A., Farnsworth, E., Morrison, G., New England Wildflower Society, 2011. New England Wildflower Society's flora novae angliae: A manual for the identification of native and naturalized vascular plants of New England. Framingham, Mass.; New Haven, Conn; New England Wild Flower Society.
- Halpern, C., Halaj, J., Evans, S., Dovciak, M., 2012. Level and pattern of overstory retention interact to shape long-term responses of understories to timber harvest. *Ecol. Appl.* 22 (8), 2049-2064.
- Halpern, C.B. and Lutz, J.A., 2013. Canopy closure exerts weak controls on understory dynamics: A 30-year study of overstory–understory interactions. *Ecol. Monographs* 83 (2), 221-237.
- Halpern, C., McKenzie, D., Evans, S.A., Maguire, D., 2005. Initial responses of forest understories to varying levels and patterns of green-tree retention. *Ecol. Appl.* 15 (1), 175-195.
- Keeton, W.S., 2006. Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. *For. Ecol. Manag.* 235 (1), 129-142.
- Kern, C.C., Burton, J.I., Raymond, P., D'Amato, A.W., Keeton, W.S., Royo, A.A., Walters, M.B., Webster, C.R., Willis, J.L., 2017. Challenges facing gap-based silviculture and possible solutions for mesic northern forests in North America. *Forestry* 90, 4-17.
- Kern, C.C., Montgomery, R.A., Reich, P.B., Strong, T.F., 2014. Harvest-created canopy gaps increase species and functional trait diversity of the forest ground-layer community. *For. Sci.* 60 (2), 335.
- Kern, C.C., Palik, B.J., & Strong, T.F., 2006. Ground-layer plant community responses to even-age and uneven-age silvicultural treatments in Wisconsin northern hardwood forests. *For. Ecol. Manag.* 230 (1), 162-170.
- Kneeshaw, D.D., Kobe, R.K., Coates, K.D., Messier, C., 2006. Sapling size influences shade tolerance ranking among southern boreal tree species. *J. Ecol.*, 94 (2), 471-480.
- Lilles, E., Dhar, A., Coates, K.D., Haeussler, S., 2018. Retention level affects dynamics of understory plant community recovery in northern temperate hemlock-cedar forests. *For. Ecol. Manag.* 421, 3-15.
- Lindenmayer, D.B., Franklin, J.F. 2002., *Conserving forest biodiversity: a comprehensive multiscaled approach.* Island Press, Washington, D.C.
- Maine Natural Areas Program, 2015. Maine Rare Plant List and Rare Plant Fact Sheets.
- McGrath, T., 2017. Nova Scotia's forest management guide. Dept of Lands and Forestry, Halifax, NS. FOR 2017-16.
- Meier, A.J., Bratton, S.P., Duffy, D.C., 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. *Ecol. Appl.* 5 (4), 935-946

Moores, A.R., Seymour, R.S., Kenefic, L.S., 2007. Height development of shade-tolerant conifer saplings in multiaged Acadian forest stands. *Can. J. For. Res.* 37 (12), 2715-2723.

Mosseler, A., Lynds, J.A., Major, J.E., 2003. Old growth forests of the Acadian forest region. *Environmental Reviews* 11.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., 2018. vegan: Community Ecology Package. R package version 2.4-6. <https://CRAN.R-project.org/package=vegan>

Olson, E., Kenefic, L.S., Dibble, A.C., Brissette, J.C., 2011. Nonnative invasive plants in the Penobscot Experimental Forest in Maine, USA: Influence of site, silviculture, and land use history. *J. Torrey Bot. Soc.* 138 (4), 453-464.

Olson, M.G., Wagner, R.G., 2011. Factors affecting species richness of tree regeneration in mixed-wood stands of central Maine: Factors affecting tree species richness during regeneration. *J. Veg. Sci.* 22 (2), 303-311.

Oswalt, C.M., Oswalt, S.N., 2007. Winter litter disturbance facilitates the spread of the nonnative invasive grass *Microstegium vimineum* (Trin.) A. Camus. *For. Ecol. Manag.* 249 (3), 199-203.

