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REGENERATION RESPONSE TO SALVAGE LOGGING FOLLOWING TORNADO DISTURBANCE

By

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By Colby Bosley-Smith

Thesis Advisor: Dr. Shawn Fraver

An Abstract of the Thesis Presented
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In an era of increasing natural disturbances, successful tree regeneration has grown more difficult to achieve. Salvage logging, a common management response to disturbance, may further impede regeneration success, although published literature currently remains inconclusive. In 2013, a rare tornado in northcentral Maine, USA, and subsequent salvage operation created three clear 'treatments' for evaluation of post-disturbance regeneration: blowdown, blowdown followed by salvage logging and an undisturbed control. In the summers of 2022 and 2023, (nine and ten) years post-tornado, we revisited this site to examine regeneration outcomes.

During the summer of 2022, we evaluated stand structure and regeneration success of the sapling layer. Our objectives focused on understanding (1) how salvage logging alters regeneration abundance and species composition of woody species and (2) whether the greater abundance of coarse woody material (CWM) remaining in the blowdown restricts moose browse through a natural 'exclosure effect'. We inventoried tree regeneration within these treatments to evaluate differences in sapling abundance, species composition, size structure, and browsing intensity. In addition, we inventoried CWM, including the height above forest floor. Results revealed significant differences in sapling composition and browsing intensity among treatments with the salvage treatment containing the highest proportion of browsed saplings. Binomial generalized linear models revealed that browsing probability was a function of mean CWM height and an interaction between sapling density and proportion of sapling hardwoods. Thus, browsing damage was less likely in plots with greater CWM heights and more likely in plots with greater sapling density and more hardwood saplings.

During the summer of 2023, we revisited these stands to understand treatment effects on understory plant communities and microclimates. Our objectives explore (1) understory community differences among undisturbed, blowdown and salvage conditions, (2) relationships between conifer sapling abundance and early successional, recalcitrant species, and (3) relationships between microclimate factors and understory communities. We inventoried understory vegetation, took hemispherical photographs to characterize canopy openness and installed sensors to track temperature and soil moisture throughout the growing season. Results indicate distinct understory community differences among each of the treatments, with the salvage treatment supporting a higher richness and abundance of early successional, shade intolerant taxa, while the blowdown and control treatments were characterized by later successional, shade tolerant taxa. Abundance of conifer regeneration was notably lower in plots with high abundance of *Rubus idaeus* or *Pteridium aquilinum*. Ordination results suggest that canopy openness and surface temperature fluctuations were the primary factors associated with these compositional differences.

This study furthers our understanding of ecosystem recovery following the successive disturbances of blowdown and salvage logging. Results suggest that salvage logging created important differences in CWM abundance and height distribution, when compared to un-salvaged areas, and that these differences in turn altered sapling size structure and browsing intensity. Further, distinct differences in species ordination and microclimate results suggest salvage logging may create conditions more favorable to shade-intolerant, recalcitrant understory vegetation. Together, these findings highlight the potential long-term effects of successive disturbances and provide forest managers insight on possible post-disturbance conditions.

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CHAPTER 1

THE NATURAL ‘EXCLOSURE EFFECT’ AND TREE REGENERATION FOLLOWING POST-WINDSTORM SALVAGE LOGGING

Understanding the influence of post-disturbance forest management practices on tree regeneration is critical for assessing ecosystem recovery and guiding future responses. In particular, the influx of elevated coarse woody material (CWM) following wind disturbance, if left in situ, may impede herbivore access, thereby protecting saplings from browsing damage through a natural ‘exclosure effect.’ In 2013, a tornado in northcentral Maine, USA and subsequent salvage logging operations created three clear ‘treatments’ for evaluation of the exclosure effect: blowdown, blowdown plus salvage logging, and an undamaged control. Nine years post-tornado, we inventoried tree regeneration within these treatments to evaluate differences in sapling abundance, species composition, size structure, and browsing intensity. In addition, we inventoried CWM, including the height above forest floor. Results revealed significant differences in sapling composition and browsing intensity among treatments. The salvage treatment had the highest proportion of browsed saplings (56 ± 28%; mean ± standard error), followed by the control (9 ± 10%) and blowdown (5 ± 8%). Blowdown had by far the greatest mean (50 ± 9 cm) and average maximum (169 ± 43 cm) heights for CWM. Binomial generalized linear models revealed that browsing probability was a function of mean CWM height and an interaction between sapling density and proportion of sapling hardwoods. Thus, browsing damage was less likely in plots with greater CWM heights and more likely in plots with greater sapling density and more hardwood saplings. This study furthers our understanding of ecosystem recovery following the successive disturbances of blowdown and salvage logging. Results suggest that salvage logging created important differences in CWM abundance and height distribution, when compared to un-salvaged areas, and that these differences in turn altered sapling size structure and browsing intensity. These findings highlight the potential long-term effects of successive disturbances, as the differences evident in these early stages may persist for decades or longer. Importantly, we provide evidence of the exclosure effect, suggesting that CWM retained in the un-salvaged area protected saplings from moose browsing. Considering these results, we recommend that managers leave CWM in place in areas where browsing is a primary threat to regeneration.

1.1 Introduction

Studies suggest that climate change is increasing the frequency and severity of forest disturbances such as windstorms, insect outbreaks, and fire (Dale et al., 2001; Turner 2010; Johnstone et al., 2016; Seidl et al., 2017). Given that disturbances strongly influence forest structure, processes, and species composition, changes in natural disturbance regimes can have profound and lasting impacts (Turner 2010; Seidl et al., 2017). Specifically, changes in disturbance frequency and intensity can shift forest composition and limit tree regeneration success for some species (Johnstone et al., 2016). Thus, forest management in a future with more intense and frequent disturbances presents a novel challenge for practitioners and policy makers.

Salvage logging, the practice of removing commercially valuable wood following a natural disturbance, is a common management response to catastrophic disturbance (Lindenmayer et al., 2008). Though primarily conducted to reduce timber revenue losses, salvage logging has also been used to aid in site preparation (Greene et al., 2006), to abate future disturbance risk (bark beetle outbreaks, fire severity) (Dodds et al., 2019; Fraver et al., 2011; Johnson et al., 2013), and to promote coexistence of important hardwood tree species (Royo et al., 2016). In contrast, salvage logging has been shown to impede tree regeneration (D'Amato et al., 2011; Santoro & D'Amato, 2019), reduce plant community diversity (Leverkus et al., 2014, Kleinman et al., 2017), eliminate the aerial seedbanks of serotinous species (Greene et al., 2006), and slow post-disturbance recovery (Taeroe et al., 2019; Li et al., 2023). These negative aspects of salvage logging are often centered around the loss of coarse woody material (CWM), given that standing and downed wood left after disturbance enhances forest structure, stimulates nutrient cycling, and provides substrate for regeneration, among other benefits (Lindenmayer et al., 2004).

One understudied benefit of CWM is its function as a physical barrier to ungulate browsing (a natural ‘exclosure effect’), thereby protecting seedlings and saplings (de Chantal & Granström, 2007; Hagge et al., 2019). Moose (*Alces* species) are considered overpopulated in many parts of northern North America and northern Europe and play a significant role in altering forest composition (Bergeron et al., 2011; Liang & Seagle, 2002). Selective browsing by moose may create conditions in which only the less-palatable (and often less desired timber species) survive to maturity (Relva et al., 2009; Smallidge et al., 2021). Exclusion fencing is one common way to prevent browsing, yet cost and labor demands make it difficult to implement (Smallidge et al., 2021). Practitioners have found success in the construction of slash walls (piles of discarded non-commercial woody material) following harvest (Grisez, 1960; Smallidge et al., 2021). Similarly, piles of fallen conifers (i.e., ‘jackstraws’) killed by fire can provide browsing refugia for aspen and willow regeneration (Ripple & Larsen, 2001). Large influxes of CWM from windstorms might serve a similar purpose; however, this potential exclosure effect remains poorly understood (but see Morimoto et al. 2021, Konôpka et al., 2021 and Hagge et al., 2019).

Several studies have demonstrated that the effects of salvage logging can persist as long as 50 to 70+ years post-harvest (Mabry and Korsgren 1998, Sass et al. 2018, Morimoto et al. 2019); however, such long-term studies are quite uncommon. More common are studies conducted several years post-salvage, although authors acknowledge the limitations of using short-term studies to project long-term stand outcomes (Palik & Kastendick, 2009; Royo et al., 2016). Further, salvage logging studies that follow regeneration for only a few years post-salvage often use seedling (not sapling) composition to examine regeneration success (Donato et al., 2006; Santoro & D’Amato, 2019; Slyder et al., 2020). Vickers et al. (2017) demonstrate that models relying on short-term seedling regeneration data (less than three years) have high uncertainty. Regeneration success is particularly precarious and unpredictable in areas with dense herbivore populations (Boerner & Brinkman, 1996; Hidding et al., 2012). Taken together these considerations point to the need for longer-term studies of post-salvage regeneration, particularly as it relates to herbivore pressure.

A series of events beginning in 2013 provides an ideal setting in which to address these knowledge gaps. In July of 2013, a tornado struck the northeastern portion of Baxter State Park, Maine, USA, causing significant canopy loss to an approximate 200-ha swath of mixed-species conifer forest (Fraver et al., 2017). A portion of this area was salvaged that winter (2013-2014) while other areas were left untouched. This series of events generated three clear “treatments” in close proximity: tornado blowdown, blowdown followed by salvage logging, and undisturbed control that could be compared with respect to tree regeneration and browsing intensity.

The overarching goal of this study is to document how salvage logging following severe wind disturbance shapes forest regeneration outcomes. More specifically, our objectives explore (1) how salvage logging alters regeneration abundance and species composition of woody species and (2) whether the greater abundance of coarse woody material (CWM) remaining in the blowdown restricts moose browse through the exclosure effect. This study contributes to a growing body of literature aimed at understanding appropriate management responses to forest disturbance, particularly in light of other stressors such as elevated herbivory, and can inform future management decisions.

1.2 Methods

1.2.1 Field Sampling

Our study was conducted within the Baxter State Park Scientific Forest Management Area (SFMA) of northcentral Maine, USA (Figure 1.1). Established in 1955, this 12,000 ha tract is maintained to demonstrate sustainable forest management practices (Whitcomb, 2008). The mean annual temperature of the SFMA is 4.4 °C with an average of 1084 mm of annual precipitation distributed evenly throughout the year (PRISM Climate Group, 2022). Topography in the SFMA ranges from 244 to

390 m a.s.l., and soils are derived from glacial till. The tornado of July, 2013, with windspeeds exceeding 40 m s^{-1}, caused extensive canopy loss in a 200-ha swath of forest in the SFMA (Fraver et al., 2017). By comparing structural characteristics of the control stands to those of the blowdown immediately post-disturbance (see Fraver et al. 2017), we estimate that the tornado reduced basal area by 87% and tree density by 85%. Salvage harvesting in portions of the wind-damaged area began in the winter of 2013-2014 using a fixed-head cut-to-length processer and forwarder, with slash left on site (Fraver et al., 2017).

Three treatments (blowdown, blowdown plus salvage, and undamaged control; Figure 1.1) were initially identified and inventoried in the summer of 2014 (Fraver et al., 2017). Prior to the tornado, these stands were dominated by red spruce (*Picea rubens* Sarg.) with lesser components of balsam fir (*Abies balsamea* (L.) Mill), northern white-cedar (*Thuja occidentalis* L.), eastern white pine (*Pinus strobus* L.), red maple (*Acer rubrum* L.) and paper birch (*Betula papyrifera* Marshall) (Fraver et al., 2017). Control stands were chosen for their similarity in composition and proximity to blowdown and salvage sites. Although many of these stands had experienced prior management (light partial harvests ca. 20 years before the blowdown), pre-blowdown differences in structure and composition among stands were deemed negligible based on pre-blowdown inventories and post-blowdown woody material and stump surveys (Fraver et al., 2017).

