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RESEARCH ARTICLE

The natural 'exclosure effect' and tree regeneration following post-windstorm salvage logging

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Abstract

1. Understanding the influence of post-disturbance forest management 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'.
2. In 2013, a tornado in northcentral Maine, United States 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. We also inventoried CWM, including the height above forest floor.
3. 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.
4. *Synthesis and applications*. This study furthers our understanding of ecosystem recovery following blowdown and salvage logging. Results suggest that salvage logging created important differences in coarse woody material (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. Thus, in post-disturbance areas where browsing threatens regeneration, we recommend that managers consider retaining CWM to serve as a natural exclosure.

KEYWORDS
Alces, compound disturbances, salvage harvesting, spruce-fir forest, ungulate browse, wind disturbance, woody debris, woody material

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; Johnstone et al., 2016; Seidl et al., 2017; Turner, 2010). Given that disturbances strongly influence forest structure, processes and species composition, changes in natural disturbance regimes can have profound and lasting impacts (Seidl et al., 2017; Turner, 2010). 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). Although 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 (Kleinman et al., 2017; Leverkus et al., 2014), eliminate the aerial seedbanks of serotinous species (Greene et al., 2006) and slow post-disturbance recovery (Li et al., 2023; Taeroe et al., 2019). These negative aspects of salvage logging are often centred 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 labour 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 Hagge et al., 2019; Konôpka et al., 2021; Morimoto et al., 2021).

Several studies have demonstrated that the effects of salvage logging can persist as long as 50 to 70+ years post-harvest (Mabry & Korsgren, 1998; Morimoto et al., 2019; Sass et al., 2018); 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). Furthermore, 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 3 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, United States, 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 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.

2 | MATERIALS AND METHODS

2.1 | Field sampling

Our study was conducted within the Baxter State Park Scientific Forest Management Area (SFMA) of northcentral Maine, United States (Figure 1; permission granted by the Baxter State Park Research Committee). Established in 1955, this 12,000 ha tract is maintained to demonstrate sustainable forest management practices (Whitcomb & Friends of Baxter State Park, 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) 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

