

RESEARCH ARTICLE

Understorey vegetation response to post-tornado salvage logging

Colby Bosley-Smith¹  | Anthony W. D'Amato² | Nicole S. Rogers¹ | Nava Tabak³ | Shawn Fraver¹

¹School of Forest Resources, University of Maine, Orono, Maine, USA

²Rubenstein School of the Environment and Natural Resources, University of Vermont, Burlington, Vermont, USA

³Baxter State Park, Millinocket, Maine, USA

Correspondence

Colby Bosley-Smith, School of Forest Resources, University of Maine, 5755 Nutting Hall, Orono, ME 04469, USA.
Email: colby.bosleysmith@maine.edu

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Abstract

Questions: How does salvage logging alter understorey vegetation composition? To what extent does abundance of recalcitrant understorey species influence conifer tree regeneration? How does salvage logging influence microclimate conditions?

Location: Scientific Forest Management Area, Baxter State Park, Maine, USA.

Methods: In 2013, a rare tornado and subsequent salvage operation created three clear “treatments” for evaluation of post-disturbance understorey community response: blowdown, blowdown followed by salvage logging and an undisturbed forested control. Ten years post tornado, we inventoried understorey vegetation at 10 sampling points within each of these treatments. We installed automated sensors to track temperature and soil moisture throughout a growing season and used hemispherical photographs to characterize canopy openness.

Results: Non-metric multidimensional scaling (NMDS) ordination based on species importance values indicated distinct species groupings according to treatment, with the salvage treatment supporting a higher abundance of the recalcitrant species, *Rubus idaeus* and *Pteridium aquilinum*. Abundance of conifer regeneration was notably lower in areas with high abundance of *Rubus idaeus* or *Pteridium aquilinum*. Daily soil surface temperature fluctuations and canopy openness (both factors that influence seed germination) decreased in the order salvage > blowdown > control. Ordination results suggest that these two factors were the primary drivers of the observed compositional differences.

Conclusions: This study furthers our understanding of the interactions among disturbance, microclimate, and understorey communities, highlighting the need for increased consideration of long-term effects on vegetation development following salvage logging. Our findings support recommendations to intermingle salvage patches within blowdown areas to promote landscape heterogeneity and species diversity.

KEYWORDS

compound disturbances, microclimate, *Pteridium*, recalcitrant species, *Rubus*, spruce–fir forest, wind disturbance

1 | INTRODUCTION

Tree regeneration success (i.e., establishment and recruitment of desired species) has recently grown more difficult to achieve as forests face compounding pressures from climate change, invasive species, forest pathogens, forest fragmentation and herbivory (Dey et al., 2019; Miller et al., 2023). In addition, natural disturbances such as windstorms, insect outbreaks, and fire limit 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 forest management gains additional relevance.

Salvage logging, a common management response following severe natural disturbances, remains controversial, as published literature is limited regarding its effect on tree regeneration and other ecosystem processes (Lindenmayer et al., 2008). Some 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; Bosley-Smith et al., 2024), impair microsite conditions for tree seedling survival (Marañón-Jiménez et al., 2013) and increase competition between seedlings and understorey vegetation (Jonášová & Prach, 2008; Palm et al., 2022). These differing conclusions reflect the fact that (1) forest types likely respond differently to salvage logging and (2) salvage operations may differ markedly from one situation to another. These considerations highlight the remaining knowledge gaps surrounding this issue.

The role of forest canopies in buffering environmental extremes, and hence maintaining understorey microclimates and plant communities, has recently gained much attention (De Frenne et al., 2021; Sanczuk et al., 2023). Although several studies have investigated the influence of salvage logging on microclimate conditions (Thorn et al., 2014; Marcolin et al., 2019), this topic remains relatively understudied given the importance of microclimate on tree regeneration (Campanello et al., 2007). Coarse woody material (CWM)—which is left in abundance after natural disturbances but removed by salvage logging—contributes to this buffering effect by providing shade and reducing the warming of soil surfaces, decreasing evaporation, and maintaining soil moisture (Devine & Harrington, 2007; Marañón-Jiménez et al., 2013; Goldin & Hutchinson, 2015). 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 unsalvaged sites, creating less favorable environments for seed germination of their study species.

Alterations to microclimate may also make conditions more favorable for the growth of recalcitrant understorey vegetation (Royo & Carson, 2006). For example, germination of some *Rubus* species is triggered by high daily temperature fluctuations (Marcuzzi & Demartinez, 1993; Suzuki, 1997; Donoso & Nyland, 2006). Similarly, *Pteridium aquilinum* (bracken fern) emergence is closely related to

high daily temperature fluctuations and increased light (Cody & Crompton, 1975; Engelman & Nyland, 2006). These native, shade-intolerant taxa (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 provided an ideal setting to investigate connections between salvage logging, microclimate conditions and understorey vegetation. In July 2013, a tornado struck the northeastern portion of Baxter State Park, Maine, USA, causing significant canopy loss in a swath of approximately 200 ha of mixed-species conifer forest (Fraver et al., 2017). Salvage logging took place in a portion of this area 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 adjacent undisturbed control. In this study, we compare these three treatments with respect to understorey vegetation and microclimate conditions.

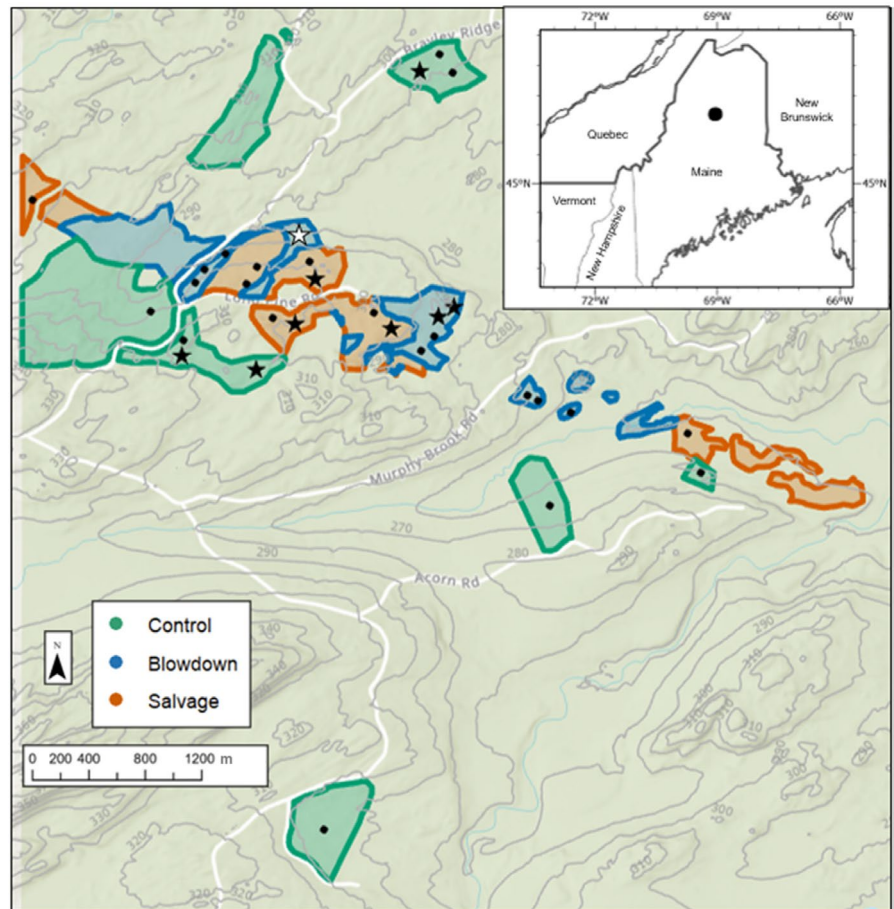
The goal of this study is to understand how salvage logging following severe wind disturbance alters understorey plant communities and microclimates. Our objectives were to explore (1) understorey community differences among undisturbed, blowdown and salvage conditions, (2) relationships between conifer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