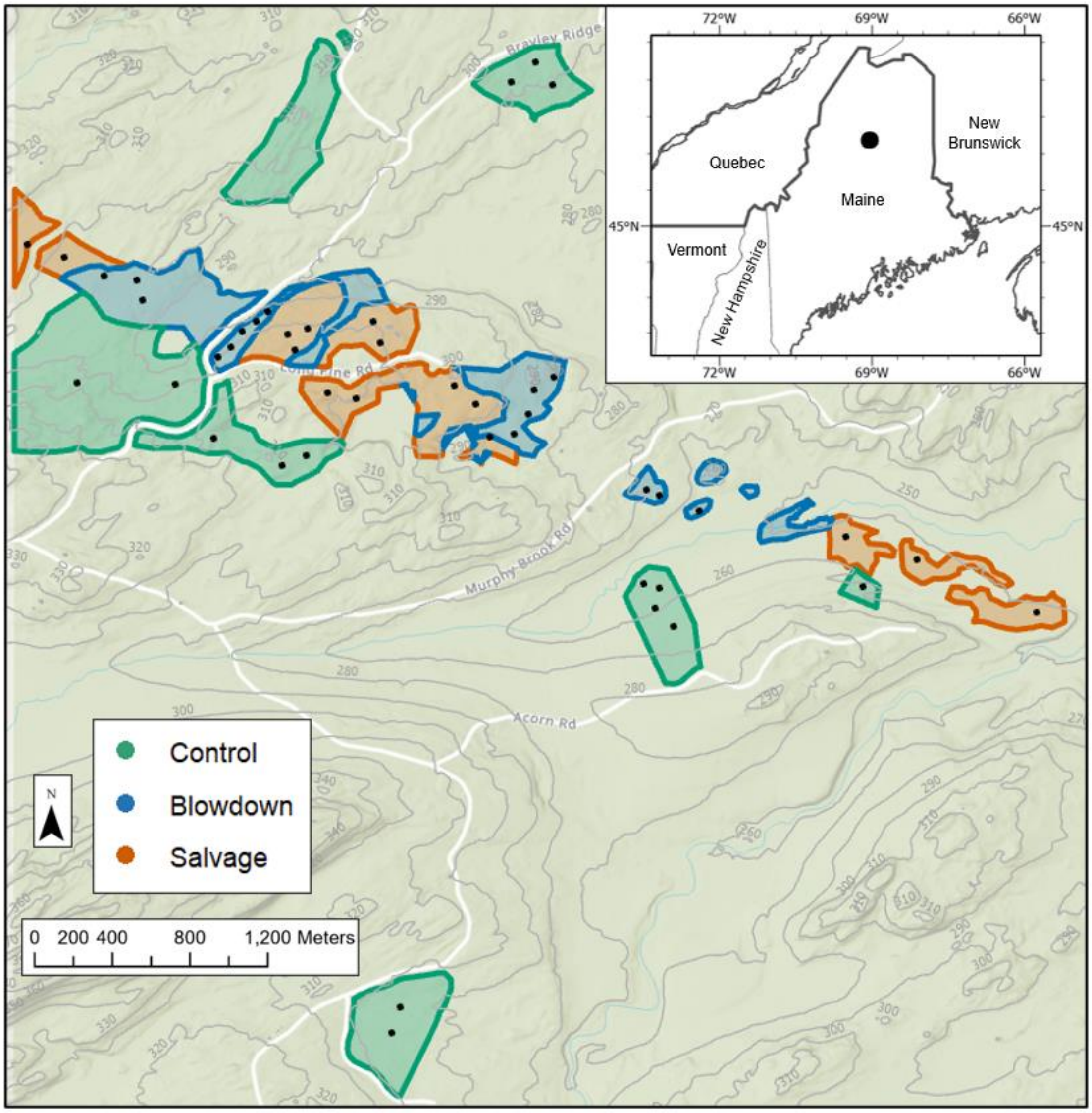

Figure 1.1. Treatment and plot locations within the Scientific Forest Management Area (SFMA), Baxter State Park, Maine, USA. Orange and blue polygons show the extent of tornado damaged patches, dots indicate plot locations. Sampled units color coded by treatment: control, blowdown, and salvage (blowdown followed by salvage). The western border of map is the western border of the SFMA. Contour lines in meters.

Nine years post-tornado, in the summer of 2022, these stands were revisited to assess regeneration and downed coarse woody material (CWM) structure within 45 plots (fifteen plots per treatment). Plot locations were designated randomly in ArcGIS with occasional on-the-ground adjustments made based on the location of recent harvests not seen in aerial imagery. Four circular sapling subplots (25 m^2, i.e., 2.8 m radius) were established in each cardinal direction 5.5 m from plot center. Within each subplot, all saplings (defined as diameter at breast height [DBH] ≤10 cm and taller than 1 m) were identified to species and tallied by four DBH classes: ≤2.5 cm, 2.6 - 5 cm, 5.1 - 7.5 cm and 7.6 - 10 cm. Each sapling was also assessed for moose browse (evidenced by torn branch tips; Pierson and deCalesta, 2015) and tallied as browsed or not browsed. Four 25-m-long CWM line-intersect transects (Van Wagner, 1968) were established within each of the 45 plots, radiating out from plot center in the four cardinal directions (total length 100 m per plot). For each CWM piece ≥ 10 cm diameter at the point of transect intersection, species was identified (when not precluded by decay), diameter, and height to the top of each piece were measured at the point of intersection, and decay class was assigned according to the five-class system (Sollins, 1982). Finally, we estimated canopy openness using 2017 LiDAR discrete-return point cloud data sourced from the US Geological Survey (US Geological Survey, 2017). These data were normalized in RStudio (R Core Team, 2021) and used to create a 5-m canopy-height model from which canopy closure was calculated for each plot (later converted to canopy openness).

1.2.2 Data Analysis

1.2.2.1 *Forest Structure*

CWM volume for each plot was calculated as,

$$V = (\pi \sum \frac{d^2}{8L}) \times 10{,}000$$

where *V* is the area-based volume ($m^3\ ha^{-1}$), *d* is the diameter (m) of each CWM piece at the point of intersection, and *L* is the total transect length (m) per plot (from Van Wagner, 1968). Volume reduction factors were applied for advanced decay class 4 and 5 logs, to account for their collapse through decay (Fraver et al. 2013). CWM height (to the top of each piece) was summarized using the plot-level mean, as it better captured height variability compared to other measures of central tendency. Potential treatment differences in CWM volume and height metrics were evaluated using separate analyses of variance (ANOVA) in R (R Core Team, 2021). Differences ultimately revealed by the ANOVAs were further tested by Tukey's HSD post-hoc test. In addition, Kolmogorov-Smirnov goodness-of-fit tests (K-S test) were conducted to assess differences in CWM height distributions among treatments (plots pooled), including Bonferroni adjustments for multiple comparisons.

1.2.2.2 Sapling Communities

Sapling composition was assessed through analysis of sapling species, size, and abundance. Species composition per hectare was summarized by treatment means, and differences in saplings per hectare and proportion of hardwoods (logit transformed) among treatments were evaluated using ANOVA followed by Tukey’s HSD test. Kolmogorov-Smirnov goodness-of-fit tests were conducted to assess differences in sapling diameter distributions (plots pooled) among treatments, including Bonferroni adjustments for multiple comparisons.

1.2.2.3 Browse Response

To evaluate the exclosure effect, we created a series of binomial generalized linear models to predict the probability of a sapling being browsed. Sapling density and sapling hardwood proportion were identified as baseline predictor variables based on prior findings suggesting that moose are drawn to areas with more hardwood regeneration (McLaren et al., 2000; Pastor et al., 1998). Random forest modeling using the R package *VSURF* (Genuer et al., 2015) was used to assess the influence of site characteristics such as distance to the nearest road, elevation, slope, aspect, and canopy openness against probability of browsing. These variables were not identified as significant predictors of browsing and were thus excluded from further analysis (See Appendix Table A1). Additional potential predictor variables were tested for collinearity, and those found to be collinear were excluded from the same model. For example, all CWM variables (e.g., mean height, median height, maximum height, volume) were collinear; however, we selected CWM mean as the variable most likely responsible for an exclosure effect, that is, impeding access by moose. Models of the three variables of interest – mean CWM height, sapling density, and hardwood proportion – were compared in all possible model combinations (including interactions) based on the Akaike Information Criterion (AIC), using the R package *AICcmodavg* (Mazerolle 2020). The top five models were ranked according to the lowest AIC score.

Finally, differences in the probability of browsing among treatments were examined. The logit-transformed proportion of browsed saplings was calculated for each plot, and differences among treatments were tested using ANOVA followed by Tukey's HSD test.

1.3 Results

1.3.1 *Forest Structure*

Mean CWM volume did not differ significantly between salvage and control (Tukey's HSD $p = 0.96$), while blowdown differed from both salvage and control ($p < 0.001$; Table 1.1). The height distribution of CWM pieces differed somewhat between salvage and control (K-S test after Bonferroni adjustment to $p = 0.017$), while blowdown differed markedly from both salvage and control (adjusted $p < 0.001$; Table 1.1; Figure 1.2). Here the trends in CWM structure among treatments are clear: control and salvage had relatively low volume and low mean height, while blowdown had relatively high volume and high mean height (Figure 1.3a). We note that mean CWM height and volume are positively correlated (*rho* = 0.73).

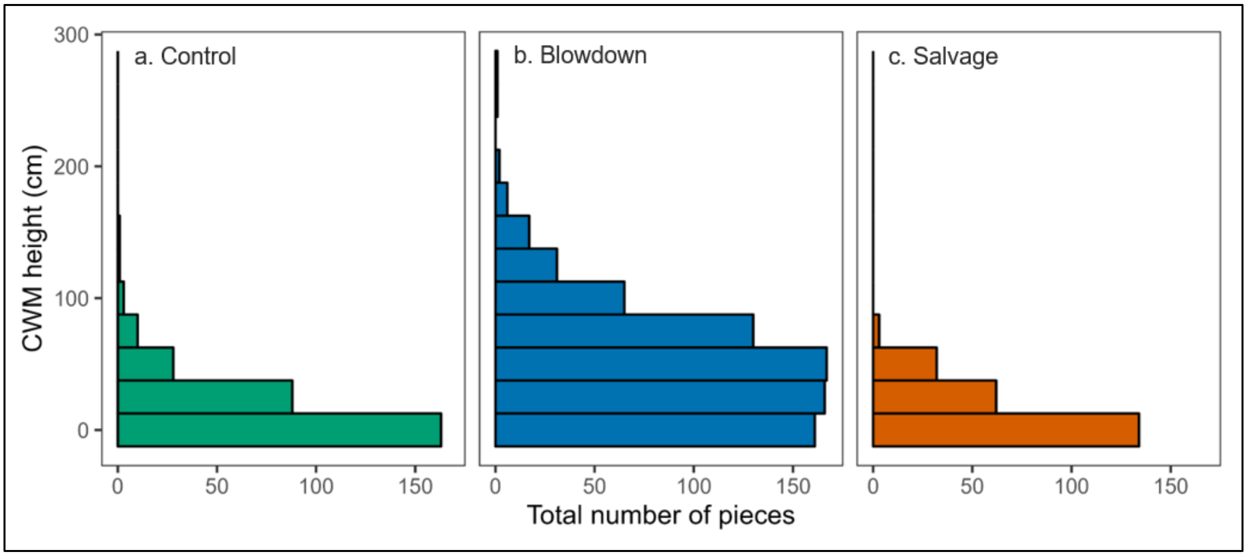

Figure 1.2. Vertical height distribution (to the top of each piece) of coarse woody material (CWM). Plot data pooled by treatment: control, blowdown, and salvage (i.e., blowdown followed by salvage).

