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Effects of harvest treatments anticipating emerald ash borer invasion on northern hardwood forests in New England, USA

Hanusia Higgins [a,1,*], Anthony W. D'Amato [a], Nathan W. Siegert [b]

[a] University of Vermont, Rubenstein School of Environment and Natural Resources, Burlington, VT, USA
[b] USDA Forest Service, State, Private & Tribal Forestry, Eastern Region, Forest Health Protection, Durham, NH, USA

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ABSTRACT

Management practices reacting to a present or encroaching non-native forest pest can have different and sometimes greater impacts than the pest itself. The emerald ash borer, *Agrilus planipennis* (EAB), has emerged as one of the most destructive invaders in North America, and management responses have shifted as EAB's invasive range has rapidly expanded over the past several decades. In response to the EAB invasion, forest management practices including pre-salvage logging and strategies to improve ash regeneration (*Fraxinus* spp.) have been implemented to meet economic, ecological, cultural, and safety objectives. Although studies have indicated landowners, foresters, and loggers are changing their management practices because of EAB, less is known about the realized ecological impacts of forest management in response to this pest. In summer 2020, we measured forest structure and composition at sites across New England, USA, that included white ash harvests (*F. americana*) motivated by the threat of EAB impacts. In the overstory, we found a lower proportion of white ash basal area in harvested study sites compared to unharvested control sites. However, white ash regeneration at the seedling and sapling stages was higher in harvested than in unharvested plots. EAB presence or proximity did not have a significant effect on overstory composition or ash health in our stands at the time of data collection. Our findings indicate that forest management practices that align with ash species' silvics, such as the greater light availability needed to successfully recruit new white ash cohorts, can bolster ash regeneration and perpetual presence in New England forests. Although EAB remains a significant threat, our work confirms the importance of promoting ash regeneration, supported by recent findings that ash survival and resistance to EAB is more prevalent, and more variable, than previously thought. This work will help inform future management decisions in response to this invasive pest that ensure long-term ecological and economic options are maintained on site.

1. Introduction

Biological invasion has become an increasingly prominent and costly global problem, both from an ecological and economic perspective (Pimentel et al., 2005). Forest pests are a particular challenge because they may functionally eliminate a given canopy tree species, generating far-reaching ecological impacts that are challenging to anticipate (D'Amato et al., 2023a; Lovett et al., 2016). Increasing global trade introduces forest pests to novel environments each year, and the problem of invasion is particularly severe in the northeastern United States, given the region's high density of shipping ports and long history of international trade (Aukema et al., 2010; Liebhold et al., 2013). In addition to their direct effects, invasive pests influence forest management decisions—often even before the pest itself is present locally—as landowners and managers concerned about their economic and ecological impacts have been shown to shift management practices tied to the tree species and ecosystems threatened by a given pest (Markowski-Lindsay et al., 2023, 2020). As such, invasive pests are one of the most pressing issues facing the future structure and functioning of forests in this and other regions of the globe and represent a significant challenge to those tasked with sustaining forest systems in an era of unprecedented environmental change (Lovett et al., 2016).

Forest management in response to invasive pests may generate impacts greater than the pest itself (Kizlinski et al., 2002). Salvage logging is one such management practice with the intent to recoup timber value following a biotic or abiotic forest disturbance (Lindenmayer et al.,

* Corresponding author.
E-mail address: thehanusia@gmail.com (H. Higgins).
[1] Present address: University of Georgia, Warnell School of Forestry and Natural Resources, Athens, Georgia, USA

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2008). Pre-salvage logging is employed in anticipation of spreading or worsening forest pest outbreaks, harvesting vulnerable trees before the primary disturbance occurs (Foster and Orwig, 2006). Management responses, including salvage and pre-salvage logging, can reduce the abundance of structural legacies, such as surviving and dead trees, left following invasion (Foster and Orwig, 2006; Lindenmayer et al., 2008). These practices affect more species than the pest alone, both directly by removing additional non-host tree species in harvest operations, or indirectly due to ecosystem impacts of the salvage or pre-salvage harvest. For example, structural changes such as deadwood removal can reduce habitat and food availability for wildlife including birds and insect herbivores, altering community composition (Castro et al., 2010; Norvez et al., 2013; Thorn et al., 2018). Salvage and pre-salvage logging change biotic and abiotic states and processes in forests, and their effects can be distinct from both typical forest management practices and from the natural disturbances that precipitate them (Lindenmayer et al., 2008).

Harvesting, including salvage and pre-salvage logging, also affects forest regeneration, altering ecosystem recovery pathways after disturbance (Leverkus et al., 2018; Morimoto et al., 2019). First, it changes the abiotic characteristics of the seedbed: removing overstory trees increases light reaching the forest floor, while the physical action of harvesting can have variable impacts on the soil, including compaction, scarification, higher temperatures, and lower moisture content, depending on the harvesting methods or machinery used (Ares et al., 2005; Londo et al., 1999; Picchio et al., 2020; Reisinger et al., 1988). These conditions can all affect seedling germination and survival; for example, increased light availability favors shade-intolerant regeneration, while soil scarification creates conditions beneficial to species that prefer to germinate in bare soil (Kizlinski et al., 2002; Orczewska et al., 2019). Harvesting can also mechanically damage existing regeneration, affecting its future growth (Stringer, 2006; White et al., 2014). Finally, if management outcomes include changing the overstory species composition of a stand, the makeup of the seedbed and future regeneration will shift (Lindenmayer et al., 2008; Smith and Ashton, 1993). Modified light and seedbed conditions can also lead to increased abundance and richness of nonnative plant species (Burnham and Lee, 2010; Eschtruth and Battles, 2009; McIver and Starr, 2001). Importantly, the magnitude of these changes can vary with time and with the intensity of disturbance (Peterson and Leach, 2008; Royo et al., 2016). Given the prevalence of pre-emptive harvests in response to invasive insects (MacLean et al., 2020), understanding the ecological impacts of these management actions is crucial to informing adaptation strategies for addressing one of the largest threats currently facing global forest ecosystems.

One of the most devastating exotic forest insects in North America is the emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) (Kovacs et al., 2010). EAB was likely introduced to North America in the 1990s and was first detected in Michigan in 2002 (Cappaert et al., 2005; Siegert et al., 2014). Since its initial introduction, it has spread across eastern North America, now known to be present in 36 U.S. states, the District of Columbia, and six Canadian provinces (Canadian Food Inspection Agency, 2024; USDA Animal and Plant Health Inspection Service, 2024). Native to Asia, this wood-boring beetle has caused widespread mortality of tree species in the *Fraxinus* genus, generating significant ecological and economic impacts on urban and rural forested environments (Herms and McCullough, 2014). Near the epicenter of EAB invasion in Michigan, over 99 % of ash trees were killed (Klooster et al., 2014); however, white ash trees have also shown highly variable levels of survival (Robinett and McCullough, 2019). In addition to killing most of the mature ash, EAB invasion has reduced seed availability and lowered regeneration rates, leaving behind an "orphaned cohort" of seedlings and small-diameter ash that have not yet been attacked by EAB (Klooster et al., 2014). The widespread mortality and subsequent gap creation generated by the EAB infestation have also impacted the forest communities of which ash is a component, including more aggressive invasion of non-native plants and altered successional pathways (Klooster et al., 2018). To contextualize the secondary impacts of this pest through forest management, it is also important to grasp its significant primary impacts as a point of comparison.