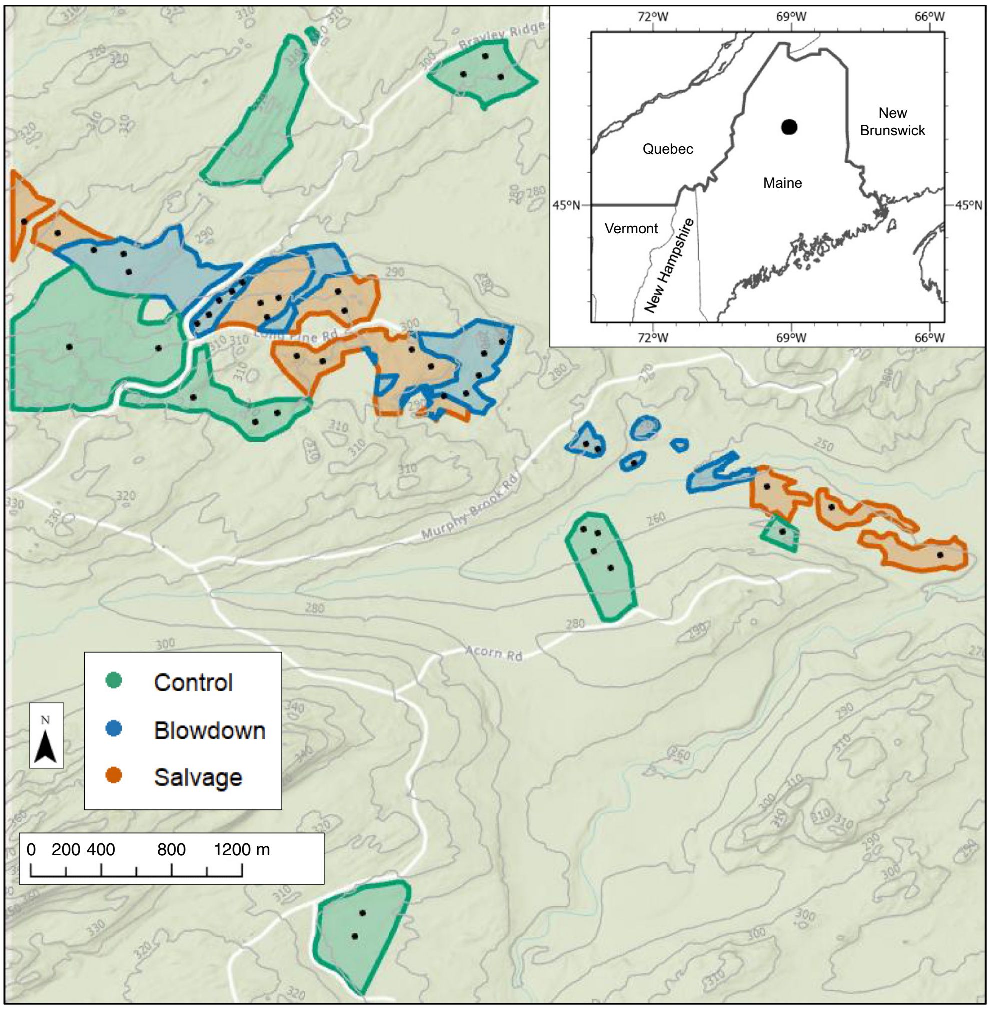

FIGURE 1 Treatment and plot locations within the Scientific Forest Management Area, Baxter State Park, Maine, United States. Orange and blue polygons show the extent of tornado damaged patches, dots indicate plot locations. Sampled units colour coded by treatment: control, blowdown and salvage (blowdown followed by salvage). The western border of map is the western border of the SFMA. Contour lines in metres.

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).

Nine years post-tornado, in the summer of 2022, these stands were revisited to assess regeneration and downed CWM structure within 45 plots (15 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 centre. 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 & 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 centre 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).

2.2 | Data analysis

2.2.1 | Forest structure

Coarse woody material volume for each plot was calculated as,

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

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.

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.

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 modelling 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 (complete model details can be found in Data S1). 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 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.

3 | RESULTS

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). 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; Figure 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 3A). We note that mean CWM height and volume are positively correlated (*rho* = 0.73).

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). 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). Sapling size class distributions differed among all treatments (K–S test $p < 0.001$; Figure 4).

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 (Table 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 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 5).

Furthermore, treatments differed significantly with respect to the proportion of saplings browsed. The salvage treatment had the

TABLE 1 Structural metrics for coarse woody material (CWM) and saplings by treatment, including standard deviations.

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})	4347 ± 2047[a]	11,013 ± 4203[b]	9373 ± 4562[b]
Sapling abundance (stems ha^{-1})			
Abies balsamea	2653 ± 1585	4880 ± 2579	2087 ± 1766
Acer rubrum	567 ± 682	1653 ± 1286	3387 ± 2537
Picea rubens	733 ± 859	1240 ± 1412	1593 ± 1812
Prunus pensylvanica	0	1340 ± 2369	933 ± 2413
Betula alleghaniensis	80 ± 152	687 ± 1308	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

Note: Different lowercase 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.

