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The effects of intensive eradication efforts for Asian longhorned beetle on understory plant communities, tree regeneration, and forest structure in southern New England hardwood forests

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ABSTRACT

The United States has been experiencing an influx of nonnative pests due to increased globalization, and these pests have the potential to permanently alter the composition, structure, and function of forests. Asian longhorned beetle (ALB) is an invasive pest detected in Worcester, MA in 2008, where it invaded both urban and natural forested areas. As a part of the eradication measures (full host removals, herbicide treatments, and stump grinding), all host tree species, primarily *Acer spp*. were removed to prevent the spread of ALB. While these eradication measures successfully eliminate ALB, little is known about their effects on forest structural and compositional conditions and recovery over time. To address this, we examined forest compositional and structural development following eradication treatments and in adjacent unimpacted forested areas. Overall, our results indicated forest recovery followed similar pathways documented after natural disturbances in southern New England forests. There was little difference among eradication treatments in terms of the resultant forest composition and structure. Overall, forest types shifted to primarily oak-hickory or pine dominance following the removal of all *Acer spp*. Notably, maple species were present in high numbers in the regeneration layer regardless of treatment, followed by other early colonizing species. Red maple (*Acer rubrum*) was the most abundant sapling and seedling species and stump sprouting occurred at 60% of sites but was absent in untreated areas. These results suggest that ALB management does not drastically alter forest compositional dynamics in these mixed species forests in the short term, despite significant reductions in the abundance of mature host species through eradication treatments.

1. Introduction

Increased globalization has contributed to the introduction of nonnative pests and pathogens via trade with estimates suggesting that 2.5 new invasive pests are introduced to the United States per year (Aukema et al., 2011; Krist et al. 2014; Lovett et al. 2016). Several nonnative pests have become extensively established in forests in the United States and have greatly affected the distribution and health of tree species and ecosystems. For example, beech bark disease, a scale insect, *Cryptococcus fagisuga*, and fungi *Neonectria* complex established in North America in the late 1800s, has since shifted the structure and density of northern hardwood forests, including reducing the number of large diameter *Fagus grandifolia* and creating extensive beech thickets (Forrester et al. 2003; Lovett 2016). Beech leaf disease, caused by an invasive nematode, *Litylenchus crenatae mccannii*, now threatens these same forests (Carta et al. 2020). More recently, the invasion of hemlock woolly adelgid, *Adelges tsugae*, from East Asia in the 1950s, has caused widespread loss of the foundation species, *Tsuga canadensis* and is responsible for cascading effects on ecosystem-level dynamics, including water quality and soil ecosystem processes such as nutrient leaching (Ellison et al., 2018; Jenkins et al., 1999). Widespread ash mortality caused by emerald ash borer, *Agrilus planipennis*, also threatens the persistence of these tree species in North America (Klooster et al., 2018). These and other invasive pests have resulted in potentially permanent effects on the ecosystems they have invaded.

Invasive pests present both short and long-term effects on ecosystems

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and the communities they invade. Short-term impacts on trees and forests include defoliation, decreased vigor, and reduced growth (Ellison et al., 2018; Heuss et al., 2018; Engelken et al., 2020). Long-term impacts include ecosystem-wide effects such as species loss, tree death, shifts in nutrient cycling, alterations in wildlife habitat, and changes to above and belowground productivity, with these changes often constituting a lasting driver of processes in an ecosystem (Lovett et al., 2006). Evaluating the potential ecological impacts of a given invasive pest requires consideration of the distinctiveness and abundance of the host species impacted and the short and long-term effects on individual trees and ecosystem functions and dynamics (Lovett et al., 2006).

Asian longhorned beetle (ALB), *Anoplophora glabripennis* (Coleoptera: Cerambycidae), is an invasive pest that has caused significant ecological and economic effects on urban forests in North America. First detected in the mid-1990s in North America, ALB is native to China and Korea (Hu et al., 2009; Haack et al., 2009; Haack et al., 1997; USDA, 2018; Nowak et al., 2001). This woodboring polyphagous beetle attacks several genera of trees in North America that constitute major components of temperate forests, including *Acer* spp., *Aesculus* spp., *Betula* spp., *Salix* spp., and *Ulmus* spp. (Gao et al, 1993; UMASS, 2016). Female ALB chew into the bark to lay their eggs in the phloem in the summer. Larvae hatch under the bark and feed in the phloem before moving into the sapwood and heartwood where they cause significant structural damage to trees. Adult emergence occurs the following year or longer in some regions (Hu et al., 2009). Successive years of attacks on the same trees compromise internal tree function and lead to a loss of vigor, and ultimately widespread tree mortality after 5–10 years (UMASS, 2016; Hull-Sanders et al., 2017).