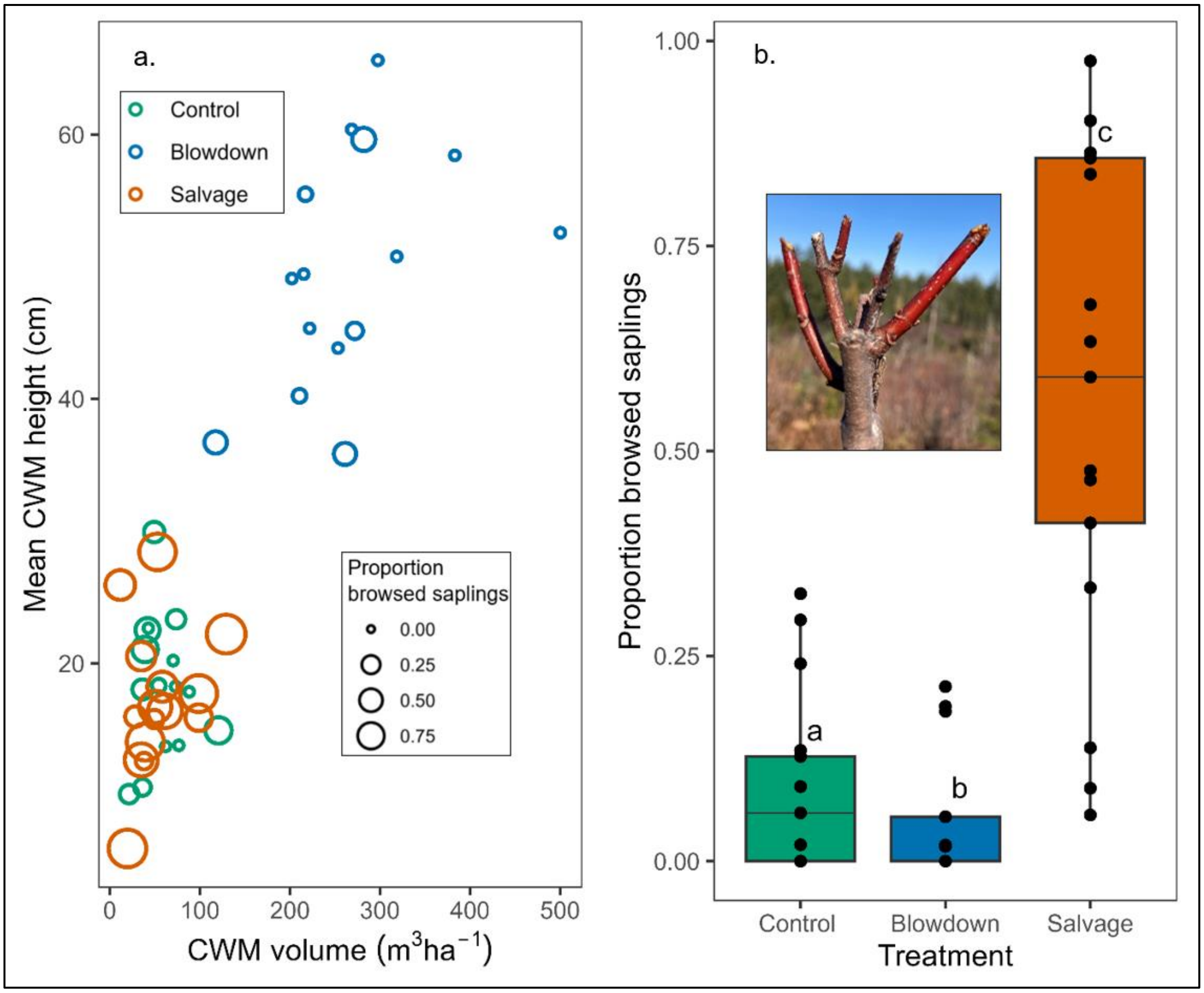

Figure 1.3. a. Mean height (to the top of each piece) and total volume of coarse woody material (CWM) for each plot. Point size scaled relative to the proportion of browsed saplings within each plot. Spearman's Rank correlation coefficient (*rho*) for the relationship between mean CWM height and mean volume = 0.73. b. Proportion of browsed saplings by treatment. Different lower-case letters indicate significant treatment differences at α < 0.05. Photo insert: moose-browsed *Acer rubrum*. Note: salvage = blowdown followed by salvage.

1.3.2 Sapling Communities

Nine years following disturbance, sapling recruitment was evident in both salvage and blowdown treatments. As expected, the disturbed blowdown and salvage treatments had mean sapling abundances 2.5 and 2.2 times (respectively) that of the undisturbed control (Tukey HSD $p < 0.001$; Table 1.1). Compositionally, *Abies balsamea* was more common in the blowdown treatment, while *Acer rubrum* was more common in the salvage treatment; however, both disturbed treatments contained similar proportions of hardwood saplings (Table 1.1). Sapling size class distributions differed among three treatments (K-S test $p < 0.001$; Figure 1.4).

Table 1.1. Structural metrics for coarse woody material (CWM) and saplings by treatment, including standard deviations. Different lower-case letters indicate significant treatment differences at $\alpha < 0.05$. Species-level composition and browsing intensity (means and standard deviations) included for the six most abundant sapling species. (Note: salvage = blowdown followed by salvage). Species listed in order of overall decreasing abundance.

Variable	**Control**	**Blowdown**	**Salvage**
Structural Metrics			
Mean CWM Height (cm)	18 ± 5^{a}	50 ± 9^{b}	17 ± 5^{a}
Median CWM Height (cm)	11 ± 6^{a}	44 ± 10^{b}	12 ± 6^{a}
Max. CWM Height (cm)	70 ± 31^{a}	169 ± 43^{b}	50 ± 14^{a}
CWM Volume (m^3 ha^{-1})	59 ± 25^{a}	268 ± 88^{b}	53 ± 32^{a}
Hardwood Proportion (%)	20 ± 17^{a}	41 ± 24^{b}	55 ± 30^{b}
Sapling Density (stems ha^{-1})	4,347 ± 2,047^{a}	11,013 ± 4,203^{b}	9,373 ± 4,562^{b}
Sapling Abundance (stems ha^{-1})			
Abies balsamea	2,653 ± 1,585	4,880 ± 2,579	2,087 ± 1,766
Acer rubrum	567 ± 682	1,653 ±1,286	3,387 ± 2,537
Picea rubens	733 ± 859	1,240 ± 1,412	1,593 ± 1,812
Prunus pensylvanica	0	1,340 ± 2,369	933 ± 2,413

Table 1.1 continued

Betula alleghaniensis	80 ± 152	687 ± 1,308	140 ± 338
Pinus strobus	33 ± 90	133 ± 232	347 ± 380
Percent Browsed Saplings (%)			
Abies balsamea	2 ± 5	0	28 ± 35
Acer rubrum	50 ± 40	19 ± 29	90 ± 20
Picea rubens	1 ± 5	0	1 ± 4
Prunus pensylvanica	N/A	10 ± 23	95 ± 11
Betula alleghaniensis	8 ± 17	4 ± 11	93 ± 6
Pinus strobus	0	0	9 ± 30

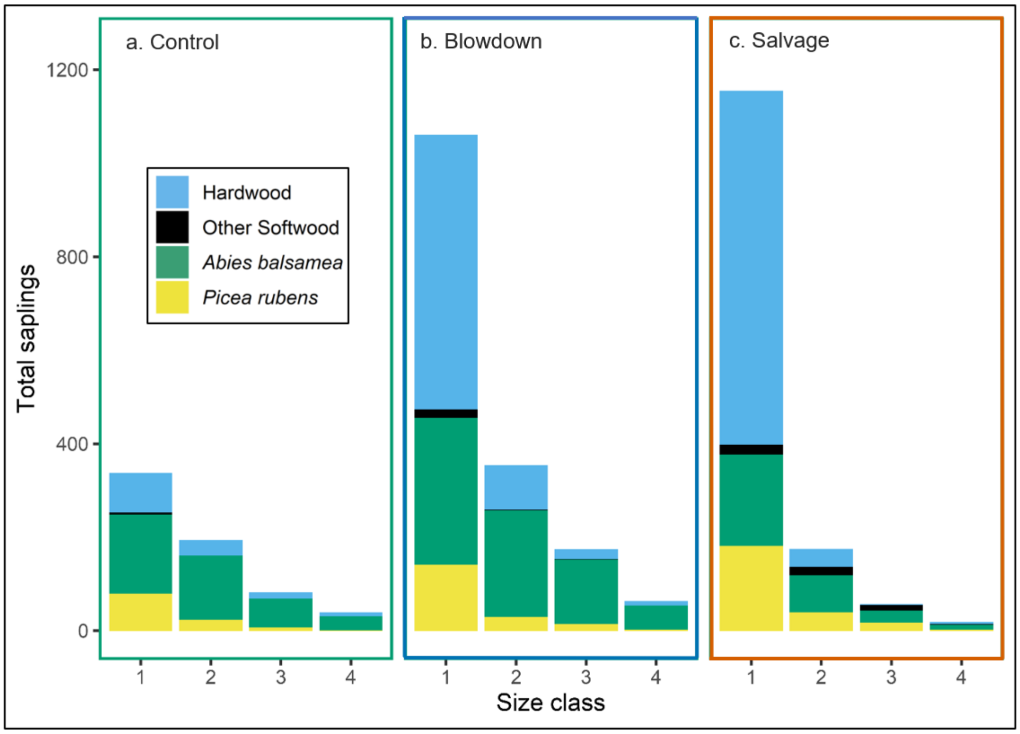

Figure 1.4. Diameter class distribution (at breast height) of all measured saplings, plot data pooled by treatment: control, blowdown, and salvage (i.e., blowdown followed by salvage). Class 1: ≤2.5 cm, class 2: 2.6 - 5 cm, class 3: 5.1 - 7.5 cm, class 4: 7.6 - 10 cm.

1.3.3 Browse Response

Probability of browsing was a function of mean CWM height and the interaction between sapling density and proportion of sapling hardwoods, based on the best approximating binomial generalized linear model in the candidate set (Table 1.2). This model carried nearly 100% of the cumulative model weight and had a relatively high ratio of residual deviance to null deviance (or McFadden's pseudo R^2). The probability of browsing was higher in plots with more hardwoods, greater sapling density, and lower CWM heights (Figure 1.5). The influence of hardwood proportion in predicting browsing was greater at lower sapling densities as indicated by the greater divergence of the probability curves at first quartile sapling density (Figure 1.5).

Further, treatments differed significantly with respect to the proportion of saplings browsed. The salvage treatment had the highest proportion (56 ± 28%), followed by the control (9 ± 10) and blowdown (5 ± 8%; Tukey HSD, all pairwise $p < 0.001$; Figure 1.3b). Blowdown and salvage notably had similar sapling densities and proportions of hardwood species (Table 1.1), two of the variables identified as significant predictors of browsing. Differences in browsing percent also varied by species within each treatment, with hardwood species and *Abies balsamea* browsed more commonly in the salvage treatment (Table 1.1).

Table 1.2 Top five models for predicting sapling browsing probability. Models ranked according to AICc scores using the variables CWM_{HT} (mean coarse woody material height above forest floor), Sapl. Dens. (sapling density) and HW Prop. (hardwood proportion, logit transformed). k = number of model parameters; AICc = corrected Akaike information criterion; ΔAICc = change in Akaike information criterion relative to the top model; AICc wt. = corrected Akaike information criterion weights; R^2 = McFadden's pseudo R^2 for a binomial distribution.