2 | METHODS

2.1 | Field sampling

Our study was conducted within the Baxter State Park Scientific Forest Management Area (SFMA) of northcentral Maine, USA (Figure 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, 2014). 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 (i.e., stems

FIGURE 1 Treatment and sampling point locations within the Scientific Forest Management Area (SFMA), Baxter State Park, Maine, USA. Orange and blue polygons show the extent of tornado-damaged patches, stars indicate sampling point locations, dots indicate sampling points containing microclimate sensors (note that the white star indicates a microclimate sampling point that was removed from analysis). Sampled units color-coded by treatment: control, blowdown, and salvage (blowdown followed by salvage).



ha^{-1}) by 85%. Salvage logging in portions of the wind-damaged area began in the winter of 2013–2014 using a fixed-head cut-to-length processor and forwarder, with slash left on site (Fraver et al., 2017). During the salvage operation, accessible standing living trees that survived the tornado were also harvested.

Three treatments (blowdown, blowdown plus salvage, and undamaged control; Figure 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*) and lesser components of balsam fir (*Abies balsamea*), northern white-cedar (*Thuja occidentalis*), eastern white pine (*Pinus strobus*), red maple (*Acer rubrum*) and paper birch (*Betula papyrifera*) (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).

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 (Bosley-Smith et al., 2024). Fifteen sampling points per treatment were designated randomly in ArcGIS with occasional on-the-ground adjustments made to exclude the locations of recent

harvests (Bosley-Smith et al., 2024). In July and August of 2023, 30 of the original 45 sampling points (10 per treatment) were revisited to inventory understorey plant communities, including all sampling points that previously had sensors and seven additional randomly selected sampling points per treatment.

Within each of the 30 understorey vegetation sampling points, eight 1×1-m sampling frames (i.e., quadrats) were placed 2.5 and 5 m from point center in each cardinal direction. Percent cover of all vascular herbaceous plants and tree regeneration (stem diameter at breast height < 10 cm) were estimated to a whole number for all taxa rooted within each frame and covering more than 1% of the area. We acknowledge that some of the larger stems may have existed prior to the tornado; however, these larger stems (>7.5 and <10 cm) were uncommon, representing only 3.3% of all regeneration (Bosley-Smith et al., 2024). Percent cover of exposed rock and deadwood unsuitable for plant colonization was recorded in the field; during data processing the cover of plants in these frames was converted to percent cover of available substrate to account for this unsuitable area. Doing so allowed for equal comparisons of species' relative cover among sampling points and treatments. To avoid observer bias, the same observer estimated percent cover for each frame.

On 21 May 2022, three TMS-4 soil moisture and temperature sensors (TOMST®, Prague, Czech Republic) (Wild et al., 2019) were installed within three randomly selected sampling points per treatment. At each sampling point, one sensor was installed at point

center, and two were 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 programmed to record data every 15 minutes and were left to collect data through the growing season (May 22nd until October 22nd, 2022). The TMS-4 sensors have a resolution of 0.063°C and an accuracy of $\pm 0.5^\circ\text{C}$ (Wild et al., 2019).

Canopy openness was measured during the summer of 2023. Hemispherical photographs were taken at each of the 30 point 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 | Data analysis

To examine gradients in understorey community composition across treatments, sampling point-level importance values (mean of relative percent cover and relative frequency, eight quadrats pooled) were calculated for each species, and used as the response variable in the following analyses. Trends in understorey 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). A pairwise permutational multivariate analysis of variance (PERMANOVA) was used to test for differences among treatment groups with Sørensen's dissimilarity, including a Bonferroni adjustment for multiple comparisons, using the R package *RVAideMemoire* (Hervé, 2022). We used analysis of variance (ANOVA) followed by a Tukey honestly significant difference (HSD) test to test for treatment differences in *Rubus idaeus* and *Pteridium aquilinum* importance. Finally, species–area curves were constructed for each treatment using *vegan* (Oksanen et al., 2022).

To assess the potentially negative relationship between conifer regeneration (*Abies balsamea*, *Picea rubens*, *Pinus strobus*, *Thuja occidentalis*, pooled) and recalcitrant understorey species (*Rubus idaeus* and *Pteridium aquilinum*), we created a series of linear regression models based on importance values. In addition to the linear model, we tested two non-linear models (negative exponential and rational) and ultimately found that the differences in the root-mean-squared error among models were inconsequential; therefore, we chose the simplest (linear) model. Conifer species were lumped to obtain adequate sample size for analysis; they collectively represent the dominant overstorey species in the undisturbed control areas and consequently the most sought-after regeneration species in the SFMA. *Rubus idaeus* and *Pteridium aquilinum* were tested as predictor species for this analysis because of their association with disturbance conditions and abundance across the study area. The top 10 most common herbaceous species (based on species importance values) and the cumulative herbaceous importance (importance values for all species summed) were also tested individually

as predictors of conifer importance. Additional predictor variables modeled were canopy openness, sapling density and CWM volume. The Akaike information criterion (AIC) was used to compare all possible model combinations of these predictors using the R package *AICcmodavg* (Mazerolle, 2020). Predictor variables were tested for co-linearity, and those found to be colinear were evaluated in separate models. Models focusing on *Rubus idaeus* and *Pteridium aquilinum* were tested separately, and the top five models for each were ranked according to the lowest AIC score.