In New England, the three native ash species constitute small but important components of rural forests and are often planted in urban settings (Hudgins et al., 2022). Prior to EAB invasion, white ash, black ash (*F. nigra*), and green ash (*F. pennsylvanica*) combined made up less than 5 % of total trees across all size classes in New England (FIA, 2021). However, local abundance of ash species can be much higher, such as in lowland ecosystems where black ash and green ash can dominate the canopy layer, as well as rich, mesic northern hardwood forests where white ash frequently constitutes over 20 % of the standing volume (FIA, 2021) and is a common species included in commercial timber harvests. To this end, given its rapid growth potential, white ash often disproportionally represents some of the largest trees in these forests (Brooks et al., 1992), serving critical ecological functions and representing high economic values; it is one of the most valuable sawlog species per board foot in the region (VT FPR, 2019). As a result, there are strong economic motivations for pre-salvage harvesting of white ash before EAB reduces the value of this species (MacLean et al., 2020; Markowski-Lindsay et al., 2020).

Forest management practices in response to pests like EAB may have to balance the long-term viability of host species with the health of the broader forest. One common management response for EAB and other invasive pests is preemptive removal of host trees as part of pre-salvage harvests to recoup their economic value before presumably dying from the infestation (Markowski-Lindsay et al., 2020). To manage EAB, a practice analogous to pre-salvage harvesting, termed "phloem reduction," has also been employed with the goal of slowing EAB population growth by reducing viable host material (McCullough et al., 2015). Functionally, this entailed prioritizing removal of large-diameter ash (Mercader et al., 2011). A major drawback to this approach is that some trees may be resistant and might have survived the EAB infestation had they been left standing (Robinett and McCullough, 2019; Steiner et al., 2019). While the surviving trees (termed "lingering ash") could hold the key to a future of breeding EAB-resistant ash populations, waiting until the invasion continues to identify the seemingly resistant trees that remain on the landscape is a crucial part of that process (Steiner et al., 2019). Furthermore, because ash is dioecious, trees of both sexes must be present at high enough densities for pollination and regeneration to occur (Wallander, 2008). Because white ash is a component of mixed stands, its wholesale removal in anticipation of EAB could lead to the loss of this species due to infilling by others (Burr and McCullough, 2014; Klooster et al., 2018). Concern for ash's role in the ecosystem is also shaping management practices, as more than half of foresters and loggers surveyed in Massachusetts and Vermont changed their management activity because of EAB's potential ecological impact on the forests they work in (Markowski-Lindsay et al., 2023).

Losing ash trees to EAB invasion has far-reaching cultural, economic, and ecological consequences (D'Amato et al., 2023b), spurring exploration of the best management practices to mitigate EAB impacts on ash trees and the communities they inhabit (D'Amato et al., 2018; Herms and McCullough, 2014; Klooster et al., 2018; McCullough et al., 2015). While the direct impact of EAB on ash trees has been studied extensively, the broader impacts of forest management practices used to control or reduce the detrimental effects of this invasive species, especially in areas of its more recent invasive range expansion such as the northeastern United States, are less understood. Moreover, key knowledge gaps remain regarding adaptive management strategies that may increase ecosystem recovery from EAB impacts through recruitment of desirable non-ash species, while maintaining future options for ash establishment.

This study inventoried the woody vegetation of northern hardwood and rich northern hardwood forests containing white ash in New England, including stands managed to mitigate the ecological and economic impacts of EAB and others that were not recently harvested. In doing so, we set out to answer the following questions: (1) What is the overall severity of disturbance caused by EAB-influenced forest management at harvested sites? (2) How do overstory species composition and forest structure differ between harvest treatments and forest types? (3) How does the regeneration layer species composition in those forests differ between harvest treatments and forest types? To achieve management goals for ash and other species in the context of EAB, it is crucial to understand the impacts of management decisions on the future of these forests. Doing so will provide valuable insight into the understudied secondary impacts of invasive species.

2. Methods

2.1. Study area

This study included 45 sites in northern hardwood forests across the states of Connecticut, Massachusetts, New Hampshire, and Vermont, USA (Fig. 1). The region's climate includes warm summers and cold winters, averaging about 100 cm of precipitation annually, with increasing variations in temperature and precipitation in recent years (Keim and Rock, 2001). Study sites varied in elevation from 181 to 701 m above sea level (The National Map Elevation, 2021). The northern hardwood forest type is characterized by an overstory dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*), and frequently includes species like white ash and eastern hemlock (*Tsuga canadensis*) (Leak and DeBald, 1987). The relative importance of each of these canopy species varies based on site fertility with sugar maple and white ash generally constituting a great proportion of canopy species on higher fertility sites (Leak and DeBald, 1987). These high-fertility sites are often classified as a distinct forest type (Edinger et al., 2014; Leak and DeBald, 1987), labeled in this study as "rich northern hardwood." Each site chosen for this study was at least four hectares in size and contained a white ash overstory component of at least 15 % by basal area.

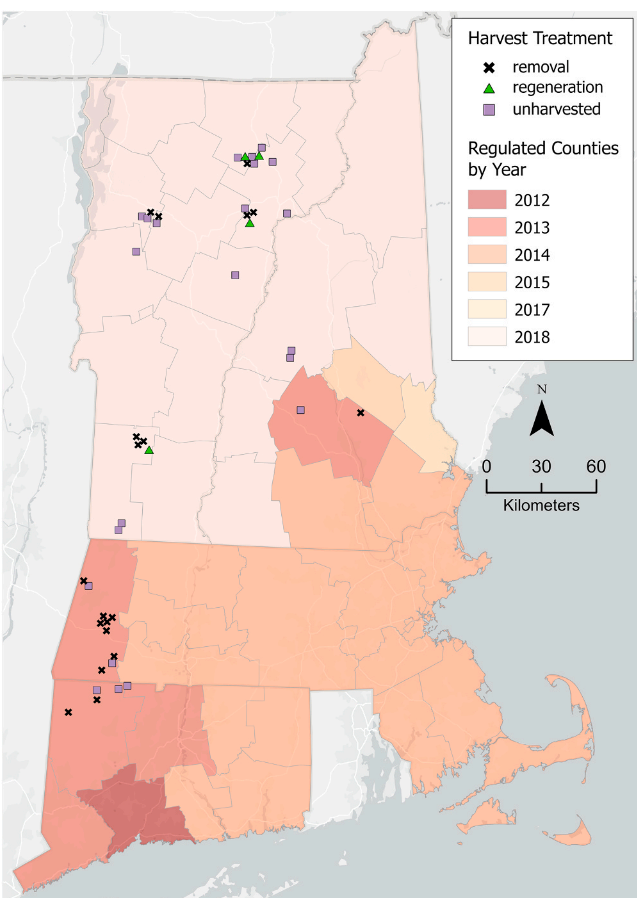

Fig. 1. Study sites across New England sampled in summer 2020, indicated by harvest treatment: unharvested, regeneration-focused, or removal-focused. Counties are shaded by the year of first EAB detection.