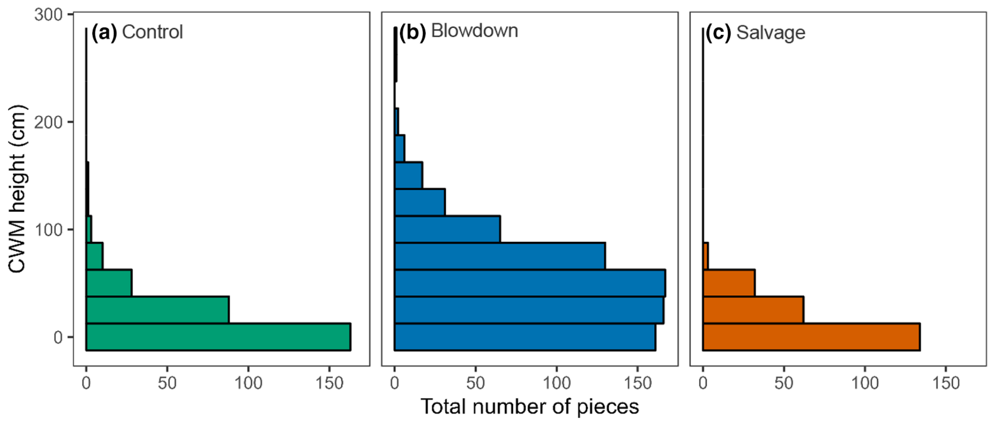

FIGURE 2 Vertical height distribution (to the top of each piece) of coarse woody material (CWM). Plot data pooled by treatment: control, blowdown and salvage (i.e. blowdown followed by salvage).

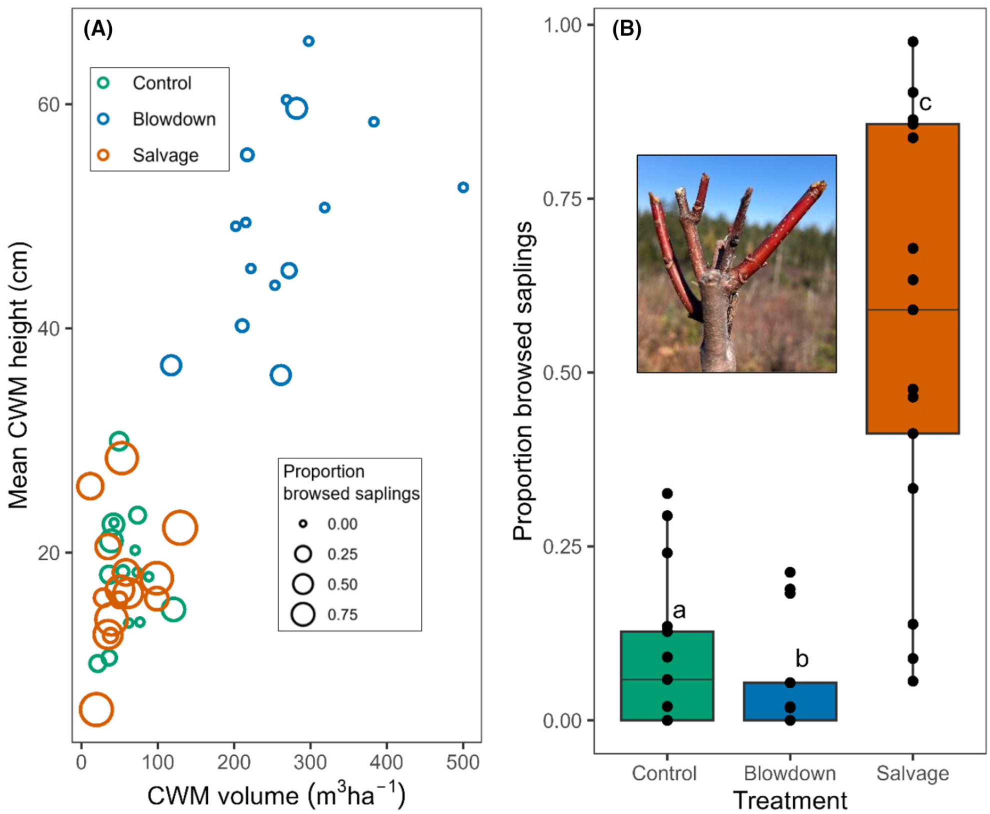

FIGURE 3 (A) Mean height (to the top of each piece) and total volume of coarse woody material (CWM) for each plot. Point size scaled relative to the proportion of browsed saplings within each plot. Spearman's rank correlation coefficient (*rho*) for the relationship between mean CWM height and mean volume = 0.73. (B) Proportion of browsed saplings by treatment. Different lowercase letters indicate significant treatment differences at $\alpha < 0.05$. Photo insert: moose-browsed *Acer rubrum*. salvage = blowdown followed by salvage.