Model Predictors	**k**	**AICc**	**ΔAICc**	**AICc wt.**	R^2
CWM_{HT} + Sapl. Dens. × HW Prop.	5	2686.4	0.0	1	0.36
CWM_{HT} + Sapl. Dens. + HW Prop.	4	2799.6	113.2	0	0.33
CWM_{HT} + HW Prop.	3	2804.4	118.0	0	0.33
CWM_{HT} + Sapl. Dens.	3	3299.1	612.7	0	0.21
Sapl. Dens. × HW Prop.	3	3445.4	759.0	0	0.17

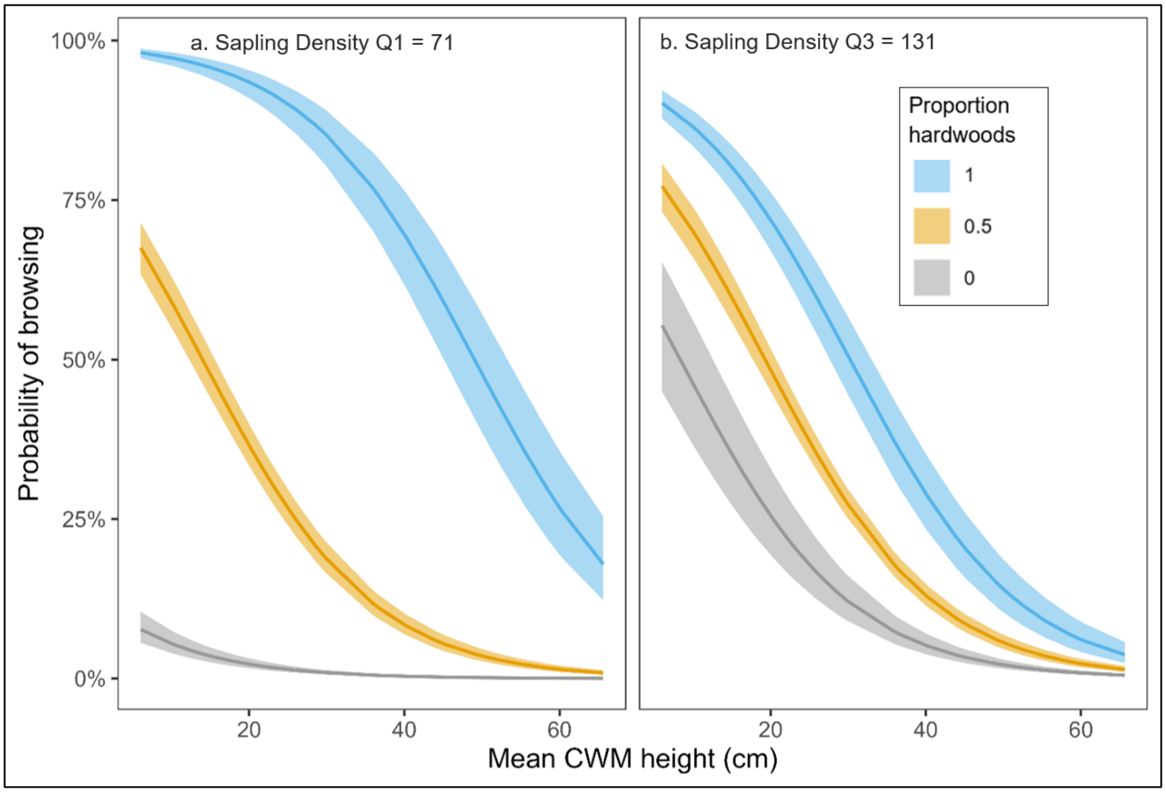

Figure 1.5. GLM model predictions of sapling probability of browsing across varying coarse woody material (CWM) heights, hardwood proportions, and sapling densities. Six scenarios are presented to illustrate the effects of the hardwood proportion × sapling density interaction: probability of browsing when all the saplings are hardwoods, probability of browsing when 50% of the saplings are hardwoods, and probability of browsing when none of the saplings are hardwoods for both the first (Q1, panel a) and third (Q3, panel b) quartile of sapling density (number per plot). Shading indicates 95% confidence intervals.

1.4 Discussion

Our results demonstrate that post-disturbance salvage logging created important differences in CWM abundance and height distribution when compared to un-salvaged areas, and that these differences in turn likely contributed to changes in sapling composition and browsing intensity. As such, our study addresses important knowledge gaps surrounding regeneration success post disturbance, as well as the role of CWM in restricting herbivory in wind disturbed areas. Although biological legacies of disturbance, such as CWM, are widely recognized as key components of ecosystem resilience (Johnstone et al. 2016), this work is among the first to demonstrate the importance of these structural legacies in minimizing impacts of herbivory on the post-disturbance sapling community.

1.4.1 Forest Structure

Structural differences between salvage and blowdown areas remained consistent with those reported by Fraver et al. (2017) eight years earlier at this same site. For example, we observed CWM volume and mean CWM height in the blowdown to be considerably greater than those in the salvaged treatment. Few studies have reported CWM heights or height distributions following severe disturbance. Those that have also included repeated measurements, which clearly show height reductions over time due to decay and settling. Morimoto et al. (2021) found that mean CWM height decreased significantly from 0.98 m to 0.38 m after 10 years, and Barker Plotkin et al. (2013) report a dramatic height reduction after 20 years (their Figure 2.4). Although our study sampled different blowdown plots than those of Fraver et al. (2017), we note that the mean CWM height had apparently decreased from 0.61 m to 0.50 m over the nine years between inventories. Although the elevated CWM following blowdown diminishes over time, it may provide an exclosure effect for a critical period (years or decades) during which saplings escape browsing via girth and height growth (Zonneyville et al., 2022). This elevated CWM, as well as greater CWM volumes, clearly distinguishes blowdown from salvage and control treatments.

1.4.2 Sapling Communities

Our results indicate that regeneration differences among treatments are both structural and compositional in nature. We note, however, that greater abundance of saplings of more advanced size classes in the blowdown may have been the result of reduced browsing (hence, faster growth) or larger seedlings or saplings that existed prior to the blowdown. Compositionally, hardwood saplings were more abundant in the more open light conditions of the blowdown and salvaged treatments when compared to control treatments. At the species level, *Acer rubrum* was more common in salvaged areas, while *Abies balsamea* was more common in blowdown areas. This finding is notable considering the life-history traits of these species. *Acer rubrum* can behave as both an early- and late-successional species with an affinity for disturbed sites (Abrams, 1998), while *Abies balsamea*, a shade-tolerant conifer, was one of the two dominant canopy species prior to the tornado (the other being *Picea rubens*). The greater abundance of *Abies balsamea* regeneration relative to that of *Picea rubens*, even in *Picea rubens* dominated stands, is well reported given that its regeneration is more robust and responds more aggressively to large canopy openings than does *Picea rubens* (Seymour 1992; Dumais and Prévost 2014). Similar compositional and structural differences between blowdown and salvage treatments are well documented in previous salvage logging studies (Royo et al., 2016; Taeroe et al., 2019; Li et al., 2023). However, we acknowledge a potential bias in our study (as well as in most previous browsing studies): seedlings that had been completely consumed would not have been tallied, as no part would have been visible (Mosbacher and Williams 2009). The magnitude of this bias remains unknown.

1.4.3 Browse Response

Perhaps the most notable finding from our study was a documentation of an exclosure effect. Although previous studies have documented the use of logging slash to physically restrict ungulate browse (Grisez, 1960; Hagge et al., 2019; Smallidge et al., 2021), ours appears to be the first to model the importance of retaining post-blowdown CWM in situ to protect saplings from browsing.

The vertical distribution of CWM in the un-salvaged treatment, represented in our model as mean CWM height, appears to restrict access by moose. For example, consider a plot with average sapling density, 100% hardwood saplings, and a mean CWM height of 65 cm. Despite the observed preference for hardwoods, model predictions suggest saplings in a plot with such elevated CWM would have only a 7% probability of being browsed. The observed effect of mean CWM height on probability of browsing is not as strong as that of hardwood proportion. For example, a plot with average sapling density of 100% hardwoods would require a mean CWM height of 38 cm to restrict the probability of browsing to 50%. The assumption that the higher vertical distribution of CWM in the un-salvaged treatment restricted access by moose is supported by studies demonstrating that snow depth limits moose movements: Melin et al. (2023) found that movement rates decreased markedly in snow depths > 40 cm, and Kelsall (1969) found that movements were ‘severely restricted’ at depths > 70 cm. Only the blowdown treatment had significant numbers of CWM pieces positioned above these critical heights.

Studies on moose feeding preference indicate that nutrient-poor taxa like *Picea* species are less preferred than nutrient-rich deciduous taxa (Pastor et al., 1998) or favored winter browse species like *Abies balsamea* (Hidding et al., 2012). For example, consider a plot with an average sapling density of 108 saplings, a mean CWM height of 0 cm, and a sapling composition of 100% hardwoods. Under such conditions, model predictions suggest that a given sapling would have a 97% probability of being browsed. Alternatively, a sapling in a plot with the same sapling density, no hardwoods, and a mean CWM height of 0 cm would have a 43% probability of being browsed. These scenarios highlight that the presence of hardwoods vastly increases the likelihood of browsing.

Nevertheless, the sapling density × proportion of hardwood interaction was the best predictor of moose browse overall. The proportion of hardwoods becomes less important under high sapling densities. This interaction is most pronounced when sapling density is low. When hardwood proportion and sapling densities are both low, browsing is also low. In contrast, sapling type (hardwood or softwood) matters less when sapling density is high. This finding suggests that moose preferentially browse hardwoods (as above), but when hardwoods are unavailable, they browse softwoods heavily in areas with high sapling density. This finding is supported by McLaren et al. (2000) who found more instances of moose browse on *Abies balsamea* in un-thinned stands containing a greater density of hardwood saplings.

Treatment effects are not named explicitly in our model, yet we did observe significant differences in browsing response among the treatments. Our results align with those from previous studies demonstrating that sapling species composition becomes less important in the presence of physical barriers (Konôpka et al., 2021; Milne-Rostkowska et al., 2020). For example, although the blowdown had sapling density and composition (including palatable species) comparable to those in the salvage treatment, the likelihood of browsing was substantially lower in the blowdown.

1.5 Conclusions

As we anticipate a future with more frequent and intense climate-related disturbances, situations for which salvage logging is considered will increase in tandem (Lindenmayer et al., 2008). Numerous studies have shown that salvage influences the trajectory of forest regeneration (D'Amato et al., 2011; Kleinman et al., 2017; Santoro & D'Amato, 2019), with desirable outcomes in some situations (Royo et al., 2016; Zonneyville et al., 2022), and undesirable outcomes in others (Taeroe et al., 2019). Results from our study system indicate that salvage logging simplified CWM structure and altered regeneration structure and composition relative to blowdown conditions. These alterations, evident early in stand development, may influence forest structure and composition for decades, as seen in previous studies (Mabry and Korsgren, 1998; Sass, et al. 2018; Li et al., 2023). Further, results suggest that retaining post-blowdown CWM in situ created an exclosure effect, thereby protecting saplings from browsing. Such protection has the additional benefit (not addressed in our study) of reducing browse-induced stem deformities, such as forks and brooms (Bergeron, et al. 2011), which persist as the damaged trees mature, thus reducing their commercial value. Importantly, rates of tree community recovery, as quantified by sapling composition and diameter distributions, were greater in un-salvaged areas, highlighting important interactions between CWM legacies and resilience to disturbance. In areas where ungulate browse presents a significant threat to regeneration, managers should consider leaving deadwood in place to act as a natural exclosure. However, the potential benefits of leaving CWM in place to protect tree regeneration, as well as provide additional ecological services, must be weighed against the use of salvage logging to mitigate subsequent catastrophic disturbance such as fire. Given the wide range of disturbance types and post-disturbance conditions possible, we encourage further exploration of regeneration outcomes following salvage operations.