To understand environmental factors driving the ordination, another NMDS ordination was conducted using only the sampling points containing sensors. One blowdown sensor point was excluded from all analyses due to being an outlier in both understorey composition and microclimate characteristics. Nine variables were examined as potential drivers of the ordination in *vegan*: soil surface temperature, surface temperature fluctuation (both 2 cm above soil temperature probe), soil moisture (all from TMS-4 sensors), canopy openness, sapling abundance, CWM volume, slope, aspect, and elevation. We were particularly interested in daily surface temperature fluctuation (difference between daily maximum and minimum temperature) because several disturbance-dependent species in this region, such as *Rubus* spp. and *Prunus pensylvanica*, respond to such fluctuations as a cue for germination post disturbance (Laidlaw, 1987; Suzuki, 1997). Surface temperature time series from each of the three TMS-4 sensors at a sampling point were averaged to generate one time series for each sampling point. Additional microclimate variables from the TMS-4 sensors (soil temperature, air temperature and associated fluctuations) were not included in the analyses, as these variables were highly correlated with surface temperature data. Potential treatment differences for canopy openness were evaluated using separate ANOVAs in R (R Core Team, 2021), and the relationship between canopy openness and surface temperature fluctuations was tested by linear regression. Differences in surface temperature fluctuations across treatments were evaluated using a slope test of each cumulative time series (each daily surface temperature fluctuation averaged by treatment summed with each prior day to generate a positive linear regression over time) with the R package *smatr* (Warton et al., 2012) and a Bonferroni adjustment for multiple comparisons. Significantly different slopes for each treatment would indicate consistent treatment differences in surface temperature fluctuation across the season.

We acknowledge that the structure of the regressions and ANOVA explained above suggests a mixed-model approach, with stand (a distinct polygon in Figure 1) as a random effect. However, eight (of 15) stands contain just one sampling point. Such “singleton” clusters are acceptable in mixed-effects models, but only in studies with many clusters (>500; Bell et al., 2008). Statistical power rapidly decreases as the number of samples per cluster and/or the number of clusters decreases (Austin & Leckie, 2018). As an alternative to mixed-effects models, we used ANOVA to evaluate the independence of sampling points, testing influence of stand on each of the modeled variables (*Rubus idaeus* importance, *Pteridium aquilinum* importance, conifer importance and canopy openness) within

each treatment. A finding of greater between-stand variability than within-stand variability would indicate the lack of independence of sampling points within stands.

3 | RESULTS

We found 68 vascular plant taxa representing 32 families across all treatments (Appendix S1). 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 2a). These results are 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 2b). A large proportion of taxa ($N=26$, or 38% of total) were shared among treatments (Figure 2a). The salvage treatment had the largest number of unique taxa ($N=15$). Two non-native species (*Hieracium caespitosum* and *Veronica officinalis*) were encountered in low abundance in the salvage treatment.

Non-metric multidimensional scaling ordination based on species importance values indicated distinct species groupings according to treatment (Figure 3). Pairwise treatment comparisons in PERMANOVA showed compositional differences between each treatment ($p < 0.001$ for all comparisons). The salvage treatment had significantly higher *Rubus idaeus* importance values than the other treatments and had higher *Pteridium aquilinum* importance compared to the blowdown treatment ($p < 0.05$). Overall, the ordination revealed greater point-to-point variation in composition (i.e., greater spread of sampling points in ordination space) within both disturbed treatments as compared with the control (Figure 3).

Rubus idaeus and *Pteridium aquilinum* alone were the best predictors of conifer regeneration importance based on AIC model rankings (Table 1). These models indicated a significant negative relationship between conifer importance and both *Rubus idaeus* and *Pteridium*

aquilinum importance values (Figure 4), with the *Rubus idaeus* model displaying a slightly better fit ($R^2=0.25$ vs 0.22, Figure 4). We note that both *Rubus idaeus* and *Pteridium aquilinum* were only present in ca. 50% of the sampling points, which reduces predictive ability (conifers were present at all sampling points). Both *Rubus idaeus* and *Pteridium aquilinum* were also associated with greater canopy openness and the salvage treatment (Figure 3). *Rubus idaeus* was present in 90% of salvaged points, while *Pteridium aquilinum* was present in 60% of salvaged points. The 10 species with the highest importance values were also modeled against conifer importance; however, none showed a significant negative relationship ($p < 0.05$). Further, no significant relationship was found between total (i.e., pooled) non-conifer importance and conifer importance.

Two environmental variables were identified as significant predictors of the ordination results: surface temperature fluctuation (from 2 cm above soil temperature probe) and canopy openness (Table 2). Both variables were positively correlated with each other and the salvage treatment (Figure 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 5b), $p=0.002$ (control vs blowdown), $p < 0.001$ (salvage vs control and blowdown). Similarly, slope test analysis of temperature fluctuation for each cumulative time series suggests that daily temperature fluctuations also differed significantly among treatments, following the same pattern (salvage > blowdown > control, Figure 5a, $p < 0.001$).

Results from the ANOVAs aimed at evaluating point-point dependence revealed a general lack of dependence within stands. However, one stand (the salvaged stand with two non-sensor sampling points, Figure 1) had greater between- than within-stand variability for *Rubus idaeus* and for conifer importance (tested at $p < 0.05$) when compared to the other salvage stands. This stand was notably not distinct when tested against *Pteridium aquilinum*