Half of the selected sites (23) had been harvested in response to regional EAB invasion within the past 10 years, including pre-salvage or salvage logging of ash and/or harvest treatments to secure ash regeneration. Most management plans for the harvested sites included responding to EAB among a list of other goals, such as improving overall forest health and resilience. The other sites (22) had not been harvested in the past 20 years and were near harvested sites. Several sites were located on the same property but were harvested in different years or consisted of different stands. Sites were located on state (27), federal (6), and privately-owned, family forest (6) and NGO (6) properties (Table 1).

To classify study sites, two categorical explanatory variables were used: harvest treatment and forest type. Unharvested sites (N = 22) constituted one treatment group, while harvested sites were separated into "removal" (N = 19) and "regeneration" (N = 4) groups for analysis. Sites that prioritized ash removal in their management were classified in the former group, while sites that prioritized ash regeneration were placed in the latter. We created these groupings based on information from management plans, prescriptions, and/or personal communication with the forester or landowner for each site. For example, a "removal" prescription listed capturing mature white ash value ahead of anticipated mortality from EAB among its goals, while a "regeneration" harvest intentionally retained both male and female white ash trees to promote regeneration. The small number of sites classified as "regeneration" harvests limited our statistical power in comparing the groups. Nonetheless, given the distinct intent of these treatments relative to pre-salvage harvests, we felt that distinguishing this group from the other harvests was warranted. Forest type was either northern hardwood (NH) or rich northern hardwood (RNH), with distinction made based on site composition, soil type, and underlying bedrock geology (Table 1).

At the time of sampling, 36 sites were in or near areas with detected EAB infestations, although reported data on known infestations from each state varied in its spatial scale so we were unable to determine the true location of EAB invasions relative to the areas being sampled. All sites where EAB had not yet been detected nearby (9) were in Vermont. The time of initial regulation for EAB in the counties where sampled sites were located ranges from the year 2013–2018 (Fig. 1). Surveys of foresters and loggers working in this region during our study period indicated they had changed their management activities in response to the threat of EAB (Markowski-Lindsay et al., 2023). In addition, EAB biological control agents had been released—and recovered—in some of the same counties as our sampled stands as early as 2013 (MapBioControl Release Site Dashboard, 2024). In one case, EAB parasitoids were released and recovered several years prior in the same property where we sampled, Shaker State Forest in New Hampshire (MapBioControl Release Site Dashboard, 2024). The effect of biological control efforts on these forests was not accounted for in our study.

Table 1
Number of study sites grouped by harvest treatment across forest type and ownership.

	Treatment			
	unharvested	*regeneration*	*removal*	**Total**
Forest type				
northern hardwood	14	2	15	31
rich northern hardwood	8	2	4	14
Ownership				
Public (national)	2	1	3	6
Public (state)	13	1	13	27
Private	4	0	2	6
Private (nonprofit)	3	2	1	6
Total sites by treatment	22	4	19	45

2.2. Vegetative sampling

We established four to ten 400 m^2 plots (11.3 m radius) in each site depending on the management regime using a stratified sampling method. In each harvested site, at least three plots were in harvest-created gaps and three in thinned or unharvested areas surrounding harvest gaps. In each unharvested site, we established at least four sampling plots to capture areas of varying ash density.

Within each plot, we recorded the species and diameter at breast height (DBH) of each overstory tree above 10.1 cm DBH, along with the diameter, height, and decay class of any stumps or snags above the same diameter (Spetich et al., 1999). If snags and stumps could not be identified to species, they were identified to genus, if possible. Downed coarse woody material (CWM) was sampled using three 11.3-m line-intercept transects at radii of 0°, 120°, and 240° originating from plot center. Diameter of CWM was recorded at the point of intersect for all CWM > 7.6 cm in diameter at its widest end and at least 1 m long. Total transect length sampled per site ($\geq$120 m) was sufficient to generate precise estimates of downed deadwood pools (Fraver et al., 2018).

In addition, we assessed the health of any ash trees at least 2.5 cm DBH within the plots using a modified version of the monitoring protocol established by Knight et al. (2014). We assigned a canopy condition from 1 to 5 and noted the presence or absence of signs of EAB infestation on each ash, including bark splitting, D-shaped exit holes, visible larval galleries, woodpecker feeding holes, epicormic branching, basal sprouting, and bark blonding (Knight et al., 2014). An ash health index was calculated from these data by adding the canopy condition (1−5) with the number of stress indicators observed on each tree, with higher numbers corresponding to stressed, less healthy trees.

To capture understory composition and structure, saplings and shrubs at least 30.5 cm tall and under 10.2 cm DBH were tallied by species in nested subplots within the 400 m^2 overstory plot. Saplings less than 10.2 cm but greater than 2.5 cm DBH were recorded in three nested 0.004 ha subplots located at azimuths of 0°, 120°, and 240° centered at 5.5 m from plot center. These saplings were tallied in 3 size classes (2.5–5.0 cm, 5.1–7.5 cm, and 7.6–10.1 cm DBH) by species. Saplings at least 30.5 cm tall and less than 2.5 cm DBH and shrub species greater than 30.5 cm tall were tallied by species in three 5 m^2 subplots nested within the larger sapling plots. Dead stems were also recorded in all subplots.

In each overstory sampling plot, we also established three 1 m^2 subplots to measure regeneration centered 4 m from plot center at 60°, 180°, and 300°, recording the number and species of seedlings in each subplot. Seedlings were defined as woody stems under 30.5 cm tall. Percent cover of vegetative life forms, categorized as herbaceous and woody vegetation, ferns and allies, sedges and grasses, bryophytes, and bare soil, were also recorded in these subplots. Percent cover for each category was assessed via "rapid sampling" using Braun-Blanquet classes (Braun-Blanquet, 1964).

2.3. Statistical analyses

We investigated relationships between harvest treatment and forest type with each response variable, as detailed below, using generalized linear mixed models and two-way ANOVAs. To assess forest structure and overstory composition, we conducted analyses at the site level, whereas responses associated with understory conditions were analyzed at the plot, nested within site, level. Most analyses were univariate because the response variables were of individual interest, and we used multivariate analyses when appropriate, as detailed below. We used the Akaike Information Criterion to choose appropriate covariance structures for ANOVAs and select the best-fitting models for each response variable, resulting in the choice of treatment group and forest type as the main explanatory variables. Ash health index, time since harvest, EAB presence, and time since county-level EAB regulation were also tested in various combinations with treatment group and forest type as possible covariates, but not included in the final models. When main factors were significant, we applied Tukey's test for post hoc analysis. All statistical analyses were conducted in R version 4.1.2 unless otherwise specified (Core Team, 2021).