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CHAPTER 2

UNDERSTORY VEGETATION RESPONSE TO POST-TORNADO SALVAGE LOGGING

In an era of increasing natural disturbances, successful tree regeneration has grown more difficult to achieve. Disturbance notably alters forest microclimates, creating open canopy conditions that might promote growth of undesirable understory communities adept at outcompeting tree seedlings. Salvage logging, a common management response to disturbance, may further impede regeneration success. In 2013, a rare tornado in northcentral Maine, USA, and subsequent salvage operation created three clear 'treatments' for evaluation of post-disturbance understory regeneration: blowdown, blowdown followed by salvage logging and an undisturbed control. Ten years post tornado, we inventoried understory vegetation within each of these treatments. We used hemispherical photographs to characterize canopy openness and installed sensors to track temperature and soil moisture throughout a growing season. Results indicate distinct understory community differences among each of the treatments, with the salvage treatment supporting a higher richness and abundance of early successional, shade intolerant taxa, while the blowdown and control treatments were characterized by later successional, shade tolerant taxa. Abundance of conifer regeneration was notably lower in plots with high abundance of *Rubus idaeus* or *Pteridium aquilinum*. Ordination results suggest that canopy openness and surface temperature fluctuations were the primary factors associated with these compositional differences. This study furthers our understanding of the interactions among disturbance, microclimate, and understory communities, highlighting the need for increased consideration of long-term effects following salvage logging.

2.1. Introduction

Tree regeneration success has recently grown more difficult to achieve as forests face compounding pressures from climate change, invasive species, forest pathogens, forest fragmentation and herbivory (Miller et al., 2023, Dey et al., 2019). In addition, natural disturbances such as windstorms, insect outbreaks, and fire hinder the ability of forest practitioners to control regeneration outcomes. As we anticipate an increase in the frequency and severity of natural disturbances (Dale et al., 2001; Johnstone et al., 2016; Seidl et al., 2017), post-disturbance management gains additional relevance.

Salvage logging, a common management response following natural disturbances, remains controversial, as published literature is inconclusive regarding its effect on tree regeneration (Lindenmayer et al., 2008). Studies suggest salvage logging can enhance site preparation and the establishment of shade intolerant hardwoods (Nelson et al., 2008; Royo et al., 2016; Slyder et al., 2020). Other studies suggest it can create conditions more favorable to ungulate herbivory (Hagge et al., 2019; Konôpka et al., 2021; Morimoto et al., 2021), can impair microsite conditions for seedling survival (Marañón-Jiménez et al., 2013) and can increase competition with understory vegetation (Jonášová & Prach, 2008; Palm et al., 2022). The disagreement among these studies highlights existing knowledge gaps surrounding this issue, in part because the influence of salvage logging appears to be system dependent.

Although several studies have investigated the influence of salvage harvesting on microclimate conditions (Marcolin et al., 2019; Thorn et al., 2014), this topic remains relatively understudied given the importance of microclimate on tree regeneration (Campanello et al. 2007). The role of forest canopies in buffering environmental extremes, and hence maintaining understory microclimates and plant communities, has recently gained much attention (De Frenne et al., 2021; Sanczuk et al., 2023). Coarse woody material (CWM) contributes to this buffering effect by providing shade and reducing the warming of soil surfaces, decreasing evaporation and maintaining soil moisture (Devine & Harrington, 2007; Goldin & Hutchinson, 2015; Marañón-Jiménez et al., 2013). For example, in the years immediately following a post-fire salvage operation, Marcolin et al. (2019) found that salvage logged sites had higher soil temperature and lower soil moisture compared to un-salvaged sites, creating less favorable environments for seed germination.

Alterations to microclimate may also make conditions more favorable for the growth of recalcitrant understory vegetation (Royo & Carson, 2006). For example, germination of *Rubus* species is triggered by daily temperature fluctuations (Donoso & Nyland, 2006; Marcuzzi & Demartinez, 1993; Suzuki, 1997). Similarly, *Pteridium aquilinum* (L.) Kuhn (bracken fern) emergence is closely related to daily temperature fluctuations and increased light (Cody & Crompton, 1975; Engelman & Nyland, 2006). These native, shade intolerant species (Hart & Chen, 2006) frequently become established post-harvest in our study region and are thought to inhibit tree regeneration (Donoso & Nyland, 2006; Engelman & Nyland, 2006; Royo & Carson, 2006), although the extent to which this occurs has not been well documented. Understanding the links between salvage logging, microclimate conditions and regeneration may provide a broader understanding of mechanisms influencing post-salvage tree regeneration.

A series of events beginning in 2013 provides an ideal setting to address connections between salvage logging, microclimate conditions and understory vegetation. In July of 2013, a tornado struck the northeastern portion of Baxter State Park, Maine, USA, causing significant canopy loss to an approximate 200-ha swath of mixed-species conifer forest (Fraver et al., 2017). A portion of this area was salvaged that winter (2013-2014) while other areas were left untouched. This series of events generated three clear “treatments”: tornado blowdown, blowdown followed by salvage logging, and undisturbed control. In this study, we compare these three treatments with respect to understory vegetation and microclimate conditions.

The goal of this study is to understand how salvage logging following severe wind disturbance alters understory plant communities and microclimates. Our objectives explore (1) understory community differences among undisturbed, blowdown and salvage conditions, (2) relationships between conifer sapling abundance and early successional, recalcitrant species, and (3) relationships between microclimate factors and understory communities. The observational nature of this study prevents us from determining mechanistic links between vegetation and microclimate, however our results provide a valuable addition to our understanding of post-salvage conditions.

2.2 Methods

2.2.1 Field Sampling

Our study was conducted within the Baxter State Park Scientific Forest Management Area (SFMA) of northcentral Maine, USA (Figure 2.1). Established in 1955, this 12,000 ha tract is maintained to demonstrate sustainable forest management practices (Whitcomb, 2008). The mean annual temperature of the SFMA is 4.4 °C with an average of 1084 mm of annual precipitation distributed evenly throughout the year (PRISM Climate Group, 2022). Topography in the SFMA ranges from 244 to 390 m a.s.l., and soils are derived from glacial till. The tornado of July, 2013, with windspeeds exceeding 40 m/s, caused extensive canopy loss in a 200-ha swath of forest in the SFMA (Fraver et al., 2017). By comparing structural characteristics of the control stands to those of the blowdown immediately post-disturbance (see Fraver et al. 2017), we estimate that the tornado reduced basal area by 87% and tree density by 85%. Salvage harvesting in portions of the wind-damaged area began in the winter of 2013-2014 using a fixed-head cut-to-length processer and forwarder, with slash left on site (Fraver et al., 2017).

Three treatments (blowdown, blowdown plus salvage, and undamaged control; Figure 2.1) were initially identified and inventoried in the summer of 2014 (Fraver et al., 2017). Prior to the tornado, these stands were dominated by red spruce (*Picea rubens* Sarg.) and lesser components of balsam fir (*Abies balsamea* (L.) Mill), northern-white cedar (*Thuja occidentalis* L.), eastern white pine (*Pinus strobus* L.), red maple (*Acer rubrum* L.) and paper birch (*Betula papyrifera* Marshall) (Fraver et al., 2017). Control stands were chosen for their similarity in composition and proximity to blowdown and salvage sites. Although many of these stands had experienced prior management (light partial harvests ca. 20 years before the blowdown), pre-blowdown differences in structure and composition among stands was deemed negligible based on pre-blowdown inventories and post-blowdown woody debris and stump surveys (Fraver et al., 2017).

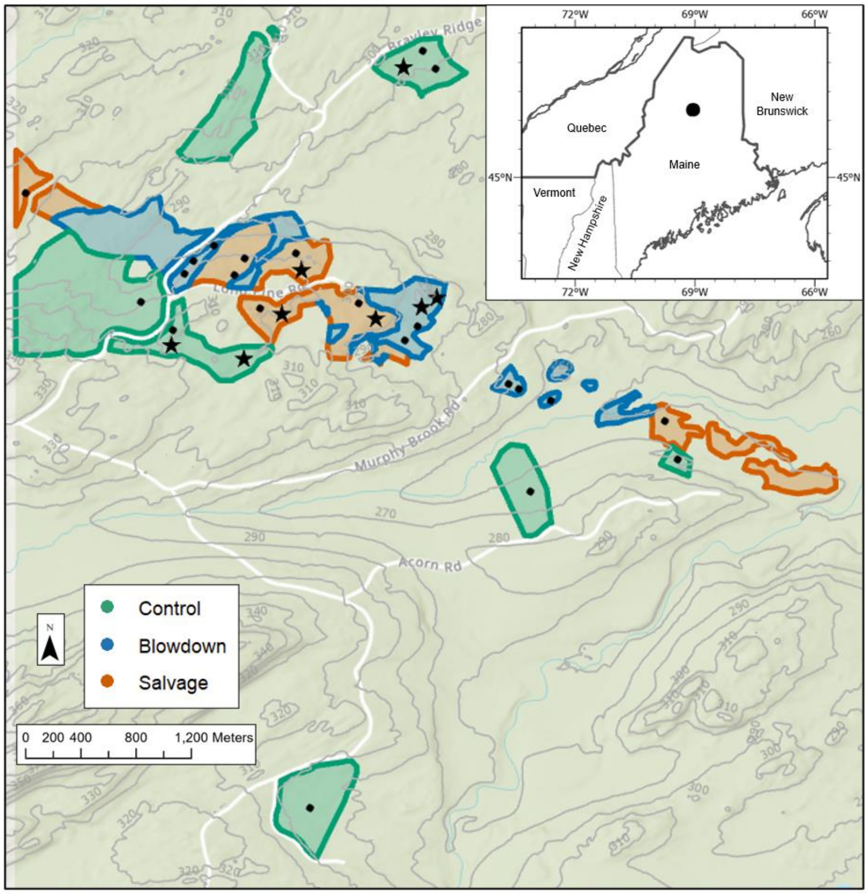

Figure 2.1: Treatment and plot locations within the Scientific Forest Management Area (SFMA), Baxter State Park, Maine, USA. Orange and blue polygons show the extent of tornado damaged patches, dots indicate plot locations, stars indicate plots containing TMS-4 sensors. Sampled units color coded by treatment: control, blowdown, and salvage (blowdown followed by salvage). The western border of map is the western border of the SFMA. Contour lines in meters.

Approximately nine years post-tornado (summer 2022), these stands were revisited to assess sapling composition, deadwood structure, browse intensity, and microclimate response across the treatments (Chapter 1). Fifteen plots per treatment were designated randomly in ArcGIS with occasional on-the-ground adjustments made based on the location of recent harvests not seen in aerial imagery (Chapter 1). On May 21st, 2022, TMS-4 soil moisture and temperature sensors (Wild et al. 2019) were installed within three randomly selected plots per treatment. In July and August of 2023, 30 of the original 45 plots (10 per treatment) were revisited to inventory understory plant communities. That is, each of the sensor plots and seven additional randomly selected plots were inventoried per treatment.

Within each of the 30 understory vegetation plots, eight 1 × 1 m vegetation frames were placed 2.5 and 5 m from plot center in each cardinal direction. Percent cover of all herbaceous plants, ferns, graminoids, tree regeneration (stem diameter at breast height < 10 cm) were estimated for all taxa rooted within each frame and covering > 1% of the area. Percent cover of exposed rock and deadwood unsuitable for plant colonization (undecayed and/or elevated logs) was recorded in the field; during data processing the cover of plants in these frames was adjusted account for this unsuitable area. To avoid observer bias, the same observer estimated percent cover for each quadrat.

Three TMS-4 sensors were installed within each of the nine sensor plots, one at plot center, and two offset 5.5 m east and west of the center. Each TMS-4 sensor monitored soil moisture and provided continuous temperature data from 6 cm below the soil surface, and 2 cm and 15 cm above the soil surface. Sensors were programed to record data every 15 minutes and were left to collect data through the growing season (collected October 22nd, 2022). The TMS-4 sensors have a resolution of 0.063°C and an accuracy of ± 0.5 °C.

Canopy openness was also measured during the summer of 2023. Hemispherical photographs were taken at each of the 30 plot centers (1 m above forest floor), using a Nikon Coolpix 995 camera with a hemispherical lens adapter. Photographs were processed using Gap Light Analyzer software (Frazer et al., 1999) to produce a canopy openness value (i.e., percent of open sky).