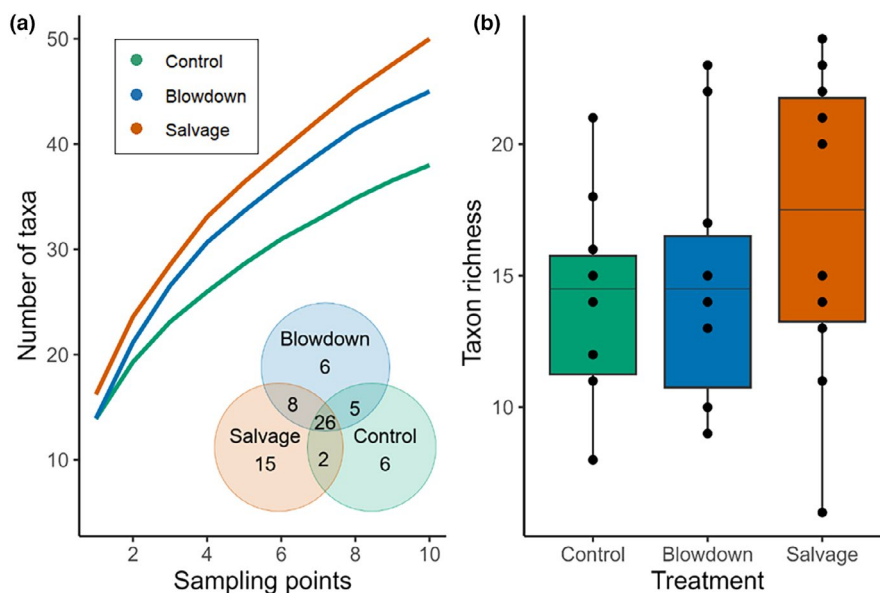


FIGURE 2 (a) Species–area curves for each treatment (Salvage = blowdown followed by salvage). Sampling points represent pooled data from eight 1×1 -m quadrats (per point), such that 10 points = 80 m^2 . Insert: Venn diagram displaying the number of unique and shared taxa within each treatment. (b) Taxon richness by treatment; each dot represents one sampling point, i.e., 8 m^2 . Horizontal lines within box plots represent medians and upper and lower quartiles.

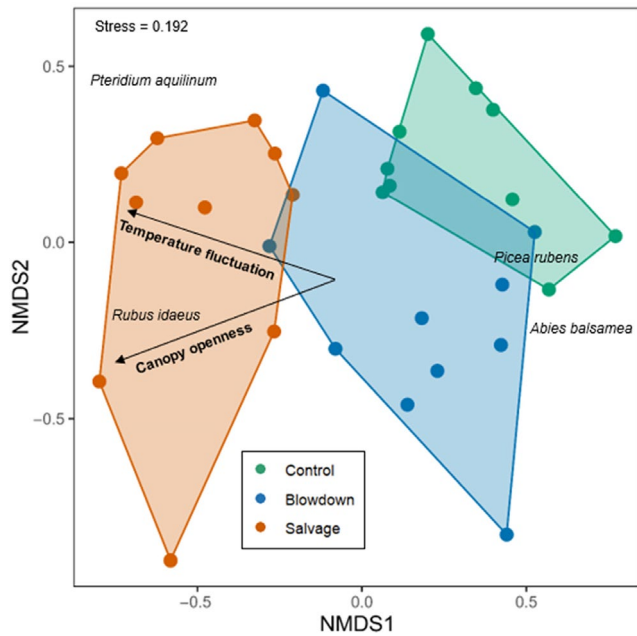


FIGURE 3 Non-metric multidimensional scaling (NMDS) ordination results based on understorey taxa importance values, outlined by treatment: Control, blowdown, and salvage (blowdown followed by salvage). The location of the recalcitrant species *Rubus idaeus* and *Pteridium aquilinum* along with the two most common conifer tree species, *Abies balsamea* and *Picea rubens* plotted along the ordination axes. Vectors indicate associations between significant environmental variable predictors and ordination axes.

TABLE 1 Results from two analyses, each showing the top five models for predicting conifer regeneration importance.

Model predictors	k	AICc	Δ AICc	AICc wt.	R^2
<i>Rubus</i>	3	-24.45	0.00	0.48	0.25
<i>Rubus</i> + CWM _{VOL}	4	-22.44	2.01	0.18	0.24
<i>Rubus</i> + Sap. Dens.	4	-21.86	2.59	0.13	0.23
Openness	3	-21.37	3.08	0.10	0.17
Sapl. Dens. + Openness	4	-19.84	4.61	0.05	0.17
<i>Pteridium</i>	3	-23.28	0.00	0.26	0.22
<i>Pteridium</i> + Openness	4	-23.06	0.22	0.24	0.26
Openness	3	-21.37	1.91	0.10	0.17
<i>Pteridium</i> + Sap. Dens.	4	-20.75	2.53	0.07	0.20
<i>Pteridium</i> + CWD _{VOL}	4	-20.66	2.62	0.07	0.19

Note: Models ranked according to AICc scores using the variables *Rubus* (*R. idaeus* importance, upper portion of table), *Pteridium* (*P. aquilinum* importance, lower portion), CWM_{VOL} (coarse woody material volume), Sap. Dens. (sapling density) and Openness (% canopy openness).

Abbreviations: AICc wt., corrected Akaike information criterion weights; AICc, corrected Akaike information criterion; k, number of model parameters; R^2 , adjusted R^2 of the linear model; Δ AICc, change in Akaike information criterion relative to the top model.

and canopy openness (i.e., no suggestion of point-point dependence). No other stands were deemed distinct when evaluated as such.

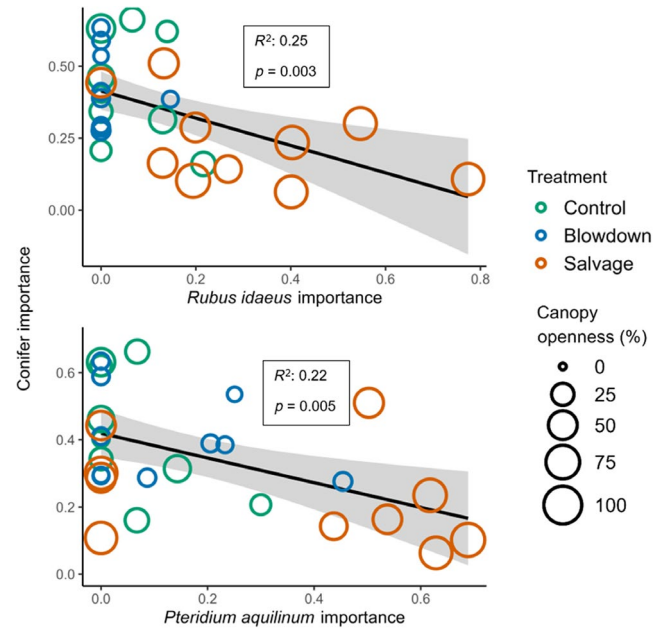


FIGURE 4 Conifer regeneration importance plotted against *Rubus idaeus* and *Pteridium aquilinum* importance, including linear regression line with shaded 95% confidence interval. Points color-coded by treatment: control, blowdown, and salvage (blowdown + salvage) and scaled according to canopy openness from hemispherical photos.

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 understorey vegetation following salvage logging 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 reduced conifer regeneration was related to increased *Rubus idaeus* and *Pteridium aquilinum* abundance, two species favored by salvage-logging disturbance, suggesting that these disturbance-adapted species may play a role in inhibiting conifer establishment in post-salvage environments.