We used mixed model regression to examine the relationship between regeneration response and disturbance severity, as approximated by the proportion of biomass removed during harvest. A disturbance severity index was calculated for each harvested plot, following methods outlined by Peterson and Leach (2008) and Kurth et al. (2020). This value represents the proportion of live aboveground biomass harvested per plot, with biomass calculated from species group and DBH (Jenkins et al., 2003). Since all sampling occurred post-harvest, for recently cut stumps in decay class 1 or 2, DBH was estimated from stump height and diameter using allometric equations (Westfall, 2010). When an equation for DBH or biomass was not available for a given species, they were assigned to the most closely related species group in Jenkins et al. (2003) for biomass estimation purposes. When the species was unknown, the species group constants given in Jenkins et al. (2003) were averaged. Aspects of the regeneration layer, including seedling and sapling density per plot, species richness, and Shannon diversity, were calculated with the diversity function in the vegan R package and regressed against the disturbance severity index value using generalized linear mixed models, with site as a random factor (Oksanen et al., 2020).

Overstory and stand structure attributes were analyzed at the site level using two-way ANOVAs with the variables of treatment type, forest type, and their interaction. Cut basal area was calculated using diameter and height for stumps in decay classes 1 and 2 (Spetich et al., 1999; Westfall, 2010), and the unharvested treatment group was excluded from the analysis of this variable. Response variables that did not conform to ANOVA expectations were natural log transformed.

Understory characteristics, including seedling and sapling counts, were analyzed at the plot level using generalized linear mixed models with a negative binomial distribution. This distribution was selected for these models because the understory count data contained many zero values (Bliss and Fisher, 1953). Response variables included total seedling/sapling densities, as well as densities for the five most prevalent overstory species in the dataset: sugar maple, white ash, American beech, yellow birch, and red maple. Unless otherwise stated, understory models included fixed effects of treatment and forest type, with site as a random effect, using the glmer.nb function in the R package lme4 (Bates et al., 2015). Models that failed to converge with these parameters were simplified by removing site or forest type variables.

Gradients in variation in understory composition across sites were examined using nonmetric multidimensional scaling (NMS) in PC-ORD 7 (McCune and Mefford, 2016). NMS was run on a matrix containing saplings and shrub species' count per plot with species occurring in fewer than three plots excluded. After running stress tests to find the optimal number of axes for the ordination space, two instances of 250 model runs each were executed with a 3-axis solution using the Sørensen distance measure, and the run with lowest minimum stress value was interpreted. Overlays of variables including treatment group and forest type were used to aid in interpretation of the resulting ordination. In addition, we conducted an indicator species analysis using this matrix for treatment groups and forest types, and applied the Bonferroni correction to the resulting p-values (McCune and Mefford, 2016).

To analyze variation in ground cover classes, we used permutational multivariate analysis of variance (PERMANOVA). The mean value of each Braun-Blanquet range used for sampling was assigned as percentage cover for each category, and these values were averaged to the plot level. PERMANOVA was executed using the adonis function in the vegan package, with treatment type and forest type as explanatory variables (Oksanen et al., 2020). Sapling composition per site was also analyzed with a PERMANOVA and the same explanatory variables, using the same subset of species present in three or more plots as in NMS analysis.

3. Results

3.1. Disturbance severity index

For harvested plots, the mean disturbance severity index was 1.5x higher in removal plots than in regeneration plots (P = 0.041) (Fig. 2). However, there was no significant relationship between disturbance severity and understory composition variables, including seedling and sapling species richness, density, and Shannon diversity.

3.2. Overstory composition and stand structure

The most prevalent overstory species across study sites were sugar maple, white ash, American beech, yellow birch, and red maple. Quadratic mean diameter did not vary significantly by treatment type but was significantly higher in northern hardwood than in rich northern hardwood sites (P = 0.0257) (Table 2). As expected, total live basal area, as well as live white ash basal area, was significantly higher in unharvested sites than in each of the harvested treatments (regeneration and removal), which did not vary significantly from one another (P = 0.4245) (Table 2). Harvested white ash basal area was higher in the removal treatment group than in the regeneration group (P = 0.0867), as was the proportion of white ash basal area cut (P = 0.0325) (Tables 2 and 3).

Snag basal area (P = 0.2459) and biomass (P = 0.480) did not differ significantly between treatment groups, but both were significantly higher in NH than in RNH sites (BA, P = 0.0032 and biomass, P = 0.017). Conversely, volume ($P < 0.0001$) and biomass ($P < 0.0001$) of CWM were both significantly higher in the removal treatment group than in unharvested sites, whereas there was no difference between the regeneration treatment group and either of the other groups. There was no significant difference in volume and biomass of CWM between forest types (volume, P = 0.105 and biomass, P = 0.121) (Table 2). For all overstory and dead wood stand-level attributes analyzed, the interaction of treatment group and forest type was not significant.

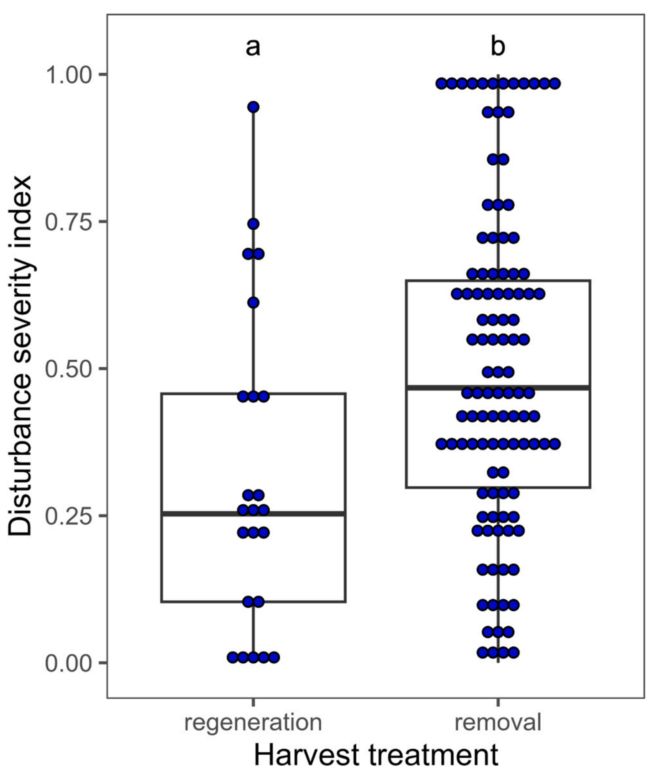

Fig. 2. Quartiles of harvested plots' disturbance severity index which measures the proportion of live aboveground biomass cut in each plot, grouped by treatment type and plotted as Tukey's box-and-whisker plot (Mcgill et al., 1978). Letters indicate significant difference at the alpha= 0.05 level.

Table 2
Stand attributes averaged by treatment and forest type. CWM=coarse woody material, BA=basal area, QMD=quadratic mean diameter.