2.2.1 Data Analysis

To examine gradients in understory community composition across treatments, plot-level importance values (mean of relative percent cover and relative frequency, eight subplots pooled) were calculated for each species. Trends in understory species composition were analyzed by Non-metric Multidimensional Scaling (NMDS) ordination, based on Sørensen (Bray-Curtis) dissimilarity, using the *vegan* package in R (Oksanen et al., 2022). The Multi-Response Permutational Procedure (MRPP) in *vegan* was used to test for differences among treatment groups based on understory community composition. Pairwise treatment comparisons in MRPP were calculated with Sørensen's dissimilarity, including a Bonferroni adjustment, using the R package *RVAideMemoire* (Hervé, 2022). Indicator species analysis was performed on species importance values to determine which species influenced patterns in the ordination and MRPP results. This test was conducted in the R package *indicspecies* (Cáceres & Legendre, 2009) using a point biserial correlation coefficient tested at $\alpha = 0.05$.

To assess the potentially negative relationship between recalcitrant understory species (*Rubus idaeus* L. and *Pteridium aquilinum*) and conifer regeneration (*Abies balsamea*, *Picea rubens*, *Pinus strobus*, *Thuja occidentalis,* pooled), we used linear regression based on importance values. Conifer species were lumped for this analysis to obtain adequate sample size for analysis, in addition to being the dominant overstory species in the undisturbed control and representing the most valuable commercial species in the SFMA. *Rubus idaeus* and *Pteridium aquilinum* were chosen as predictor species for this analysis because of their association with disturbance conditions and abundance across the study area.

To understand environmental factors driving the ordination, a secondary ordination was conducted on plots containing sensors. One blowdown sensor plot was removed from all analysis as an outlier in both understory composition and microclimate characteristics. The influence of nine variables on the gradients in community composition depicted in the ordination were examined in *vegan*: soil surface temperature, surface temperature fluctuation, soil moisture (all from TMS-4 sensors), canopy openness, saplings abundance, coarse woody material (CWM) volume, slope, aspect, and elevation. We were particularly interested in temperature fluctuation because several disturbance-dependent species in this region, such as *Rubus* spp. and *Prunus pensylvanica,* use such fluctuations as a cue for germination post-disturbance (Suzuki, 1997; Laidlaw 1987). Variables collected at the subplot level were averaged by subplot and analyzed at the plot level. Additional microclimate variables from the TMS-4 sensors (soil temperature, air temperature and associated fluctuations) were not included in analyses, as these variables were highly correlated with surface temperature data. Potential treatment differences among microclimate variables were evaluated using separate analyses of variance (ANOVA) in R (R Core Team, 2021).

2.3 Results

We found 68 vascular plant taxa representing 29 families (See Appendix Table B1). Distinct patterns in understory taxa emerged by treatment. The salvage treatment had the greatest number of taxa (N=51), followed by blowdown (N=45), followed in turn by control (N=39) (Figure 2.2a). These results are also reflected by mean richness by treatment, as well as in the species-area curves, which show this consistent richness pattern (salvage>blowdown>control) across all scales evaluated (Figure 2.2b). A large proportion of taxa (N=26, or 38% of total) were shared among treatments (Figure 2.2a), and the salvage treatment had the largest number of unique taxa (N=15), several of which were significant indicator species (Table 1). Two non-native species (*Hieracium caespitosum* Dumort. and

Veronica officinalis L.) were encountered in low abundance in the salvage treatment. *Veronica officinalis* is notably an indicator of the salvage treatment (see below).

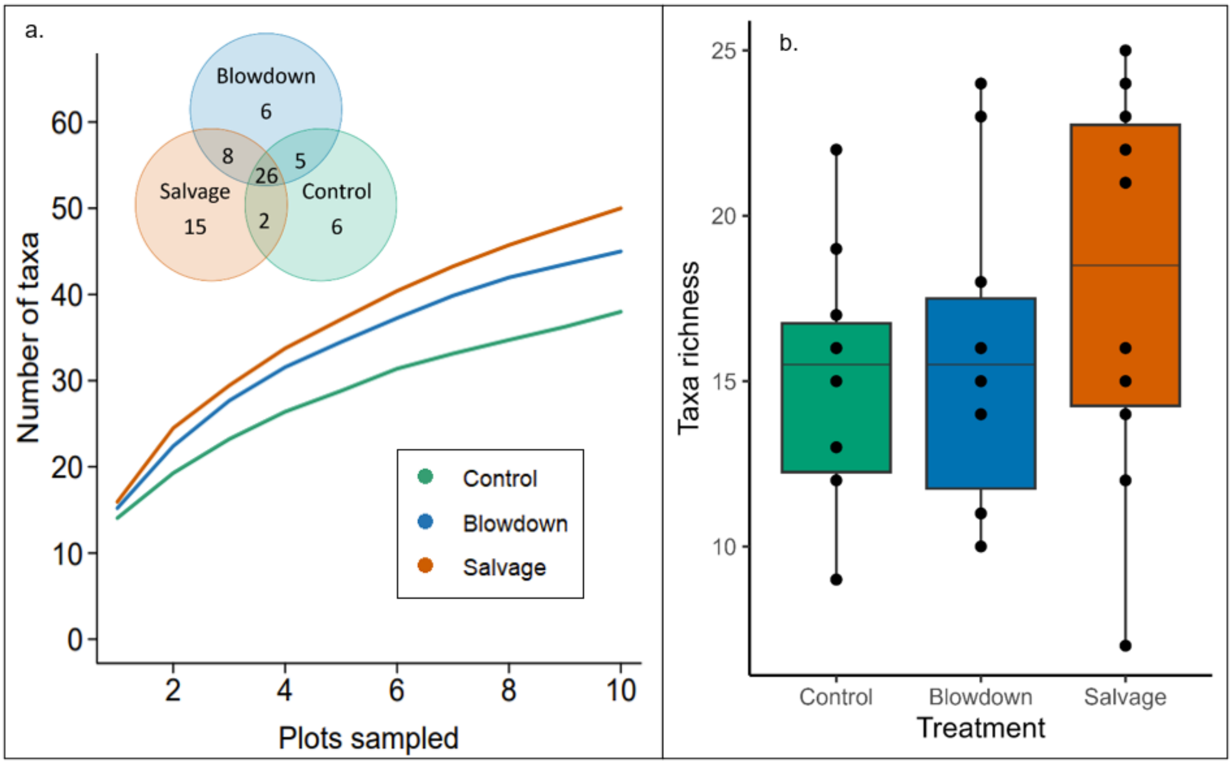

Figure 2.2: a. Species-area curves for each treatment (note: salvage = blowdown followed by salvage). Insert: Venn Diagram displaying the number of unique and shared taxa within each treatment. b. Taxa richness by treatment.

NMDS ordination based on species importance values indicated distinct species groupings according to treatment (Figure 2.3). Pairwise treatment comparisons in MRPP showed compositional differences between each treatment ($p < 0.001$, all comparisons). Indicator species analysis suggested that these patterns were driven by multiple species (Table 1.1). Canada mayflower (*Maianthemum canadense* Desf.) and starflower (*Lysimachia borealis* (Raf.) U.Manns & Anderb.) were indicators of control conditions, while wood ferns (*Dryopteris*) and northern white-cedar (*Thuja occidentalis*) seedlings were indicators of blowdown conditions. Nine taxa were indicators of salvage conditions, with paper birch (*Betula papyrifera*), sedge species (*Carex*) and raspberry (*Rubus idaeus*) showing the strongest correlation (all p < 0.001). Control and blowdown treatments shared two indicator species in common, balsam fir (*Abies balsamea*; p = 0.001), and bluebead lily (*Clintonia borealis* Aiton (Raf.); p = 0.030 The salvage treatment did not share indicator species with other treatments. Overall, the ordination revealed greater plot-to-plot variation in composition (i.e., greater spread of plots in ordination space) within both disturbed treatments (Figure 2.3).

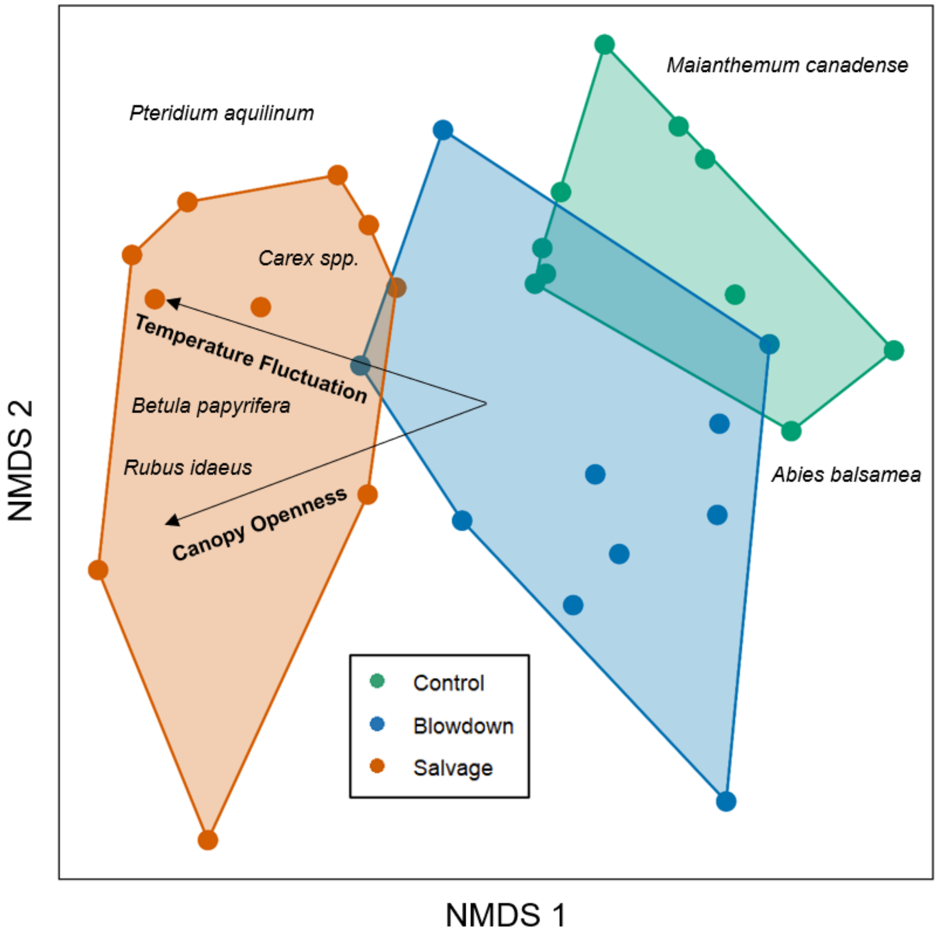

Figure 2.3: NMDS ordination results based on understory taxa importance values, outlined by treatment: control, blowdown, and salvage (blowdown followed by salvage). Location of indicator species (p < 0.001 and *Pteridium aquilinum*) plotted along both axes. Vectors indicate associations between significant environmental variable predictors and ordination axes.

Table 2.1: Indicator taxa for each treatment with associated p-values sorted by treatment and increasing p-values. Ellenberg Index for shade tolerance rankings sourced from Humbert et.al (2007), where lower numbers indicate greater tolerance. Note: salvage = blowdown followed by salvage.

Taxa	**Treatment Association**	**p-value**	**Ellenberg Index**
Maianthemum canadense	Control	0.001	4
Lysimachia borealis	Control	0.004	3
Dryopteris spp.	Blowdown	0.002	3
Thuja occidentalis	Blowdown	0.016	3
Abies balsamea	Control + Blowdown	0.001	3
Clintonia borealis	Control + Blowdown	0.030	4
Betula papyrifera	Salvage	0.001	7
Carex spp.	Salvage	0.001	3-9
Rubus idaeus	Salvage	0.001	7
Pteridium aquilinum	Salvage	0.011	6
Veronica officinalis	Salvage	0.021	--
Diervilla lonicera	Salvage	0.030	6
Prunus pensylvanica	Salvage	0.033	9
Vaccinium spp.	Salvage	0.045	7
Fragaria virginiana	Salvage	0.048	9

Linear regressions revealed significant negative relationships between conifer seedlings and both *Rubus idaeus* and *Pteridium aquilinum* abundance, based on importance values (Figure 2.4), with the *Rubus idaeus* model displaying a slightly better fit (R^2 0.25 vs 0.22, Figure 2.4). We note that both

Rubus idaeus and *Pteridium aquilinum* were only present in ca. 50% of the plots, which reduces predictive ability (conifers were present in all plots). Both *Rubus idaeus* and *Pteridium aquilinum* were also associated with greater canopy openness and the salvage treatment. *Rubus idaeus* was present in 90% of salvaged plots, while *Pteridium aquilinum* was present in 60% of salvaged plots.