Outerbridge, R.A., Trofymow, J.A., 2009. Forest management and maintenance of ectomycorrhizae: A case study of green tree retention in south-coastal British Columbia. *J. Eco. Manag.* 10 (2).

Palik, B.J., Mitchell, R.J., Hiers, J.K., 2002. Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: balancing complexity and implementation. *For. Ecol. Manag.* 155 (1-3), 347-356.

Paluch, J.G., 2005. The influence of the spatial pattern of trees on forest floor vegetation and silver fir (*Abies alba* mill.) regeneration in uneven-aged forests. *For. Ecol. Manag.* 205 (1), 283-298.

Peck, J.E., Zenner, E.K., Palik, B., 2012. Variation in microclimate and early growth of planted pines under dispersed and aggregated overstory retention in mature managed red pine in Minnesota. *Can. J. For. Res.* 42 (2), 279-290.

Prévost, M., 2008. Effect of cutting intensity on microenvironmental conditions and regeneration dynamics in yellow birch conifer stands. *Can. J. For. Res.* 38 (2), 317-330.

Prévost, M., Raymond, P., 2012. Effect of gap size, aspect and slope on available light and soil temperature after patch-selection cutting in yellow birch–conifer stands, Quebec, Canada. *For. Ecol. Manag.* 274, 210-221.

Quinn, G.P., Keough, M.J., 2002. *Experimental design and data analysis for biologists*. Cambridge, UK: Cambridge University Press.

R Core Team., 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>

- Raymond, P., Bédard, S., Roy, V., Larouche, C., Tremblay, S., 2009. The irregular shelterwood system: review, classification, and potential application to forests affected by partial disturbances. *J. For.* 107, 405-413.
- Raymond, P., Royo, A.A., Prévost, M., Dumais, D., 2018. Assessing the single-tree and small group selection cutting system as intermediate disturbance to promote regeneration and diversity in temperate mixedwood stands. *For. Ecol. Manag.* 430, 21-32.
- Revelle, W., 2017. psych: Procedures for personality and psychological research, Northwestern University, Evanston, Illinois, USA, <https://CRAN.R-project.org/package=psych> Version = 1.7.5.
- Reuling, L.F., D'Amato, A.W., Palik, B.J., Martin, K.J., Fassnacht, D.S.A., 2019. Initial tree regeneration response to natural-disturbance-based silviculture in second-growth northern hardwood forests. *Can. J. For. Res.* 49 (6), 628-639.
- Richardson, D.M., Pyšek, P., 2006. Plant invasions: Merging the concepts of species invasiveness and community invasibility. *Prog. Phys. Geogr.* 30 (3), 409-431.
- Ricketts, T.H., Dinerstein, E., Olson, D.M., Loucks, C., 1999. Who's where in North America? Patterns of species richness and the utility of indicator taxa for conservation. *BioScience* 49 (5), 369-381.
- Roberts, M.W., D'Amato, A.W., Kern, C.C., Palik, B.J., Marini, L., 2016. Long-term impacts of variable retention harvesting on ground-layer plant communities in *Pinus resinosa* forests. *J. Appl. Ecol.* 53 (4), 1106-1116.
- Roberts, M.W., D'Amato, A.W., Kern, C.C., Palik, B.J., 2017. Effects of variable retention harvesting on natural tree regeneration in *Pinus resinosa* (red pine) forests. *For. Ecol. Manag.* 385, 104-115.
- Royo, A.A. and Carson, W.P., 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Can. J. For. Res.* 36 (6), 1345-1362.
- Runkle, J.R., 1982. Patterns of disturbance in some old-growth mesic forests of Eastern North America. *Ecology* 63 (5), 1533-1546.
- Saunders, M.R., Wagner, R.G., 2005. Ten-year results of the Forest Ecosystem Research Program – successes and challenges. In: Peterson, C.E., Maguire, D.A. (Eds.), *Balancing Ecosystem Values: Innovative Experiments for Sustainable Forestry*. USDA For. Serv. PNW-GTR-635, 147–152.
- Seymour, R.S., 1992. The red spruce-balsam fir forest of Maine: evolution of silvicultural practice in response to stand development patterns and disturbances. In: Kelty, M.J., Larson, B.C., Oliver, C.D. (Eds.), *The Ecology and silviculture of mixed-species forests: a festschrift for David M. Smith*. Kluwer Academic Publishers, 217–244.
- Seymour, R.S., 2005. Integrating disturbance parameters into conventional silvicultural systems: experience from the Acadian forest of northeastern North America. In: Peterson, C.E., Maguire, D.A.,