Statistic (mean ± SE)	Treatment			Forest type	
	unharvested	*regeneration*	*removal*	*NH*	*RNH*
CWM volume (m^3/ha)	32.0^{a} ± 4.3	67.9^{ab} ± 18.6	86.1^{b} ± 9.7	65.8^{a} ± 8.1	40.9^{a} ± 7.1
CWM biomass (Mg/ha)	9.2^{a} ± 1.4	21.4^{ab} ± 5.5	32.4^{b} ± 3.9	23.1^{a} ± 3.3	13.5^{a} ± 2.6
snag BA (m^2/ha)	11.9^{a} ± 1.6	21.8^{a} ± 7.2	14.2^{a} ± 3.6	16.5^{a} ± 2.4	7.6^{b} ± 1.2
snag biomass (Mg/ha)	26.1^{a} ± 4.4	45.9^{a} ± 20.1	31.7^{a} ± 10.8	36.9^{a} ± 7.3	15.3^{b} ± 1.9
trees per hectare	588.4^{a} ± 27.4	317.3^{b} ± 80.6	285.3^{b} ± 21.6	392.3^{a} ± 35.0	533.6^{b} ± 37.0
QMD (cm)	27.8^{a} ± 0.8	30.8^{a} ± 3.5	28.7^{a} ± 0.6	29.2^{a} ± 0.7	26.8^{b} ± 0.8
live tree BA (m^2/ha)	34.8^{a} ± 1.2	20.5^{b} ± 1.2	18.1^{b} ± 1.2	25.0^{a} ± 1.8	29.7^{a} ± 2.0
live white ash BA (m^2/ha)	13.3^{a} ± 1.0	6.4^{b} ± 1.0	3.8^{b} ± 0.6	8.2^{a} ± 1.2	9.8^{a} ± 1.2
cut white ash BA (m^2/ha)	—	3.5^{a} ± 0.6	8.4^{a} ± 1.1	4.3^{a} ± 1.0	2.8^{a} ± 1.2
proportion white ash BA cut	—	0.36^{a} ± 0.05	0.65^{b} ± 0.05	0.35^{a} ± 0.07	0.21^{a} ± 0.07
ash canopy rating (1–5)	2.1^{a} ± 0.1	2.1^{a} ± 0.3	2.4^{a} ± 0.2	2.4^{a} ± 0.1	2.0^{a} ± 0.1

Notes: Levels were compared within each factor (treatment and forest type), and letters indicate significant differences at the alpha= 0.05 level.

3.2.1. EAB infestation context

At the time of sampling in 2020, EAB was present or nearby in 36 of the 45 sites studied, according to each state's detection data. The mean ash canopy rating per stand, on a 1–5 scale with 1 representing a healthy canopy, ranged from 1.0 to 4.1. Overall, mean ash canopy rating was not significantly different across forest types and harvest treatments (Table 2). Ash canopy rating also did not vary significantly between stands where EAB was present and stands where it was absent (P = 0.124), or by the years since county-level EAB regulation (P = 0.0598). Overstory variables, including live and cut basal area both for white ash and including all species, did not vary significantly with the factors EAB presence or time since EAB regulation. Although we did not directly measure the effects of EAB, the above tests provide our best effort to account for any confounding introduced by EAB's presence or impacts.

3.3. Understory abundance and composition

Total understory seedling density did not vary significantly between forest type, treatment type, or their interaction. However, the removal treatment had a significant positive effect on the number of seedlings of white ash (P = 0.0421) and yellow birch (P = 0.0062), and a significant negative effect on sugar maple (P = 0.0107), when compared to the unharvested group (Table 4; Fig. 3a).

Sapling densities were a function of treatment group, forest type, and their interaction. Across forest types, total sapling density was greater in the regeneration treatment than in unharvested control plots (P = 0.0183). White ash saplings were significantly more numerous in both the regeneration (P = 0.0251) and removal (P = 0.0001) treatments compared to unharvested areas, as were yellow birch saplings in the regeneration treatment (P = 0.0153). For American beech, the rich northern hardwood forest type had significantly fewer saplings than did northern hardwood plots (P = 0.0373) (Table 4; Fig. 3b).

A 3-axis NMS solution was found to be optimal for explaining variation in sapling composition and had a minimum stress value of 12.280

Table 3
Most abundant overstory species' basal area and importance values averaged by treatment and forest type. Importance values are based on relative basal area (BA) and stems per hectare.

Species	Statistic (mean ± SE)	Treatment			Forest type	
		unharvested	*regeneration*	*removal*	*NH*	*RNH*
sugar maple	live BA (m^2/ha)	12.1 ± 1.1	10.7 ± 2.2	8.2 ± 1.0	9.1 ± 0.7	13.0 ± 1.7
	cut BA (m^2/ha)	—	3.2 ± 1.6	3.5 ± 0.9	2.1 ± 0.6	1.0 ± 0.6
	Importance value	78.0 ± 6.1	113.8 ± 15.6	95.0 ± 8.4	83.5 ± 5.8	99.2 ± 9.5
white ash	live BA (m^2/ha)	13.3 ± 1.0	6.4 ± 1.0	3.8 ± 0.6	8.2 ± 1.2	9.8 ± 1.2
	cut BA (m^2/ha)	—	3.5 ± 0.6	8.4 ± 1.1	4.3 ± 1.0	2.8 ± 1.2
	Importance value	60.6 ± 3.5	50.5 ± 7.7	34.1 ± 4.1	47.0 ± 4.1	51.8 ± 4.4
American beech	live BA (m^2/ha)	1.7 ± 0.4	0.3 ± 0.2	0.8 ± 0.2	1.4 ± 0.3	0.6 ± 0.2
	cut BA (m^2/ha)	—	0.2 ± 0.1	1.0 ± 0.4	0.6 ± 0.3	0.0 ± 0.0
	Importance value	14.1 ± 2.9	6.5 ± 4.2	17.2 ± 4.9	18.3 ± 3.4	6.9 ± 2.2
yellow birch	live BA (m^2/ha)	1.8 ± 0.4	1.6 ± 0.7	1.4 ± 0.4	1.6 ± 0.3	1.5 ± 0.5
	cut BA (m^2/ha)	—	0.5 ± 0.2	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.2
	Importance value	10.8 ± 2.4	15.6 ± 7.1	16.1 ± 4.5	14.1 ± 2.8	11.4 ± 4.0
red maple	live BA (m^2/ha)	1.6 ± 0.4	0.1 ± 0.1	1.1 ± 0.3	1.3 ± 0.3	1.2 ± 0.6
	cut BA (m^2/ha)	—	0.0 ± 0.0	0.7 ± 0.4	0.3 ± 0.2	0.3 ± 0.2
	Importance value	9.6 ± 2.5	0.9 ± 0.9	12.4 ± 3.8	10.9 ± 2.5	8.0 ± 3.7

Table 4
Seedling and sapling densities per species and treatment, and F statistics for fixed effects and their interactions in generalized linear mixed models for sample plot understory (seedling and sapling) tallies. Given the large difference in sample size between treatment groups, several main effects with large F-values were not significant and did not result in any significant pairwise differences between levels.