highest proportion (56 ± 28%), followed by the control (9 ± 10) and blowdown (5 ± 8%; Tukey HSD, all pairwise $p < 0.001$; Figure 3b). Blowdown and salvage notably had similar sapling densities and proportions of hardwood species (Table 1), two of the variables identified as significant predictors of browsing. Differences in browsing also varied by species within each treatment, with hardwood species and *Abies balsamea* browsed more commonly in the salvage treatment (Table 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

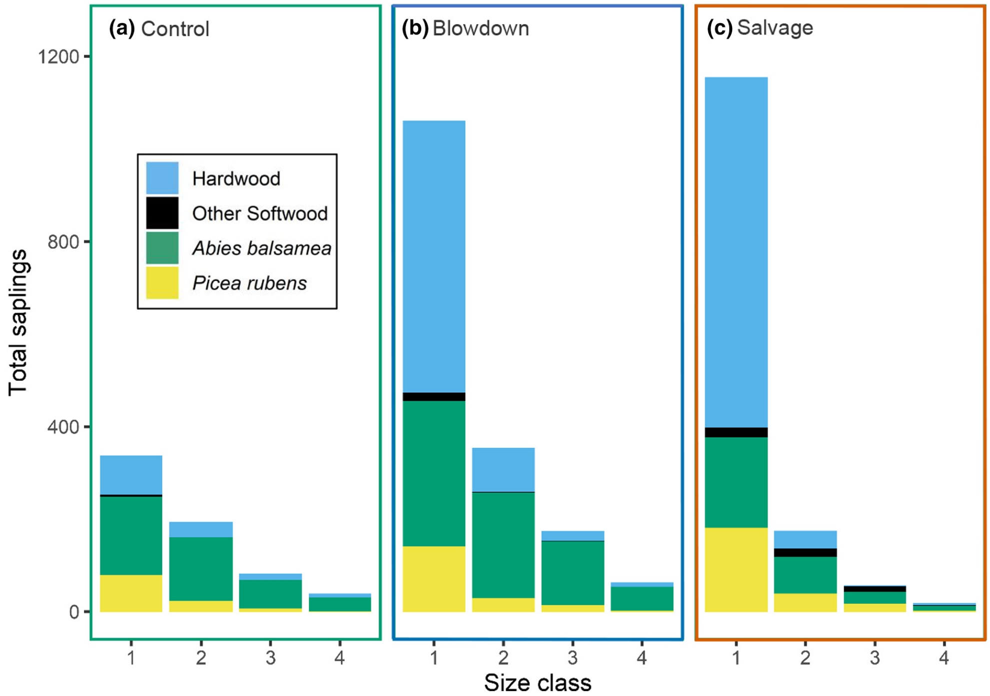

FIGURE 4 Diameter class distribution (at breast height) of all measured saplings, plot data pooled by treatment: control, blowdown and salvage (i.e. blowdown followed by salvage). Class 1: ≤2.5 cm, class 2: 2.6–5 cm, class 3: 5.1–7.5 cm, class 4: 7.6–10 cm.

TABLE 2 Top five models for predicting sapling browsing probability.

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

Note: 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).

Abbreviations: AICc wt., corrected Akaike information criterion weights; AICc, corrected Akaike information criterion; *k*, number of model parameters; R^2, McFadden's pseudo R^2 for a binomial distribution; ΔAICc, change in Akaike information criterion relative to the top model.

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.

4.1 | Forest structure

Structural differences between salvage and blowdown areas remained consistent with those reported by Fraver et al. (2017) 8 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 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 9 years between inventories. While 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 (Zonnevylle et al., 2022). This elevated CWM, as well as greater CWM volumes, clearly distinguishes blowdown from salvage and control treatments.