- (Eds.), *Balancing Ecosystem Values: Innovative Experiments for Sustainable Forestry*. USDA For. Serv. PNWGTR-635, pp. 41–48.
- Seymour, R.S., Guldin, J., Marshall, D., Palik, B., 2006. Large-scale, long-term silvicultural experiments in the United States: historical overview and contemporary examples. *Allg. For. Jagdztg.* 177, 104–112.
- Seymour, R.S., Hunter Jr., M.L., 1999. Principles of ecological forestry. In: Hunter, M.L., Jr. (Ed.), *Maintaining Biodiversity in Forest Ecosystems*. Cambridge University Press, Cambridge, UK, 22–61.
- Seymour, R.S., White, A.S., de Maynadier, P.G., 2002. Natural disturbance regimes in northeastern North America – evaluating silvicultural systems using natural scales and frequencies. *For. Ecol. Manag.* 155, 357–367.
- Siira-Pietikäinen, A., & Haimi, J., 2009. Changes in soil fauna 10 years after forest harvestings: Comparison between clear felling and green-tree retention methods. *For. Ecol. Manag.* 258 (3), 332-338.
- Stohlgren, T.J., Bull, K.A., Otsuki, Y., 1998. Comparison of rangeland vegetation sampling techniques in the central grasslands. *J. Range Manag.* 51 (2), 164-172.
- Troup, R.S., 1955. *Silvicultural systems* 2nd ed. New York: Oxford University Press. 216p.
- Urgenson, L.S., Halpern, C.B., Anderson, P.D., 2013. Twelve-year responses of planted and naturally regenerating conifers to variable-retention harvest in the pacific northwest, USA. *Can. J. For. Res.* 43 (1), 46-55.
- Van Couwenberghe, R., Collet, C., Lacombe, E., Pierrat, J., Gégout, J., 2010. Gap partitioning among temperate tree species across a regional soil gradient in windstorm-disturbed forests. *For. Ecol. Manag.* 260 (1), 146-154.
- von Ende, C., 1993. Repeated-measures analysis: growth and other time-dependent measures. *Design and Analysis of Ecological Experiments* (eds S.M. Scheiner & J. Gurevitch), 113–137. Chapman & Hall, Inc., New York.
- Walters, M.B., Farinosi, E.J., Willis, J.L., Gottschalk, K.W., 2016. Managing for diversity: Harvest gap size drives complex light, vegetation, and deer herbivory impacts on tree seedlings. *Ecosphere* 7 (8).
- Whigham, D.F., 2004. Ecology of woodland herbs in temperate deciduous forests. *Annu. Rev. Ecol. Evol. Syst.* 35 (1), 583-621.
- Widen, M.J., Petras O'Neil, M.A., Dickinson, Y.L., Webster, C.R., 2018. *Rubus* persistence within silvicultural openings and its impact on regeneration: The influence of opening size and advance regeneration. *For. Ecol. Manag.* 427, 162-168.
- Wolf, A.T., Parker, L., Fewless, G., Corio, K., Sundance, J., Howe, R., Gentry, H., 2008. Impacts of summer versus winter logging on understory vegetation in the Chequamegon-Nicolet National Forest. *For. Ecol. Manag.* 254 (1), 35-45.
- Worrall, J.J.T., Lee, D., Harrington, T.C., 2005. Forest dynamics and agents that initiate and expand canopy gaps in *Picea abies* forests of Crawford Notch, New Hampshire, USA. *J. Ecol.* 93 (1), 178-190.