	Seedling density by treatment (seedlings per square meter)			Fixed effect F statistic		
	unharvested	*regeneration*	*removal*	*Treatment*	*Forest type*	*Treatment x Forest type*
Seedlings						
all species	11.1631	16.2754	6.2507	1.1517	1.4773	1.7162
sugar maple	9.1986	13.5652	3.2065	**3.8188**	3.9161	1.4865
white ash	0.1667	0.2899	0.4897	**2.5704**	0.1782	0.0736
American beech	0.0674	0.0290	0.1091	1.5236	6.7181	0.7022
yellow birch	0.0284	0.0290	0.1888	**3.7487**	—	—
red maple	0.7340	0.4348	0.5251	0.0582	2.4392	**3.2091**
	Sapling density by treatment (saplings per hectare)			**Fixed effect F statistic**		
	unharvested	*regeneration*	*removal*	*Treatment*	*Forest type*	*Treatment x Forest type*
Saplings						
all species	1312.399	2772.947	1487.381	**5.1299**	0.0877	**4.0200**
sugar maple	319.1489	560.3865	317.2730	0.7212	13.7978	2.2243
white ash	40.1891	190.0161	180.2688	**8.0402**	0.0789	0.7933
American beech	360.9141	466.9887	413.6349	0.0777	**6.9414**	1.4153
yellow birch	58.3163	383.2528	78.6627	**2.6113**	0.4735	0.7451
red maple	18.1245	28.9855	30.8096	0.8200	0.0401	1.1818

Notes: F statistics of significant effects for each species are bolded.

(instability=0.00000, P = 0.0040). In order of decreasing importance, axis 1 explained 36.3 % of the variation in sapling data, axis 2 explained 29.9 % of the variation, and axis 3 explained 19.2 % of the variation, for a total of 85.4 % of variation explained (Fig. 4). Axis 1 was positively associated with sugar maple ($\tau = 0.429$) and negatively associated with brambles (*Rubus* spp.; $\tau = -0.590$) and ranged from harvested treatments in the negative portion to unharvested treatments in the positive portion, meaning that sugar maple saplings were more dominant in unharvested sites and more *Rubus* spp. dominated the sapling layer in harvested sites. Axis 2 was negatively correlated with American beech ($\tau = -0.597$). No significant indicator species were identified for treatment groups or forest types based on Bonferroni-corrected p-values.

Site-level sapling composition varied between forest types and treatment types, although their interaction was not significant (P = 0.231). Each of the harvested treatment groups, removal (P = 0.001) and regeneration (P = 0.006), were significantly different from the unharvested group, but they did not differ significantly from each other (P = 0.201). In addition, sapling composition was significantly different between NH and RNH forest types (P = 0.002).

Ground cover composition, as described by plant lifeform, was affected by treatment type, but not forest type (P = 0.665) or their interaction (P = 0.172). Ground cover composition differed between unharvested and each harvested treatment group (removal, P = 0.003 and regeneration, 0.018), but not between the two harvested groups (P = 0.930).

4. Discussion

In this study, we assessed the condition of northern hardwood forests harvested in response to or anticipation of the invasive EAB. This work complements previous studies that inferred management responses to EAB via existing inventories or surveys (Holt et al., 2021; MacLean et al., 2020; Markowski-Lindsay et al., 2023) by documenting the on-the-ground impacts of EAB's influence on forest management practices in a recently invaded region. It also contributes to the body of literature capturing ecological effects of salvage and pre-salvage logging (Leverkus et al., 2018; Lindenmayer et al., 2008; Thorn et al., 2018). At the overstory level, we expectedly observed decreased basal area for the EAB-host species, white ash, in harvested sites, with a higher proportion removed in ash reduction-focused treatments relative to

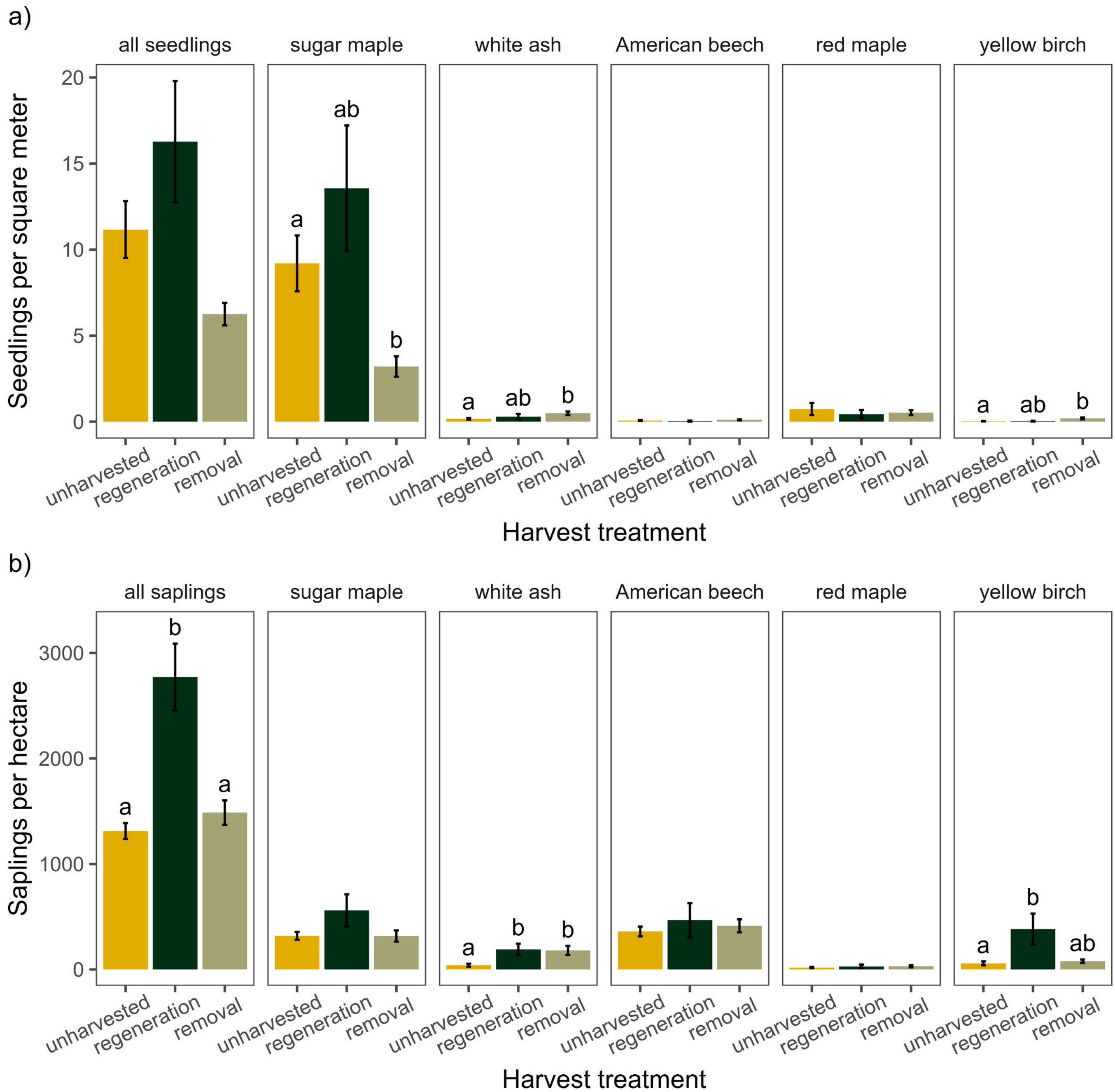

Fig. 3. a) Seedling and b) sapling density for all species and for each of the 5 most prevalent overstory species, per harvest treatment group. Within each species, groups that differ significantly from each other are noted with different letters.