Observed compositional differences among treatments generally align with the findings of previous studies. Several studies report 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, likely due to a greater abundance of shade-intolerant taxa, similar to findings reported by Lang et al. (2009) and Slyder et al. (2020). This relationship between salvage logging and greater abundance of shade-intolerant species is well established (Elliott et al., 2002; Palik & Kastendick, 2009; D'Amato et al., 2011; Georgiev et al., 2022); however, no studies (to our knowledge) have explored the relationship between recalcitrant species and salvage logging. Furthermore, several studies report increases in non-native

TABLE 2 Environmental predictor variables assessed for the NMDS ordination, sorted from lowest to highest p -value.

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

Note: Association with the two ordination axes, R^2 and p -value displayed. Significant predictors ($p < 0.05$) are indicated with asterisk.

Abbreviations: CWM, coarse woody material; NMDS, non-metric multidimensional scaling.

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 precluded a robust analysis.

One critical finding from this study is the relationship between conifer regeneration importance and the importance of recalcitrant understorey species. Specifically, we found sampling points with lower conifer regeneration abundance (assessed by importance values) were associated with greater *Rubus idaeus* and *Pteridium aquilinum* importance, and that these species alone were better predictors of conifer abundance than candidate models including additional site conditions. Notably, the importance of other common herbaceous species, whether tested individually or in sum, were not associated with lower conifer 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. 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 for hardwood species; instead, we found reduced conifer importance at sampling points containing *Rubus idaeus*, suggesting that conifer regeneration may still be inhibited by *Rubus* nine years post disturbance. The slower growth of *Picea rubens* and *Abies balsamea*, (Seymour, 1992) our dominant conifer species, may make them more vulnerable to suppression by *Rubus* compared to the northern hardwoods. Further, the salvage treatment may have created conditions more favorable for *Rubus* growth (i.e., removal of advance regeneration) compared to environmental conditions in the Donoso and Nyland (2006) study. While few studies have explored the competitive effect of *Rubus* on conifer growth, an earlier study in northern Maine found that *Abies balsamea* seedlings that were 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* on *Abies balsamea* can persist for 25 years.

Pteridium aquilinum is known to inhibit tree regeneration and seedling growth across its range (e.g., Dolling, 1996; Humphrey & Swaine, 1997; Hartig & Beck, 2003). It primarily reproduces vegetatively, allowing it to rapidly colonize disturbed areas (Cody & Crompton, 1975). Working within our region, George and Bazzaz (1999) found that *Pteridium aquilinum* litter creates an impenetrable barrier preventing germinating seeds from reaching the soil beneath and restricting emergence for seeds germinating below the litter layer. These authors also report that the presence of *Pteridium aquilinum* reduces light levels necessary for the emergence of tree seedlings. Additionally, *Pteridium aquilinum* contains allelopathic chemicals that reduce the growth of *Populus* spp. and *Prunus serotina* seedlings (Horsley, 1977; Dolling, 1996; Engelman & Nyland, 2006).

The primary environmental drivers of the understorey 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 the germination of *Rubus* species and *Pteridium aquilinum* benefits from both daily temperature fluctuations and high light levels (Cody & Crompton, 1975; Suzuki, 1997; Engelman & Nyland, 2006). Importantly, these factors were associated with our treatments, as salvage conditions displayed the highest average surface temperature fluctuations and the greatest canopy openness (Figure 5), a finding also reported by Marcolin et al. (2019). The reduced canopy openness in blowdown (relative to salvage) may be due to (1) shading by deadwood that was stacked or hung up above the ground (Palik & Kastendick, 2009) and (2) the remaining undisturbed advance regeneration, which was less abundant in the salvage areas because of additional disturbance from this harvest. Interestingly, soil moisture, a factor often correlated with CWM abundance (Devine & Harrington, 2007; Harrington et al., 2013; Goldin & Brookhouse, 2015) was not identified as a significant driver of plant community composition. Finally, we acknowledge that these microclimate results should be viewed with caution, given the small number of sensors deployed.