APPENDIX A: SPECIES LIST

Table A.1: Species list. Taxonomy and nomenclature follow Haines et al. (2011).

FAMILY	TAXA
Anacardiaceae	<i>Toxicodendron rydbergii</i> (Small ex Rydb.) Greene
Apiaceae	<i>Aralia hispida</i> Vent.
Araceae	<i>Arisaema triphyllum</i> (L.) Schott
Araliaceae	<i>Aralia nudicaulis</i> L.
Asteraceae	<i>Anaphalis margaritacea</i> (L.) Benth. & Hook.
Asteraceae	Asteraceae
Asteraceae	<i>Cirsium discolor</i> (Muhl. ex Willd.) Spreng.
Asteraceae	<i>Erechtites hieraciifolius</i> (L.) Raf. ex DC.
Asteraceae	<i>Euthamia graminifolia</i> (L.) Nutt.
Asteraceae	<i>Hieracium caespitosum</i> Dumort.
Asteraceae	<i>Hieracium</i> L.
Asteraceae	<i>Hieracium pilosella</i> L.
Asteraceae	<i>Lactuca canadensis</i> L.
Asteraceae	<i>Oclemena acuminata</i> (Michx.) Greene
Asteraceae	<i>Solidago altissima</i> L.
Asteraceae	<i>Solidago canadensis</i> L.
Asteraceae	<i>Solidago</i> L.
Asteraceae	<i>Solidago puberula</i> Nutt.
Asteraceae	<i>Solidago rugosa</i> Mill.
Asteraceae	<i>Symphyotrichum lateriflorum</i> (L.) A. Love & D. Love
Asteraceae	<i>Symphyotrichum puniceum</i> (L.) A. Love & D. Love
Asteraceae	<i>Taraxacum officinale</i> F. H. Wigg.
Balsaminaceae	<i>Impatiens capensis</i> Meerb.
Betulaceae	<i>Alnus incana</i> (L.) Moench
Betulaceae	<i>Betula alleghaniensis</i> Britton
Betulaceae	<i>Betula cordifolia</i> Regel
Betulaceae	<i>Betula</i> L.
Betulaceae	<i>Betula papyrifera</i> Marsh.
Betulaceae	<i>Betula populifolia</i> Marsh.
Betulaceae	<i>Corylus cornuta</i> Marsh.
Betulaceae	<i>Ostrya virginiana</i> (Mill.) K. Koch
Brassicaceae	<i>Cardamine pensylvanica</i> Muhl. ex Willd.
Caprifoliaceae	<i>Diervilla lonicera</i> Mill.
Caprifoliaceae	<i>Linnaea borealis</i> L.
Caprifoliaceae	<i>Lonicera canadensis</i> Bartram ex Marsh.
Caprifoliaceae	<i>Viburnum nudum</i> L.
Cornaceae	<i>Chamaepericlymenum canadense</i> (L.) Aschers. & Graebn.