regeneration-focused treatments. In the understory, however, white ash saplings were more prevalent in both harvested treatment groups than in unharvested control plots. Most prior work on insect pests' direct and indirect impacts has focused on communities where the host trees are among the dominant overstory species (e.g., Grinde et al., 2022). This study parses effects of EAB-motivated management in forests where the target species is a minor component, and where landowners have had more time to anticipate and respond to its arrival (FIA, 2021; Grinde et al., 2022; Herms and McCullough, 2014; Klooster et al., 2018). In these systems, accounting for regeneration dynamics following partial canopy disturbances due to mortality from EAB or associated management are critical to developing management practices that consider not only the pest and its hosts, but the broader natural community and future of the forest.

4.1. Harvest impacts to overstory and deadwood dynamics

The harvests captured in this study removed a higher proportion of basal area compared to regional averages. In particular, the mean percentage of overstory basal area removed from harvested plots in our study was 45.7 % ± 28.7 %. In northern hardwood forests across the northeastern United States, the average percentage of basal area removed in FIA plots harvested from 2002 to 2008 was 37.7 % ± 28.9 % (Canham et al., 2013). Despite differences in proportion of basal area removed, the harvest severities we documented based on proportion of aboveground biomass removed (50 % for ash removal-focused treatments and 31.7 % for ash regeneration-focused treatments) are more consistent with recent examinations of FIA plots in our study region (MacLean et al., 2020). These findings may reflect an increasing severity

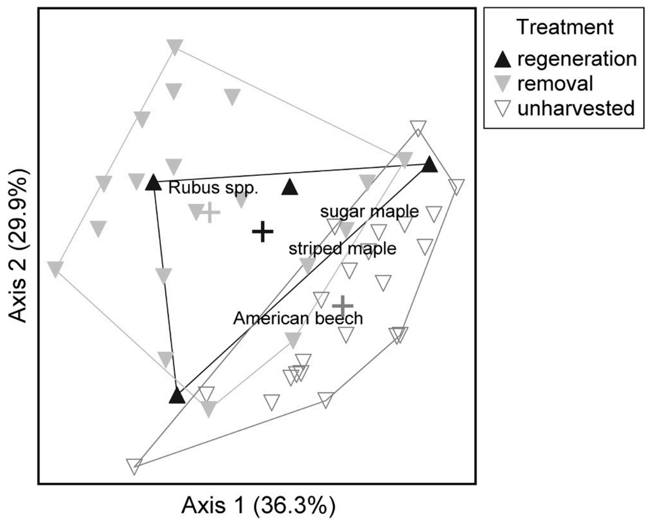

Fig. 4. Nonmetric multidimensional scaling ordination of stand-level sapling composition including the two axes that explain the most variance in the data, with centroids (plus signs) and hulls for each of stands' treatment groups. Locations of species labels represent the weighted average location and are only presented for species significantly correlated with a given axis.

of harvest in these forests to address regeneration challenges posed by American beech (Leak, 1999), as well as a potential increase in removals due to the threat of species loss to EAB.

Our study measured less removal of overall basal area than other pest-related salvage harvests. In a study of salvage logging impacts relating to the hemlock woolly adelgid (*Adelges tsugae* Annand), over two-thirds of total basal area was removed from salvaged sites (Kizlinski et al., 2002); another survey of the same phenomenon found a 54 % reduction in basal area from precut conditions (Brooks, 2004). Following a spruce budworm (*Choristoneura fumiferana* Clemens) outbreak in Canada, basal area was over four times greater in unsalvaged than salvaged stands (Norvez et al., 2013). Salvage harvests following a spongy moth (*Lymantria dispar* L.) outbreak and subsequent oak mortality removed, on average, 56 % of basal area per stand (Sewall et al., 1995). Ash is a smaller constituent of the forests we sampled than the more dominant target species of other pests, which is likely a reason for this difference. In addition, given the high commercial value of white ash during the period our study sites were harvested, the need to harvest other non-ash species to make treatments economically viable was likely far less than assumed by work predicting an increase in non-ash harvesting in response to EAB (MacLean et al., 2020).

Removal of non-target species in salvage operations is a frequent concern because it can be ecologically and economically significant (Lindenmayer et al., 2008; Thorn et al., 2018). For example, yellow birch, a species that often co-occurs with white ash in northern hardwood forests, is an important wildlife resource generating food, shelter, and unique microhabitat conditions via its leaf litter quality and rooting structure (Burns et al., 1990; Jonczak et al., 2020). In the case of eastern hemlock, many higher-value hardwood species were removed during salvage and pre-salvage logging operations in addition to hemlocks for economic reasons (Foster and Orwig, 2006). In New England forests, white ash is both rarer at the stand level and more economically valuable than another target species like the eastern hemlock (VT FPR, 2019); this means that overall harvest severity can be lower, and that fewer non-target species can be included as "harvest bycatch," to reap similar financial gains from a salvage logging operation. The lower proportion of non-ash biomass harvested in the sites we examined is in contrast to the predictions of MacLean et al. (2020), which indicated up to 81 % of biomass removed by family forest owners in response to EAB would be from species other than ash. 52 % of the total biomass cut in our harvested plots was from non-ash species. Moreover, our study design balancing the number of gap and matrix plots sampled within each harvested site may have inflated this value, overrepresenting the gap plot condition (where virtually all overstory biomass was removed, regardless of species) relative to the forest matrix (where trees were removed singly and species seen as vulnerable, including ash, were often prioritized for cutting).

Another study comparing harvests before and after EAB detection found that the presence of EAB correlated with increased intensity of ash harvesting, but decreased probability of harvest for non-ash species (Holt et al., 2021). Given this work was focused on harvesting after EAB detection, it may have obscured the effects of pre-salvage harvesting prior to local EAB detection (Holt et al., 2021). In the present study, most of the harvests we sampled were explicitly preemptive, with the assumption that EAB was present nearby and would be spreading to those forests soon or was already present without detection. Although we could not evaluate the probability of a given plot being harvested, we found that harvest severity was higher in sites where treatments focused on ash removal, with this difference related to a higher proportion of ash removed in the removal treatments; the percentage of non-ash biomass harvested did not differ between treatment groups.