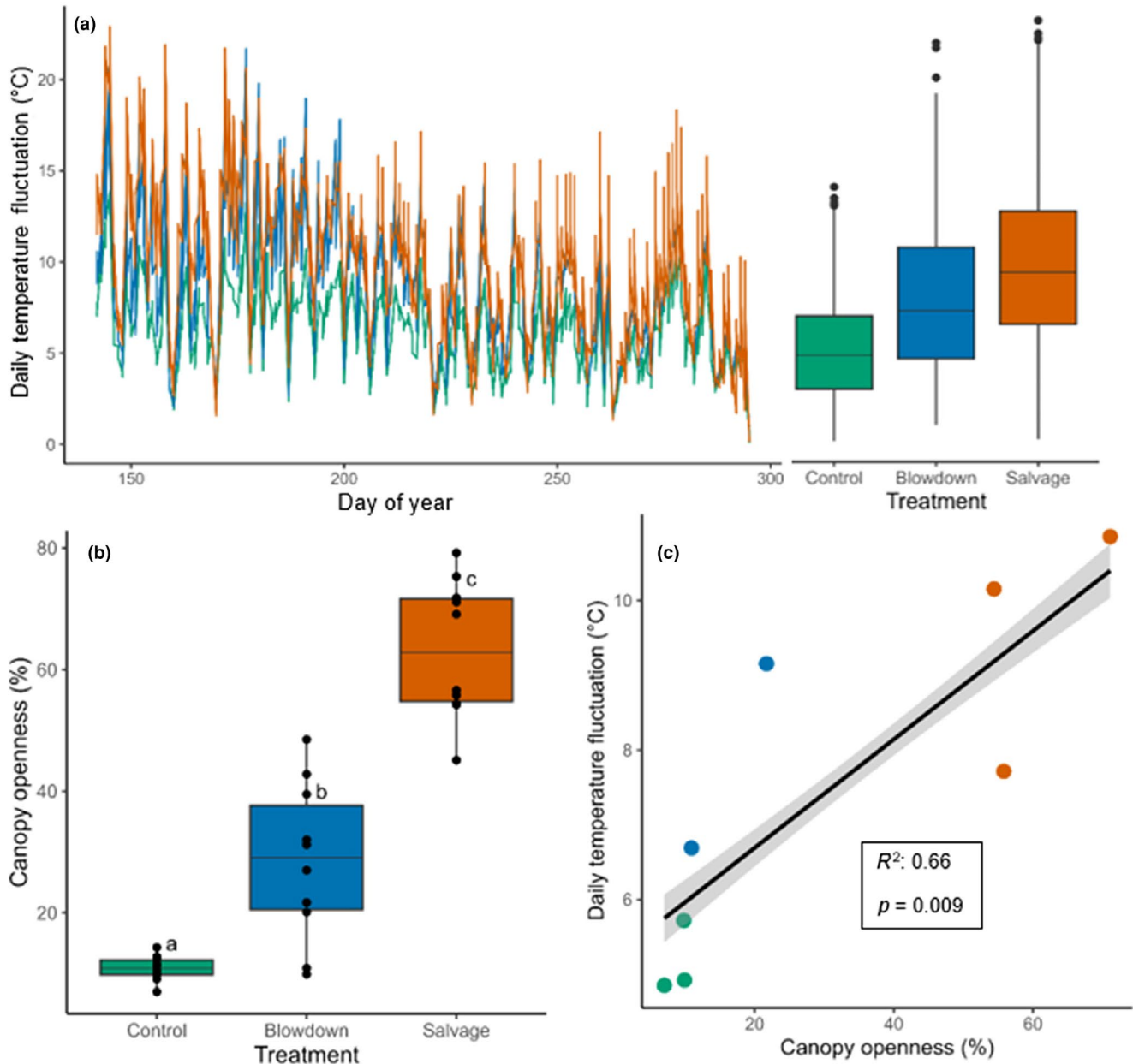


FIGURE 5 (a) Daily temperature fluctuation (difference between daily maximum and minimum temperature at each sampling points averaged by treatment) throughout the 2022 growing season, color-coded and summarized by treatment. (b) Canopy openness by treatment. Different lower-case letters indicate significant treatment differences at $\alpha < 0.05$. (c) Daily temperature fluctuation (averaged across the season) versus 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. Horizontal lines within box plots represent medians and upper and lower quartiles.

5 | CONCLUSIONS

As with other salvage-logging studies, management recommendations must be context- and priority-oriented. The greater taxonomic richness sometimes 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 et al., 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, delays in tree regeneration. These potential consequences of

salvage must be weighed against the benefits associated with greater canopy openness. Several studies recommend a middle ground, that is, intermingling patches of blowdown within salvaged areas (as was done by SFMA managers) to promote landscape heterogeneity and species diversity (Kleinman et al., 2017; Georgiev et al., 2022). Our findings support this recommendation, although we caution that management decisions should be site- and objective-specific.

These results are an important first step in understanding the mechanistic links among understory communities, environmental conditions, and salvage logging. 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 importance of conifer regeneration was related to increased importance of *Rubus idaeus* and *Pteridium aquilinum*. Our cursory identification 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.

AUTHOR CONTRIBUTIONS

C.B.-S. and S.F. conceived the ideas and designed methodology; C.B.-S., S.F., and N.T. collected the data; C.B.-S. and S.F. analyzed the data; C.B.-S. and S.F. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare to have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.w0vt4b90z> (Bosley-Smith et al., 2024).

ORCID

Colby Bosley-Smith  <https://orcid.org/0000-0002-4185-1333>

REFERENCES

Austin, P.C. & Leckie, G. (2018) The effect of number of clusters and cluster size on statistical power and type I error rates when testing

random effects variance components in multilevel linear and logistic regression models. *Journal of Statistical Computation and Simulation*, 88(16), 3151–3163. Available from: <https://doi.org/10.1080/0094655.2018.1504945>

- Bell, B.A., Ferron, J.M. & Kromrey, J.D. (2008) Cluster size in multilevel models: the impact of sparse data structures on point and interval estimates in two-level models. In: *Proceedings of the survey research methods section*. Alexandria, VA: American Statistical Association 2010.
- Bosley-Smith, C., D'Amato, A.W., Rogers, N.S., Tabak, N. & Fraver, S. (2024) Understorey vegetation response to post-tornado salvage logging. *Dryad*. <https://doi.org/10.5061/dryad.w0vt4b90z>
- Bosley-Smith, C., Fraver, S., D'Amato, A.W., Rogers, N.S., Tabak, N. & Wason, J. (2024) The natural 'exclusion effect' and tree regeneration following post-windstorm salvage logging. *Journal of Applied Ecology*, 61, 260–270. Available from: <https://doi.org/10.1111/1365-2664.14560>
- Campanello, P.I., Gatti, M.G., Ares, A., Montti, L. & Goldstein, G. (2007) Tree regeneration and microclimate in a liana and bamboo-dominated semideciduous Atlantic Forest. *Forest Ecology and Management*, 252(1–3), 108–117. Available from: <https://doi.org/10.1016/j.foreco.2007.06.032>
- Cody, W.J. & Crompton, C.W. (1975) The biology of Canadian weeds: 15. *Pteridium aquilinum* (L.) Kuhn. *Canadian Journal of Plant Science*, 55(4), 1059–1072. Available from: <https://doi.org/10.4141/cjps75-165>
- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D. et al. (2001) Climate change and Forest disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *Bioscience*, 51(9), 723–734. Available from: [https://doi.org/10.1641/0006-3568\(2001\)051\[0723:CCAFD\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2)
- D'Amato, A.W., Fraver, S., Palik, B.J., Bradford, J.B. & Patty, L. (2011) Singular and interactive effects of blowdown, salvage logging, and wildfire in sub-boreal pine systems. *Forest Ecology and Management*, 262(11), 2070–2078. Available from: <https://doi.org/10.1016/j.foreco.2011.09.003>
- De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J. et al. (2021) Forest microclimates and climate change: importance, drivers and future research agenda. *Global Change Biology*, 27(11), 2279–2297. Available from: <https://doi.org/10.1111/gcb.15569>
- Devine, W.D. & Harrington, C.A. (2007) Influence of harvest residues and vegetation on microsite soil and air temperatures in a young conifer plantation. *Agricultural and Forest Meteorology*, 145(1–2), 125–138. Available from: <https://doi.org/10.1016/j.agrformet.2007.04.009>
- Dey, D.C., Knapp, B.O., Battaglia, M.A., Deal, R.L., Hart, J.L., O'Hara, K.L. et al. (2019) Barriers to natural regeneration in temperate forests across the USA. *New Forests*, 50, 11–40. Available from: <https://doi.org/10.1007/s11056-018-09694-6>
- Dolling, A. (1996) Changes in *Pteridium aquilinum* growth and photo-toxicity following treatments with lime, sulphuric acid, wood ash, glyphosate and ammonium nitrate. *Weed Research*, 36(4), 293–301. Available from: <https://doi.org/10.1111/j.1365-3180.1996.tb01659.x>
- Donoso, P.J. & Nyland, R.D. (2006) Interference to hardwood regeneration in northeastern North America: the effects of raspberries (*Rubus* spp.) following clearcutting and shelterwood methods. *Northern Journal of Applied Forestry*, 23(4), 288–296. Available from: <https://doi.org/10.1093/njaf/23.4.288>
- Elliott, K.J., Hitchcock, S.L. & Krueger, L. (2002) Vegetation response to large scale disturbance in a southern Appalachian Forest: hurricane opal and salvage logging. *Journal of the Torrey Botanical*