FAMILY	TAXA
Cupressaceae	<i>Thuja occidentalis</i> L.
Cyperaceae	<i>Carex arctata</i> Boott ex Hook.
Cyperaceae	<i>Carex brunnescens</i> (Pers.) Poir.
Cyperaceae	<i>Carex communis</i> L.H. Bailey
Cyperaceae	<i>Carex debilis</i> Michx.
Cyperaceae	<i>Carex deflexa</i> Hornem.
Cyperaceae	<i>Carex disperma</i> Dewey
Cyperaceae	<i>Carex gracillima</i> Schwein.
Cyperaceae	<i>Carex intumescens</i> Rudge
Cyperaceae	<i>Carex</i> L.
Cyperaceae	<i>Carex laxiflora</i> Lam.
Cyperaceae	<i>Carex leptalea</i> Wahlenb.
Cyperaceae	<i>Carex leptonevia</i> (Fernald) Fernald
Cyperaceae	<i>Carex lucorum</i> Willd. ex Link
Cyperaceae	<i>Carex merritt-fernaldii</i> Mack.
Cyperaceae	<i>Carex scoparia</i> Schkuhr ex Willd.
Cyperaceae	<i>Carex stipata</i> Muhl. ex Willd.
Cyperaceae	<i>Carex tenera</i> Dewey
Cyperaceae	<i>Carex trisperma</i> Dewey
Dennstaedtiaceae	<i>Dennstaedtia punctilobula</i> (Michx.) T. Moore
Dennstaedtiaceae	<i>Pteridium aquilinum</i> (L.) Kuhn
Dryopteridaceae	<i>Athyrium angustum</i> (Willd.) C. Presl.
Dryopteridaceae	<i>Dryopteris</i> Adans.
Dryopteridaceae	<i>Dryopteris carthusiana</i> (Vill.) H. P. Fuchs
Dryopteridaceae	<i>Dryopteris cristata</i> (L.) A. Gray
Dryopteridaceae	<i>Dryopteris intermedia</i> (Mulh. ex Willd.) A. Gray
Dryopteridaceae	<i>Dryopteris marginalis</i> (L.) A. Gray
Dryopteridaceae	<i>Gymnocarpium dryopteris</i> (L.) Newman
Dryopteridaceae	<i>Onoclea sensibilis</i> L.
Dryopteridaceae	<i>Polystichum acrostichoides</i> (Michx.) Schott
Equisetaceae	<i>Equisetum pratense</i> Ehrh.
Ericaceae	<i>Gaultheria hispidula</i> (L.) Muhl. ex Bigelow
Ericaceae	<i>Gaultheria procumbens</i> L.
Ericaceae	<i>Kalmia angustifolia</i> L.
Ericaceae	<i>Pyrola</i> L.
Ericaceae	<i>Vaccinium myrtilloides</i> Michx.
Fagaceae	<i>Fagus grandifolia</i> Ehrh.
Fagaceae	<i>Quercus rubra</i> L.
Geraniaceae	<i>Geranium</i> L.
Juncaceae	<i>Luzula multiflora</i> (Ehrh.) Lej.
Lamiaceae	<i>Lycopus uniflorus</i> Michx.
Lamiaceae	<i>Prunella vulgaris</i> L.