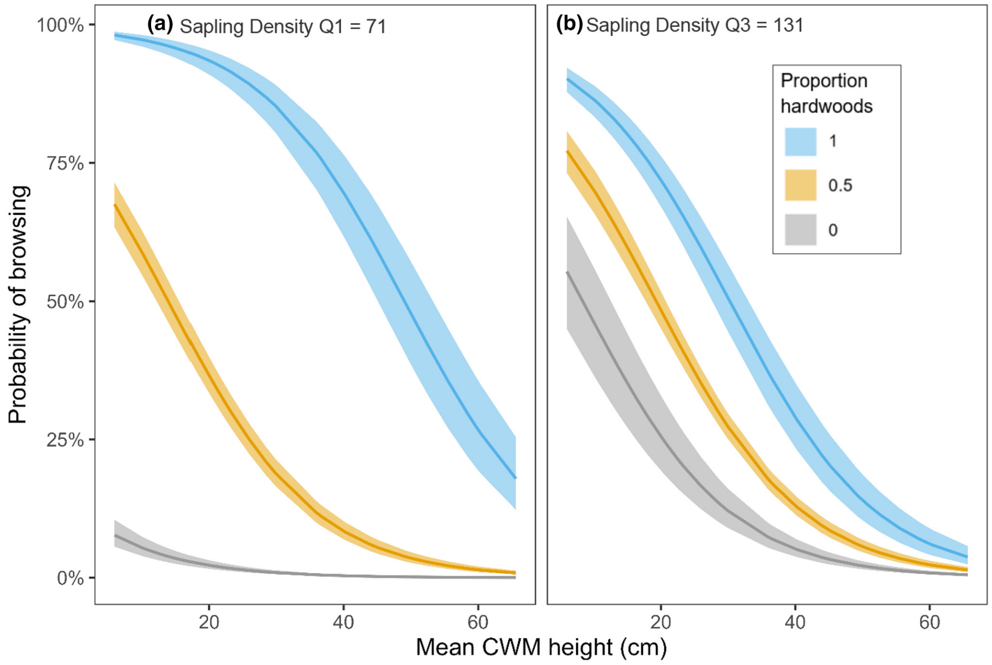

FIGURE 5 GLM model predictions of sapling probability of browsing across varying coarse woody material (CWM) heights, hardwood proportions and sapling densities. Six scenarios are presented to illustrate the effects of the hardwood proportion × sapling density interaction: probability of browsing when 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) quartiles of sapling density (number per plot). Shading indicates 95% confidence intervals.

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* (Dumais & Prévost, 2014; Seymour, 1992). Similar compositional and structural differences between blowdown and salvage treatments are well documented in previous salvage logging studies (Li et al., 2023; Royo et al., 2016; Taeroe et al., 2019). 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 & Williams, 2009). The magnitude of this bias remains unknown.

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 favoured 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 unthinned 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.

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; Zonnevylle 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 (Li et al., 2023; Mabry & Korsgren, 1998; Sass et al., 2018). 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 post-disturbance areas where ungulate browse presents a significant threat to regeneration, we recommend that managers consider retaining CWM to serve as a natural exclosure, particularly in areas where hardwood regeneration is desired. 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.

AUTHOR CONTRIBUTIONS

Colby Bosley-Smith and Shawn Fraver conceived the ideas and designed methodology; Colby Bosley-Smith, Shawn Fraver and Nava Tabak collected the data; Colby Bosley-Smith, Jay Wason and Shawn Fraver analysed the data; Colby Bosley-Smith and Shawn Fraver led the writing of the manuscript; Anthony D'Amato and Nicole Rogers provided management insight. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.bnzs7h4hh (Bosley-Smith et al., 2023).

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SUPPORTING INFORMATION

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

Data S1: Full table of models tested for predicting sapling browsing probability.

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