- Society, 129(1), 48. Available from: <https://doi.org/10.2307/3088682>
- Engelman, H.M. & Nyland, R.D. (2006) Interference to hardwood regeneration in northeastern North America: assessing and countering ferns in northern hardwood forests. *Northern Journal of Applied Forestry*, 23(3), 166–175. Available from: <https://doi.org/10.1093/njaf/23.3.166>
- Fox, T.R. (1986) Raspberry (*Rubus idaeus* L.) competition effects on balsam fir (*Abies balsamea* (L.) mill.) seedlings in northern Maine. *Tree Planter's Notes*, 37(2), 3120.
- Fraver, S., Dodds, K.J., Kenefic, L.S., Morrill, R., Seymour, R.S. & Sypitkowski, E. (2017) Forest structure following tornado damage and salvage logging in northern Maine, USA. *Canadian Journal of Forest Research*, 47(4), 560–564. Available from: <https://doi.org/10.1139/cjfr-2016-0395>
- Frazer, G.W., Canham, C.D. & Lertzman, K.P. (1999) Gap light Analyzer (GLA), version 2.0. User's Manual and Program Documentation 36.
- George, L.O. & Bazzaz, F.A. (1999) The Fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. *Ecology*, 80(3), 833–845. Available from: [https://doi.org/10.1890/0012-9658\(1999\)080\[0833:TFUAAE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[0833:TFUAAE]2.0.CO;2)
- Georgiev, K.B., Bässler, C., Feldhaar, H., Heibl, C., Karasch, P., Müller, J. et al. (2022) Windthrow and salvage logging alter β -diversity of multiple species groups in a mountain spruce forest. *Forest Ecology and Management*, 520, 120401. Available from: <https://doi.org/10.1016/j.foreco.2022.120401>
- Goldin, S.R. & Brookhouse, M.T. (2015) Effects of coarse woody debris on understory plants in a temperate Australian woodland. *Applied Vegetation Science*, 18(1), 134–142. Available from: <https://doi.org/10.1111/avsc.12120>
- Goldin, S.R. & Hutchinson, M.F. (2015) Thermal refugia in cleared temperate Australian woodlands: coarse woody debris moderate extreme surface soil temperatures. *Agricultural and Forest Meteorology*, 214–215, 39–47. Available from: <https://doi.org/10.1016/j.agrformet.2015.07.011>
- Hagge, J., Müller, J., Bässler, C., Biebl, S.S., Brandl, R., Drexler, M. et al. (2019) Deadwood retention in forests lowers short-term browsing pressure on silver fir saplings by overabundant deer. *Forest Ecology and Management*, 451, 117531. Available from: <https://doi.org/10.1016/j.foreco.2019.117531>
- Harrington, T.B., Slesak, R.A. & Schoenholtz, S.H. (2013) Variation in logging debris cover influences competitor abundance, resource availability, and early growth of planted Douglas-fir. *Forest Ecology and Management*, 296, 41–52. Available from: <https://doi.org/10.1016/j.foreco.2013.01.033>
- Hart, S.A. & Chen, H.Y.H. (2006) Understory vegetation dynamics of north American boreal forests. *Critical Reviews in Plant Sciences*, 25(4), 381–397. Available from: <https://doi.org/10.1080/07352680600819286>
- Hartig, K. & Beck, E. (2003) The bracken fern (*Pteridium arachnoideum* (Kaulf.) Maxon) dilemma in the Andes of southern Ecuador. *Ecotropica*, 9, 3–13.
- Hervé, M. (2022) RVAideMemoire: testing and plotting procedures for biostatistics. R package version 0.9-81-2. <https://CRAN.R-project.org/package=RVAideMemoire>
- Horsley, S.B. (1977) Allelopathic inhibition of black cherry by fern, grass, goldenrod, and aster. *Canadian Journal of Forest Research*, 7(2), 205–216. Available from: <https://doi.org/10.1139/x77-030>
- Humphrey, J.W. & Swaine, M.D. (1997) Factors affecting the natural regeneration of *Quercus* in Scottish oakwoods. I. Competition from *Pteridium aquilinum*. *Journal of Applied Ecology*, 34(3), 577–584. Available from: <https://doi.org/10.2307/2404908>
- Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E. et al. (2016) Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, 14(7), 369–378. Available from: <https://doi.org/10.1002/fee.1311>
- Jonášová, M. & Prach, K. (2008) The influence of bark beetles outbreak vs. salvage logging on ground layer vegetation in central European mountain spruce forests. *Biological Conservation*, 141(6), 1525–1535. Available from: <https://doi.org/10.1016/j.biocon.2008.03.013>
- Kleinman, J.S., Ford, S.A. & Hart, J.L. (2017) Catastrophic wind and salvage harvesting effects on woodland plants. *Forest Ecology and Management*, 403, 112–125. Available from: <https://doi.org/10.1016/j.foreco.2017.08.006>
- Konôpka, B., Šebeň, V. & Merganičová, K. (2021) Forest regeneration patterns differ considerably between sites with and without Windthrow wood logging in the high Tatra Mountains. *Forests*, 12, 1349. Available from: <https://doi.org/10.3390/f12101349>
- Laidlaw, T.F. (1987) Drastic temperature fluctuation: the key to efficient germination of pin cherry. *Tree Planter's Notes*, 38(3), 5210.
- Lang, K.D., Schulte, L.A. & Guntenspergen, G.R. (2009) Windthrow and salvage logging in an old-growth hemlock-northern hardwoods forest. *Forest Ecology and Management*, 259(1), 56–64. Available from: <https://doi.org/10.1016/j.foreco.2009.09.042>
- Leinonen, K., Nygren, M. & Rita, H. (1993) Temperature control of germination in the seeds of *Picea abies*. *Scandinavian Journal of Forest Research*, 8(1–4), 107–117. Available from: <https://doi.org/10.1080/02827589309382759>
- Lindenmayer, D.B., Burton, P.J. & Franklin, J.F. (2008) *Salvage logging and its ecological consequences*, 1st edition. Washington, DC: Island Press.
- Marañón-Jiménez, S., Castro, J., Querejeta, J.I., Fernández-Ondoño, E. & Allen, C.D. (2013) Post-fire wood management alters water stress, growth, and performance of pine regeneration in a Mediterranean ecosystem. *Forest Ecology and Management*, 308, 231–239. Available from: <https://doi.org/10.1016/j.foreco.2013.07.009>
- Marcolin, E., Marzano, R., Vitali, A., Garbarino, M. & Lingua, E. (2019) Post-fire management impact on natural forest regeneration through altered microsite conditions. *Forests*, 10(11), 11014. Available from: <https://doi.org/10.3390/f10111014>
- Marcuzzi, M. & Demartinez, E. (1993) Study on dormancy of raspberry seeds (*Rubus-idaeus* L.). *Phyton-International Journal of Experimental Botany*, 54(2), 139–147.
- Mazerolle, M.J. (2020) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R Package Version 2.3-1. <https://cran.r-project.org/package=AICcmodavg>
- Michalová, Z., Morrissey, R.C., Wohlgemuth, T., Bače, R., Fleischer, P. & Svoboda, M. (2017) Salvage-logging after windstorm leads to structural and functional homogenization of understory layer and delayed spruce tree recovery in Tatra Mts., Slovakia. *Forests*, 8(3), 88. Available from: <https://doi.org/10.3390/f8030088>
- Miller, K.M., Perles, S.J., Schmit, J.P., Matthews, E.R., Weed, A.S., Comiskey, J.A. et al. (2023) Overabundant deer and invasive plants drive widespread regeneration debt in eastern United States national parks. *Ecological Applications*, 33(4), e2837. Available from: <https://doi.org/10.1002/eap.2837>
- Morimoto, J., Sugiura, M., Morimoto, M. & Nakamura, F. (2021) Restoration of natural forests after severe wind disturbance in a cold, snowy region with a deer population: implications from 15 years of field experiments. *Frontiers in Forests and Global Change*, 4, 675475.
- Nelson, J.L., Groninger, J.W., Battaglia, L.L. & Ruffner, C.M. (2008) Bottomland hardwood forest recovery following tornado disturbance and salvage logging. *Forest Ecology and Management*, 256(3), 388–395. Available from: <https://doi.org/10.1016/j.foreco.2008.04.035>
- Oksanen, F.J., Simpson, G.L., Blanchet, F.G. & Kindt, R. (2022) Vegan: community ecology package. R Package Version 2.4-3. <https://CRAN.R-project.org/package=vegan>
- Palik, B. & Kastendick, D. (2009) Woody plant regeneration after blow-down, salvage logging, and prescribed fire in a northern Minnesota