FAMILY	TAXA
Lamiaceae	<i>Scutellaria lateriflora</i> L.
Liliaceae	<i>Clintonia borealis</i> (Aiton) Raf.
Liliaceae	<i>Maianthemum canadense</i> Desf.
Liliaceae	<i>Medeola virginiana</i> L.
Liliaceae	<i>Polygonatum pubescens</i> (Willd.) Pursh
Liliaceae	<i>Streptopus lanceolatus</i> (Aiton) Reveal
Liliaceae	<i>Trillium erectum</i> L.
Liliaceae	<i>Uvularia sessilifolia</i> L.
Lycopodiaceae	<i>Dendrolycopodium dendroideum</i> (Michx.) A. Haines
Lycopodiaceae	<i>Dendrolycopodium obscurum</i> (L.) A. Haines
Monotropaceae	<i>Monotropa uniflora</i> L.
Myricaceae	<i>Comptonia peregrina</i> (L.) J. M. Coult.
Oleaceae	<i>Fraxinus americana</i> L.
Oleaceae	<i>Fraxinus nigra</i> Marsh.
Onagraceae	<i>Circaea alpina</i> L.
Ophioglossaceae	<i>Botrychium</i> Sw.
Orchidaceae	<i>Cypripedium acaule</i> Aiton
Orchidaceae	<i>Epipactis helleborine</i> (L.) Crantz
Orchidaceae	<i>Goodyera pubescens</i> (Willd.) R. Br.
Orchidaceae	<i>Platanthera hookeri</i> (Torr. ex A. Gray) Lindl.
Orchidaceae	<i>Platanthera</i> Rich.
Osmundaceae	<i>Osmunda claytoniana</i> L.
Osmundaceae	<i>Osmundastrum cinnamomeum</i> (L.) C. Presl
Oxalidaceae	<i>Oxalis montana</i> Raf.
Pinaceae	<i>Abies balsamea</i> (L.) Mill.
Pinaceae	<i>Picea rubens</i> Sarg.
Pinaceae	<i>Pinus strobus</i> L.
Pinaceae	<i>Tsuga canadensis</i> (L.) Carriere
Plantaginaceae	<i>Veronica scutellata</i> L.
Poaceae	<i>Agrostis</i> L.
Poaceae	<i>Brachyelytrum aristosum</i> (Michx.) P. Beauv. ex Trel.
Poaceae	<i>Danthonia spicata</i> (L.) P. Beauv. ex Roem. & Schult.
Poaceae	<i>Dichanthelium</i> (Hitchc. & Chase) Gould
Poaceae	<i>Glyceria striata</i> (Lam.) Hitchc.
Poaceae	<i>Oryzopsis asperifolia</i> Michx.
Poaceae	Poaceae
Poaceae	<i>Schizachne purpurascens</i> (Torr.) Swallen
Polygalaceae	<i>Polygala paucifolia</i> Willd.
Polygonaceae	<i>Fallopia cilinodis</i> (Michx.) Holub
Primulaceae	<i>Lysimachia borealis</i> (Raf.) U. Manns & A. Anderb.
Pyrolaceae	<i>Moneses uniflora</i> (L.) A. Gray
Ranunculaceae	<i>Coptis trifolia</i> (L.) Salisb.

FAMILY	TAXA
Rhamnaceae	<i>Frangula alnus</i> Mill.
Rosaceae	<i>Amelanchier</i> Medik.
Rosaceae	<i>Fragaria virginiana</i> Duchesne
Rosaceae	<i>Prunus pennsylvanica</i> L. f.
Rosaceae	<i>Rubus allegheniensis</i> Porter
Rosaceae	<i>Rubus dalibarda</i> L.
Rosaceae	<i>Rubus hispidus</i> L.
Rosaceae	<i>Rubus idaeus</i> L.
Rosaceae	<i>Rubus occidentalis</i> L.
Rosaceae	<i>Rubus pubescens</i> Raf.
Rubiaceae	<i>Galium palustre</i> L.
Rubiaceae	<i>Galium triflorum</i> Michx.
Rubiaceae	<i>Houstonia caerulea</i> L.
Rubiaceae	<i>Mitchella repens</i> L.
Salicaceae	<i>Populus grandidentata</i> Michx.
Salicaceae	<i>Populus tremuloides</i> Michx.
Sapindaceae	<i>Acer pennsylvanicum</i> L.
Sapindaceae	<i>Acer rubrum</i> L.
Sapindaceae	<i>Acer saccharum</i> Marsh.
Saxifragaceae	<i>Chrysosplenium americanum</i> Schwein. ex Hook.
Saxifragaceae	<i>Mitella nuda</i> L.
Scrophulariaceae	<i>Veronica officinalis</i> L.
Thelypteridaceae	<i>Phegopteris connectilis</i> (Michx.) Watt
Thelypteridaceae	<i>Thelypteris noveboracensis</i> (L.) Ching
Tiliaceae	<i>Tilia americana</i> L.
Violaceae	<i>Viola</i> L.
Violaceae	<i>Viola labradorica</i> Schrank

BIOGRAPHY OF THE AUTHOR

Maggie grew up in the woods of western Massachusetts before heading to Maine for an interdisciplinary bachelor's degree at College of the Atlantic. After graduating in 2011 she worked as a painter, a baker, and a botanist before moving to a desk in Nutting Hall where she battled a long-term dataset with an army of untrained R code. Maggie is a candidate for the Master of Science degree in Forest Resources from the University of Maine in August 2019.