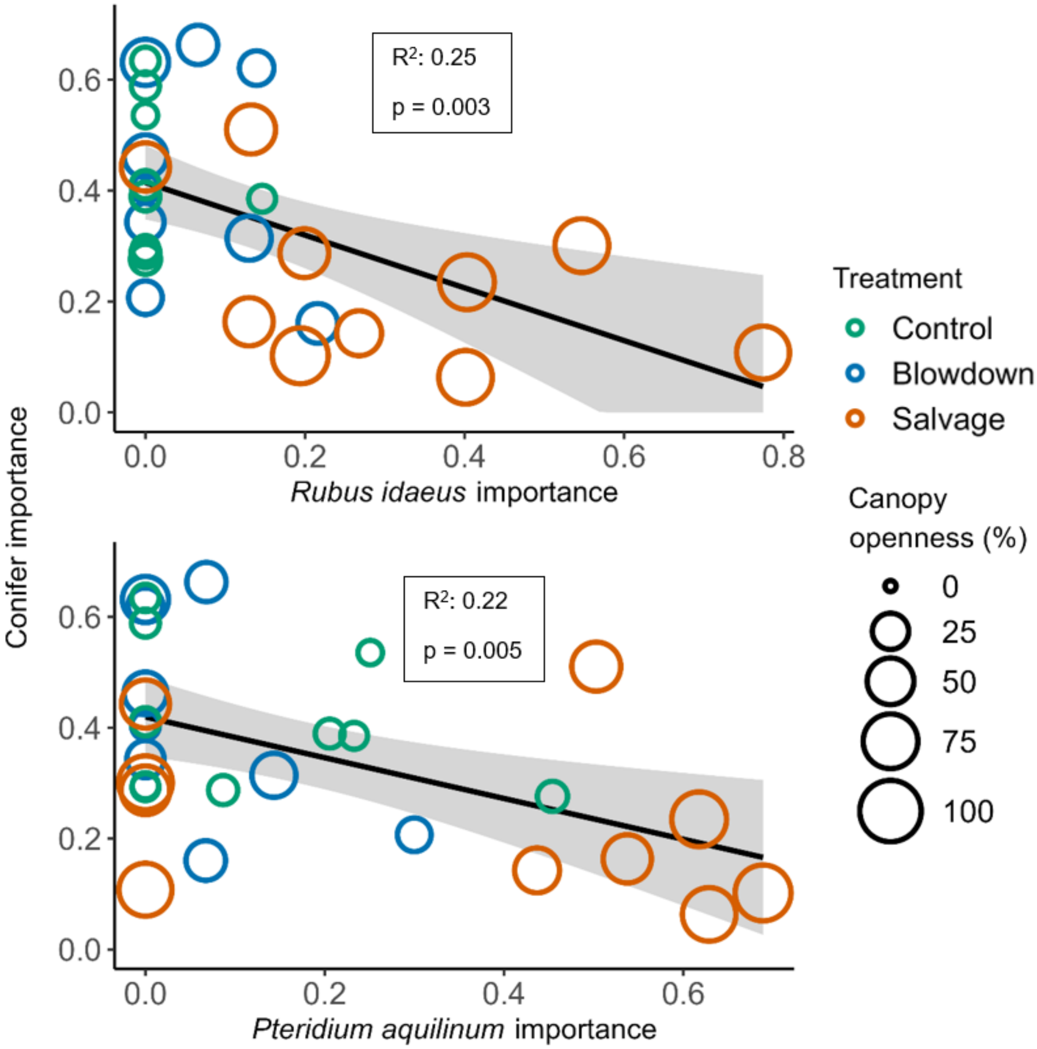

Figure 2.4: Conifer importance plotted against *Rubus idaeus* and *Pteridium aquilinum* importance, including linear regression line with shaded 95% confidence interval fit to the data. Adjusted R^2 and p-value displayed for both regressions. Plots color-coded by treatment: control, blowdown, and salvage (blowdown + salvage) and scaled according to canopy openness from hemispherical photos.

Two environmental variables were identified as significant predictors of the ordination results: surface temperature fluctuation and canopy openness (Table 2.2). Both variables were positively correlated with each other and the salvage treatment (Figure 2.5c, $R^2 = 0.66$), with canopy openness appearing to have a slightly stronger effect on ordination results. ANOVA analysis followed by Tukey HSD results suggested that canopy openness conditions differed significantly among treatments, with salvage displaying the greatest openness, and controls the least (Figure 2.5b, $p = 0.002$ (control vs. blowdown), $p < 0.001$ (salvage vs control and blowdown). Daily temperature fluctuations also differed significantly among treatments, following the same pattern (Figure 2.5a, $p < 0.001$).

Table 2.2: Environmental predictor variables assessed for the ordination, sorted from lowest to highest p-value. Association with the two ordination axes, R^2 and p-value displayed. Significant predictors ($p < 0.05$) indicated with asterisk.

Environmental Predictor	**NMDS 1**	**NMDS 2**	**R^2**	**p-value**
Canopy openness	-0.976	0.216	0.87	0.024*
Surface temperature fluctuations	-0.909	-0.417	0.73	0.044*
Mean surface temperature	-0.939	-0.343	0.54	0.123
Soil moisture	-0.354	0.935	0.55	0.138
Sapling density	-0.983	0.186	0.54	0.148
CMW volume	0.212	- 0.977	0.34	0.387
Aspect	0.292	0.956	0.28	0.414
Slope	-0.085	-0.996	0.15	0.686
Elevation	-0.808	0.589	0.02	0.950

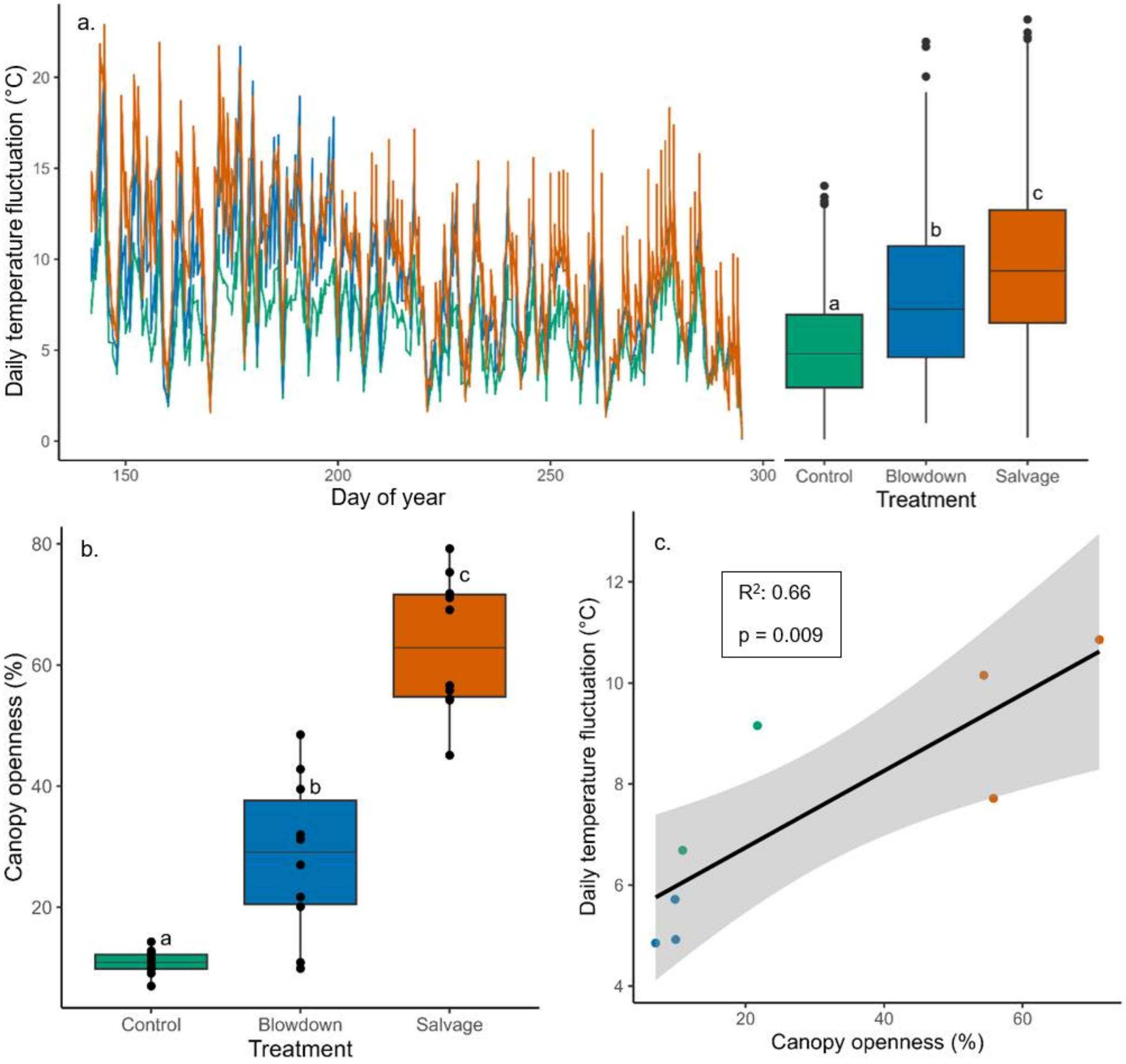

Figure 2.5: a. Daily temperature fluctuation (plots averaged by treatment) throughout the 2022 growing season, color-coded and summarized by treatment. b. Canopy openness by treatment. Different lower-case letters (panel a and b) indicate significant treatment differences at α < 0.05. c. Daily temperature fluctuation plotted against canopy openness, including linear regression line with shaded 95% confidence interval fit to the data. Adjusted R^2 and p-value displayed for the linear regression.

2.4 Discussion

Our results identify significant deviations in community composition among control, blowdown and salvage conditions and point to possible mechanisms for these differences. While differences in understory vegetation following salvage have been demonstrated in prior studies, ours is among the first to connect compositional patterns with microclimate and post salvage conditions. We also demonstrate that the abundance of conifer regeneration was related to increased *Rubus idaeus* and *Pteridium aqulinum* abundance, suggesting that these disturbance-adapted species inhibited conifer establishment.

Observed compositional differences among treatments generally align with the findings of previous studies. Several studies observed reductions in species richness following salvage due to landscape homogenization (Rumbaitis del Rio, 2006; Kleinman et al., 2017; Michalová et al., 2017). This was not the case on our site, as species richness in the salvage treatment was higher than that of the blowdown and control, due to a greater abundance of shade-intolerant taxa, similar to findings reported by Lang et al. (2009) and Slyder et al. (2019). Indicator taxa for the salvage treatment were notably all shade intolerant, while indicator taxa for control and blowdown were all shade tolerant (Humbert et.al, 2007; Table 2.1). This relationship between salvage logging and greater abundance of shade intolerant species is well established (D'Amato et al., 20011; Elliott et al., 2002; Georgiev, 2022; Palik & Kastendick, 2009). Furthermore, few studies have identified increases in non-native taxa following salvage logging relative to blowdown conditions (e.g., Rumbaitis del Rio, 2006). Our finding of two non-native taxa in the salvage treatment is notable, yet the low abundance of these species precludes robust analysis.