- forest. *Forest Ecology and Management*, 258(7), 1323–1330. Available from: <https://doi.org/10.1016/j.foreco.2009.06.034>
- Palm, K., Vodde, F., Tullus, T., Engelhart, J. & Jögiste, K. (2022) Impact of different storm severity levels and post-storm management on understory vegetation richness, diversity, and composition 19–20 years after wind disturbance. *Forest Ecology and Management*, 524, 120506. Available from: <https://doi.org/10.1016/j.foreco.2022.120506>
- PRISM Climate Group. (2014) Oregon State University. <https://prism.oregonstate.edu>. Accessed 16 Dec 2022.
- R Core Team. (2021) *R: a language and environment for statistical computing*. Vienna, Austria: R foundation for 504 statistical computing.
- Royo, A.A. & Carson, W.P. (2006) On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research*, 36(6), 1345–1362. Available from: <https://doi.org/10.1139/x06-025>
- Royo, A.A., Peterson, C.J., Stanovick, J.S. & Carson, W.P. (2016) Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence? *Ecology*, 97(6), 1566–1582. Available from: <https://doi.org/10.1890/15-1093.1>
- Ruel, J.-C. (1992) Impact de la compétition exercée par le framboisier (*Rubusidaeus* L.) et les feuillus de lumière sur la croissance du sapin (*Abiesbalsamea* (L.) Mill.) en régénération. *Canadian Journal of Forest Research*, 22(9), 1408–1416. Available from: <https://doi.org/10.1139/x92-187>
- Rumbaitis del Rio, C.M. (2006) Changes in understory composition following catastrophic windthrow and salvage logging in a subalpine forest ecosystem. *Canadian Journal of Forest Research*, 36(11), 2943–2954. Available from: <https://doi.org/10.1139/x06-169>
- Sanczuk, P., De Pauw, K., De Lombaerde, E., Luoto, M., Meeussen, C., Govaert, S. et al. (2023) Microclimate and forest density drive plant population dynamics under climate change. *Nature Climate Change*, 13(8), 840–847. Available from: <https://doi.org/10.1038/s41558-023-01744-y>
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G. et al. (2017) Forest disturbances under climate change. *Nature Climate Change*, 7(6), 395–402. Available from: <https://doi.org/10.1038/nclimate3303>
- 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*. Dordrecht, The Netherlands: Springer, pp. 217–244.
- Slyder, J.B., Wenzel, J.W., Royo, A.A., Spicer, M.E. & Carson, W.P. (2020) Post-windthrow salvage logging increases seedling and understory diversity with little impact on composition immediately after logging. *New Forests*, 51(3), 409–420. Available from: <https://doi.org/10.1007/s11056-019-09740-x>
- Suzuki, W. (1997) Germination responses of *Rubus palmatus* var. *Coptophyllus* and *Rubus parvifolius* seeds with different burial durations to a variable light and temperature regime. *Ecological Research*, 12(2), 167–174. Available from: <https://doi.org/10.1007/BF02523782>
- Thorn, S., Bässler, C., Gottschalk, T., Hothorn, T., Bussler, H., Raffa, K. et al. (2014) New insights into the consequences of post-windthrow salvage logging revealed by functional structure of saproxylic beetles assemblages. *PLoS One*, 9(7), e101757. Available from: <https://doi.org/10.1371/journal.pone.0101757>
- USDA, NRCS. (2024) *The PLANTS database*. Greensboro, NC: National Plant Data Team.
- Warton, D.I., Duursma, R.A., Falster, D.S. & Taskinen, S. (2012) Smatr 3 – an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution*, 3, 257–259.
- Whitcomb, H.R. & Friends of Baxter State Park. (2008) Governor baxter's magnificent obsession: a documentary history of baxter state park 1931–2006. Governor Percival Proctor Baxter Documents.
- Wild, J., Kopecký, M., Macek, M., Šanda, M., Jankovec, J. & Haase, T. (2019) Climate at ecologically relevant scales: a new temperature and soil moisture logger for long-term microclimate measurement. *Agricultural and Forest Meteorology*, 268, 40–47.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Importance values for all understorey taxa by treatment: control, blowdown, and salvage (blowdown followed by salvage) (USDA, NRCS, 2024).

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