Differences in our observed harvest severities and those predicted by MacLean et al. (2020) and documented by Holt et al. (2021) may be related to the differences in ownerships sampled. Our study sites, which included more public than private lands, may represent a different set of priorities and outcomes for ash and its associated species than those predicted for family forests, the largest land ownership class in EAB's invasive range (Sass et al., 2020). Management actions on public lands are subject to a different set of regulations and stakeholder inputs than privately-owned parcels (United States, 1976). However, forest management approaches vary both within and between ownership types (Holt et al., 2020; Klein and Wolf, 2007; Leahy et al., 2013; Zhao et al., 2020), and our field-based assessment provides valuable "ground truthing" of management actions in the region. A recent survey of foresters and loggers in Massachusetts and Vermont found that most respondents changed their management practices in ash stands due to EAB's ecological impacts (Markowski-Lindsay et al., 2023). In addition, managing ash in the context of EAB was not the sole or primary motivation for many of the treatments we sampled, making it difficult to isolate the effects of EAB on harvest practices. However, this reflects the reality that white ash is typically a small component of mixed forests in our study area and addressing EAB was often part of a larger suite of goals for these harvests.

For both ash and non-ash species, the volume of CWM in sites we sampled was lower across all treatment groups than the volume in Michigan forests experiencing high ash mortality due to EAB (Perry et al., 2018). In addition, CWM volume in our removal treatment group was significantly higher than in unharvested stands for both ash and non-ash species, while the Michigan forest saw an increase only in ash CWM between two sampling periods (Perry et al., 2018). Conversely, some salvage and pre-salvage logging operations decrease deadwood relative to unharvested stands, and these structural legacies can persist for decades following the disturbance, such as in balsam fir forests logged after spruce budworm outbreaks (Norvez et al., 2013). Although the stage of EAB infestation differs in our sites compared to those sampled elsewhere, this result suggests that removing trees affected by EAB will limit the increase in deadwood inputs in the forest due to EAB-induced mortality. Unharvested sites, given their higher ash basal area (Table 2), are likely to experience the greatest increase in ash deadwood inputs as EAB infestations advance. Retention of some canopy ash in areas experiencing pre-salvage operations is one option for ensuring future CWM inputs are sustained on these sites.

4.2. Regeneration and structural impacts

Regeneration of a target species post-salvage logging is highly dependent on the species' silvics and the type of management employed. For white ash, the light availability opened by thinning and group selection—practices employed in most harvested stands in this study—is beneficial to advance regeneration in the sapling stage (Burns et al., 1990). Commensurately, although ash made up a relatively small proportion of the understory in all sampled sites, both harvested treatment groups had higher density of white ash saplings than unharvested control sites (Fig. 3). In contrast, cases where harvests damage advance regeneration can alter successional pathways (Kizlinski et al., 2002; Spence and MacLean, 2012). Salvage and pre-salvage logging operations induced by the hemlock woolly adelgid led to accelerated hardwood regeneration, indicating a shift in the future forest type away from hemlock dominance (Brooks, 2004; Kizlinski et al., 2002). Elsewhere, salvage logging following a spruce budworm outbreak had different impacts on balsam fir regeneration in stands that were pre-commercially thinned to reduce hardwood density (prior to the salvage logging) and those that were not (Spence and MacLean, 2012). Clearcut salvage operations in Midwestern black ash forests altered water dynamics on a different timeline than simulated mortality due to EAB, delaying a drop down in the water table that impacted vegetation regrowth post-harvest (Slesak et al., 2014). In the upland systems we examined, canopy openings created by harvests likely promoted recruitment of white ash given it is considered a gap-obligate tree species in these ecosystems (Leak, 1999).

Aside from white ash, the plots we surveyed did not show shifts in understory prevalence of other species like those captured by Brooks et al. (2004) after hemlock woolly adelgid-induced salvage logging. Sugar maple was the most prevalent tree species in the understory across treatment groups, consistent with pre-EAB northern hardwood forests in the region (Brooks et al., 1992). The differences in sapling layer composition between harvested and unharvested sites were largely due to the prevalence of more shade-intolerant species growing in harvested sites, a common outcome of increased light availability due to harvesting (Kern et al., 2013). Whereas the diffuse canopy openings caused by EAB mortality in mixed forests elsewhere have led to accelerated forest development towards greater dominance by shade tolerant trees and shrubs (Dolan and Kilgore, 2018) and loss of ash in the understory (Burr and McCullough, 2014; Klooster et al., 2018), we found that harvests may help sustain options for this species in sites where canopy ash are removed.

4.3. Conclusions and management implications

Our study found that harvests motivated by EAB invasion exhibited a range of impacts on northern hardwood forest composition and structure. White ash was the species most intensely harvested, with a large decrease in overstory basal area, but conversely an increase in understory density. Other species were harvested as well; in all but a few cases, EAB was not the sole factor driving management activities assessed in this study. Overall severity and post-harvest basal area were in line with typical silvicultural practices in the region, and understory compositional differences between harvested and control sites were comparable to typical post-harvest succession.

Recent work demonstrating more variability in white ash mortality from EAB, in some areas even a majority of ash surviving post-invasion, has emphasized the need for a range of management approaches to ash (Robinett and McCullough, 2019; Steiner et al., 2019). Maintaining ash in the face of EAB may benefit from silviculture that both preserves mature ash and promotes new recruitment and growth, such as increasing light availability for young trees, especially considering the obstacle of a diminished seedbank resulting from EAB-induced mortality (Klooster et al., 2014). This approach is supported by our finding that harvested sites had more white ash saplings than unharvested ones.

In addition, other management approaches, such as chemical protection of ash and biological control of EAB, are being increasingly used and can work in conjunction with silvicultural strategies to promote ash persistence and regeneration (D'Amato et al., 2023b; McCullough, 2020). A combined approach to managing both ash regeneration and EAB directly is especially important in light of findings that endemic EAB populations remain in aftermath forests with reduced white ash phloem area (Robinett et al., 2021), as well as in sapling-sized ash trees (Aubin et al., 2015). This work has broadened our understanding of the outcomes of management responses to forest pests, particularly in forests where the affected species are a component of mixed stands. Future work on this topic can expand our understanding of the scale and breadth of EAB-influenced harvesting practices by observing sites over a longer period and by isolating the impacts of specific management practices through manipulative studies. This knowledge can help inform future management actions and contribute to a greater understanding of the secondary impacts of invasive forest pests.

CRediT authorship contribution statement

Higgins Hanusia: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Siegert Nathan W.:** Writing – review & editing, Visualization, Validation, Methodology, Funding acquisition, Conceptualization. **D'Amato Anthony W.:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The dataset for this study is available at the following link:

Data for: Effects of harvest treatments anticipating emerald ash borer invasion on northern hardwood forests in New England, USA (Mendeley Data)

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