One critical finding from this study is the relationship between tree seedling abundance and the abundance of recalcitrant understory species. Specifically, we found plots with lower conifer seedling abundance (assessed by importance values) were related to greater *Rubus idaeus* and *Pteridium* *aquilinum* importance. In their review of *Rubus* species in northern hardwood forests (USA), Donoso and Nyland (2006) found that *Rubus* reduced the regeneration abundance of northern hardwood stands by 40% or more. Nevertheless, they also found that hardwood species tended to escape *Rubus* competition 5-7 years post-disturbance, forming closed canopy conditions in 10-15 years (Donoso & Nyland, 2006). Our findings for conifer species do not support the escape from competition reported by these authors, as the reduced conifer importance in our plots containing *Rubus idaeus* suggests that conifer regeneration is still inhibited by *Rubus* nine years post-disturbance. An earlier study in northern Maine found *Abies balsamea* seedlings overtopped by *Rubus idaeus* exhibited growth reductions when compared to open-grown controls (Fox 1986). Similarly, Ruel (1992) found that the competitive effects of *Rubus* can persist for 25 years.

Pteridium aquilinum is known to inhibit tree regeneration and seedling growth, with evidence from studies worldwide (e.g., Dolling 1996; Humphrey & Swaine 1997; Hartig & Beck 2003). It primarily reproduces vegetatively, allowing it to quickly colonize disturbed areas (Cody & Crompton, 1975). Working within our region, George and Bazzaz (1999) found that *Pteridium aquilinum* litter can create an impenetrable barrier preventing germinating seeds reaching the soil beneath and restricting emergence for seeds germinating below the litter layer. These authors also report that the presence of *Pteridium aquilinum* reduced light levels necessary for the emergence of tree seedlings. Additionally, *Pteridium aquilinum* contains allelopathic chemicals that reduce growth of *Populus* spp. and *Prunus serotina* seedlings (Dolling, 1996; Engelman & Nyland, 2006; Horsley, 1977). Monitoring of salvaged sites into the future is necessary to determine the extent to which *Rubus idaeus* and *Pteridium aquilinum* might impede or delay growth of preferred tree species.

The primary environmental drivers of the understory community response outlined above were identified as canopy openness and surface temperature fluctuation. Both factors are well-known to influence seed germination; however, the influence could be detrimental or beneficial depending on the species. For example, germination failure has been observed in *Picea abies* (a close relative of *Picea rubens*) seeds when exposed to high temperature fluctuations (Leinonen et al., 1993), while germination of *Rubus* species and *Pteridium aquilinum* benefits from temperature fluctuations and high light (Cody & Crompton, 1975; Engelman & Nyland, 2006; Suzuki, 1997). Importantly, these factors were associated with treatments, as salvage conditions displayed the highest average surface temperature fluctuations and greatest canopy openness (Figure 2.5), a finding also reported by (Marcolin et al., 2019). The reduced canopy openness in blowdown (relative to salvage) is partially due to shading by deadwood (Palik & Kastendick, 2009) and largely due to remaining undisturbed advance regeneration. Interestingly, soil moisture, a factor often correlated with CWM abundance (Devine & Harrington, 2007; Goldin & Brookhouse, 2015; Harrington et al., 2013) was not identified as a significant driver of plant community composition.

2.5 Conclusions

As with other salvage logging studies, management recommendations must be context- and priority-oriented. The greater taxonomic richness found in salvaged areas, along with the greater abundance of shade intolerant species, indicates that salvage logging may be a useful tool for promoting species diversity (Georgiev, 2022) or regenerating shade intolerant hardwoods (Royo et al., 2016). Conversely, our results demonstrate that the microclimate changes caused by salvage logging may lead to colonization by recalcitrant species and, hence tree regeneration delays. These potential consequences of salvage must be weighed against the benefits associated with greater canopy openness. Several studies recommend a middle-ground, leaving patches of blowdown within salvaged areas (as done by SFMA managers) to promote landscape heterogeneity and species diversity (Kleinman et al., 2017, Georgiev, 2022). Our findings support this recommendation, although we caution that management decisions are site- and objective-specific.

These results are an important first step in understanding the mechanistic links between understory communities, environmental conditions, and salvage harvesting. As we anticipate a future with more frequent and severe disturbances (Dale et al., 2001; Johnstone et al., 2016; Seidl et al., 2017), exploring the consequences of post-disturbance management becomes more critical. Our results clearly indicate distinct community assemblages among control, blowdown, and salvage conditions. Further, we show that reduced abundance of conifer seedlings and saplings are related to *Rubus idaeus* and *Pteridium aquilinum*. Our discussion of the microclimate factors that might drive this compositional response requires further examination. Direct observation of germination and microclimate response immediately post-salvage would provide a deeper understanding of this phenomenon. Further, longer term monitoring of post-salvage conditions is necessary to understand how these conditions might impede or delay establishment of late-successional communities.

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APPENDIX

Table A.1. Full table of models tested for predicting sapling browsing probability. Models ranked according to AICc scores using the variables $\mathrm{CWM}_{\mathrm{HT}}$ (mean coarse woody material height above forest floor), Sapl. Dens. (sapling density), HW Prop. (hardwood proportion, logit transformed), aspect, distance to nearest road, elevation, and slope. k = number of model parameters; AICc = corrected Akaike information criterion; ΔAICc = change in Akaike information criterion relative to the top model; AICc wt. = corrected Akaike information criterion weights; R^2 = McFadden's pseudo R^2 for a binomial distribution. Top five models shown in Table 1.2.

Model Predictors	**k**	**AICc**	**ΔAICc**	**AICc wt.**	R^2
$\mathrm{CWM}_{\mathrm{HT}}$ + Sapl. Dens. × HW Prop.	5	2686.4	0	1	0.36
$\mathrm{CWM}_{\mathrm{HT}}$ + Sapl. Dens. + HW Prop.	4	2799.6	113.2	0	0.33
$\mathrm{CWM}_{\mathrm{HT}}$ + HW Prop.	3	2804.4	118.0	0	0.33
$\mathrm{CWM}_{\mathrm{HT}}$ + Sapl. Dens.	3	3299.1	612.7	0	0.21
Sapl. Dens. × HW Prop.	3	3445.4	759.0	0	0.17
Sapl. Dens. + HW Prop.	4	3446.86	760.5	0	0.17
HW Prop.	2	3450.8	764.5	0	0.17
$\mathrm{CWM}_{\mathrm{HT}}$	2	3497.6	811.2	0	0.16
Aspect	2	3837.9	1151.6	0	0.07
Canopy Openness	2	4045.9	1359.5	0	0.03
Distance to Road	2	4130.7	1444.4	0	0
Sapl. Dens.	2	4134.5	1448.1	0	0
Elevation	2	4147.8	1461.5	0	0
Slope	2	4158.6	1472.2	0	0

Table B.1. Importance values for all understory taxa found during the study.

	Control	Blowdown	Salvage
ARALIACEAE			
Aralia hispida	0	0	0.006
Aralia nudicaulis	0.223	0.076	0.108
ASTERACEAE			
Anaphalis margaritacea	0	0.013	0.013
Eurybia macrophylla	0.013	0	0.021
Hieracium caespitosum	0	0	0.021
Petasites frigidus	0.007	0.007	0
Solidago spp.	0.007	0.014	0.040
Symphyotrichum novae- angliae	0	0	0.006
BETULACEAE			
Alnus incana	0	0	0.007
Betula alleghaniensis	0.030	0.034	0.008
Betula cordifolia	0	0.043	0
Betula papyrifera	0	0.040	0.215
Corylus cornuta	0.008	0.008	0
CAMPANULACEAE			
Lobelia inflata	0	0	0.006
CAPRIFOLIACEAE			
Diervilla lonicera	0	0.027	0.114
Linnaea borealis	0.155	0.213	0.149
Lonicera canadensis	0	0.027	0.013
CORNACEAE			
Chamaepericlymenum canadense	0.263	0.100	0.211
CUPRESSACEAE			
Thuja occidentalis	0.008	0.049	0
CYPERACEAE			
Carex spp.	0.020	0.019	0.164
DRYOPTERIDACEAE			
Dryopteris spp.	0.021	0.209	0.072
ERICACEAE			
Chimaphila umbellata	0	0	0.006
Gaultheria hispidula	0	0.020	0.007
Galutheria procubens	0.026	0.029	0.013
Kalmia angustifolia	0	0	0.008
Orthilia secunda	0.026	0.020	0.006
Vaccinium corymbosum	0.007	0	0
Vaccinium spp.	0.080	0.034	0.175
FAGACEAE			
Fagus grandifolia	0	0.007	0
GROSSULARIACEAE			
Ribes spp.	0	0.007	0
LILIACEAE			
Clintonia borealis	0.122	0.101	0.020
Medeola virginiana	0.007	0	0
Streptopus lanceolatus	0	0	0.013
MELANTHIACEAE			
Trifolium aureum	0	0	0.006
Trillium erectum	0.026	0.006	0.013
MYRSINACEAE			
Lysimachia borealis	0.112	0.006	0.013
OLEACEAE			
Fraxinus americana	0	0	0.006
ONOCLEACEAE			
Onoclea sensibilis	0	0	0.023

Table B.1 continued

	Control	Blowdown	Salvage
ORCHIDACEAE			
Cypripedium acaule	0.006	0	0
Goodyera tesselata	0.007	0	0
OSMUNDACEAE			
Osmunda claytonia	0.016	0.007	0.007
OXALIDACEAE			
Oxalis montana	0.039	0	0
PLANTAGINACEAE			
Veronica officinalis	0	0	0.034
PINACEAE			
Abies balsamea	0.246	0.325	0.084
Pinus strobus	0.013	0.013	0.043
Picea rubens	0.280	0.146	0.146
RANUNCULACEAE			
Coptis trifolia	0.078	0.020	0.013
ROSACEAE			
Amelanchier spp.	0.014	0	0.013
Aronia floribunda	0	0	0.006
Fragaria virginiana	0	0.013	0.060
Prunus pensylvanica	0	0.048	0.106
Rubus pubescens	0.019	0.065	0.075
Rubus dalibarda	0.039	0.007	0
Rubus idaeus	0.015	0.055	0.305
Sorbus americana	0.020	0.024	0.013
RUSCACEAE			
Maianthemum canadense	0.319	0.092	0.097
SALICACEAE			
Populus grandidentata	0	0	0.007
Populus tremuloides	0	0.009	0
Salix spp.	0	0.006	0
Acer pensylvanicum	0.023	0	0
Acer rubrum	0.312	0.193	0.307
Acer saccharum	0.030	0.013	0.021
Acer spicatum	0.021	0.007	0
THELYPTERIDACEAE			
Parathelypteris noveboracensis	0.007	0.006	0.007
Phegopteris connectilis	0	0.028	0.020
VIOLACEAE			
Viola renifolia	0	0.009	0
WOODSIACEAE			
Gymnocarpium dryopteris	0	0	0.013

BIOGRAPHY OF THE AUTHOR

Colby, known by many as ‘The Captain’, was raised in Washington, DC where she first developed an interest in the outdoors and a concern for the environment during hikes in Rock Creek Park and weekend trips to the Chesapeake Bay. She graduated as Valedictorian from Capital City Public Charter School in 2016. Eager to live and learn closer to nature, she attended the University of Vermont where she graduated in 2020 with a Bachelor’s degree in Environmental Sciences and a minor in Forestry. Her interest in Forest Ecology and Silviculture was sparked during her time working as a field technician for Anthony D’Amato’s Silviculture and Applied Forest Ecology Lab. On one field trip she had the opportunity to work with Shawn Fraver who she later contacted about graduate assistantships. In 2021 she began her master’s assistantship as a Teaching Assistant for William Livingston’s Forest Vegetation course and a Research Assistant for Shawn Fraver. Following graduation, Colby will pursue a PhD in Forest Resources at the University of Maine advised by Shawn Fraver and Nicole Rogers. Colby is a candidate for the Master of Science degree in Forest Resources from the University of Maine in December 2023.