Most ALB infestations have occurred in urban settings, with impacts limited to boulevard trees, greenways, or isolated residential plantings; however, the 2008 infestation in Worcester, Massachusetts USA moved outside of the city and into adjacent forested areas, which were largely dominated by host species, such as *Acer* spp. The resulting quarantine area around Worcester is the largest documented for an ALB infestation with 284.9 square kilometers currently regulated. The spread of this nonnative insect into forested areas provided opportunities to study ALB in more natural forests. Stand assessments of ALB impact on composition, structure, and growth suggested no differences in radial growth between infested and unifested trees, as well as indications that *Acer rubrum* was a preferred host in these stands (Dodds and Orwig 2011). Evaluations of short-term impacts suggest ALB has the potential to significantly shift species composition in these systems away from *Acer* spp. dominance with reductions in aboveground biomass and mature forest conditions (e.g., large diameter trees) (Dodds et al., 2014). Nevertheless, assessment of ALB activity and/or eradication methods on post-eradication forests is needed to better understand longer-term effects in these forested communities.

Eradication techniques employed by USDA Animal and Plant Health Inspection Service (APHIS) and foresters following the infestation of ALB in forest stands include full host removals (mechanical removal of all host species), herbicide treatments (removals of host species with application of herbicide to cut stumps), and stump removals (removal of stumps after tree cutting) (UMASS, 2016). These eradication methods continue to be used in the areas of North America with known ALB infestations, namely Worcester, MA, Central Long Island, NY, Clermont County, OH, and Charleston County, SC. While these methods have been successful in eradicating ALB from several urban locations, it is not yet known what effect eradication efforts will have on the long-term composition, diversity, and structure of natural forests. Long-term tree mortality from ALB or host removals associated with its management has been predicted to lead to stands dominated by the non-host, *Quercus spp*., which was the species of next greatest abundance in impacted forests in Massachusetts (Dodds and Orwig, 2011).

Asian longhorned beetle is predicted to continue to be an issue in the United States and worldwide (Peterson and Hargrove, 2004). This study builds on the research surrounding the effects of ALB on forests and urban areas in Worcester County, MA and contributes to the understanding of forest and vegetation response to management associated with ALB eradication over time. The objectives of this study were to assess the impacts of the ALB eradication efforts five years post-management on different forest types and across eradication treatments by quantifying: i) the composition and structure of the overstory layer, ii) the composition, diversity, and richness of the regeneration layer and iii) the presence of invasive plant species in the herbaceous and woody shrub layers across forest types and ALB eradication treatments.

2. Methods

2.1. Study area and design

Field sites were in Worcester County in central Massachusetts and selected in conjunction with foresters from Massachusetts Department of Conservation and Recreation (DCR) and the APHIS ALB program based on two factors: 1) located within the active quarantine boundary and 2) treated with ALB eradication harvests between 2008 and 2015 (Fig. 1). Sites sampled include white pine hardwood forests ($n = 5$), oak hardwood forests ($n = 5$), and red maple hardwood forests ($n = 5$). All sites selected were subject to full host removals of all ALB host species present, including *Acer rubrum, Acer saccharum, Acer platanoides*, and *Betula* spp. Treatments included full host, FH, (removals cut all stems $\geq$2.54 cm diameter breast height [DBH, 1.3 m height] of all ALB host species), herbicide, H, (full host removal plus application of Garlon 4 Ultra and Triclopyr herbicide to cut stumps), and stump ground (SG) (full host plus stump removal and grinding) (Table 1). Controls representing one of each forest type ($n = 3$) were established within quarantine bounds and located in areas uninfested with ALB and adjacent to treated areas when possible. Given we were unable to find replicates of unimpacted control areas, these sites serve as a general benchmark for comparing treatment impacts within a given forest type but were not included in statistical analyses of treatment effects.

Worcester County is in the northeastern highlands ecoregion, with soils in our study sites largely characterized as fine sandy loam soils over schist and phyllite bedrock (NRCS Soil Survey, 1985, Zen et al, 1983). This region receives an average of 128 cm of precipitation annually with average minimum and maximum temperatures ranging from −9.1–26.0° C from 1987 to 2017 (PRISM Climate Group, 2004).

2.2. Field methods

Field sampling of woody vegetation, ground level vegetation, and coarse woody material at each site occurred 5–7 years following overstory host removal in three, circular 0.04 ha plots. Plot placement was along a transect to ensure adequate coverage of forest conditions in each area. Plots were set at least 50 m apart from one another, as well as from the forest edge or roads. Each plot was set up according to Forest Health Monitoring (FHM) program protocols (Fig. 2, Alexander and Barnard, 1994). We sampled forest types that are representative of this region.

In each plot, species and diameter at breast height (DBH) were recorded for all living and standing dead overstory trees, $\geq$10 cm DBH. Saplings were measured in 40 m^2 subplots at 5.5 m from plot center at azimuths of 0, 120, and 240°. Saplings were defined as individuals greater than 1.3 m tall and <2.54 cm DBH and were tallied by species. Seedlings <25 cm tall and <2.54 cm DBH were tallied by species in 5 m^2 subplots nested within the sapling plots.

Ground layer vegetation was tallied and recorded in three 1-m^2 subplots at 4 m from plot center at azimuths of 60°, 180°, and 300°. Percent cover of herbaceous and woody species <25 cm tall were recorded in each sub-plot by life form and cover class. Life forms were as follows: herb (H), fern (F), sedge/grass (S/G), bryophyte (B), and bare soil (S). Cover classes were classified by percent cover from 1 to 6 (1 = trace-1%, 2 = 1–5%, 3 = 6–15%, 4 = 16%-30%, 5 = 31–60%, 6 = 61–100%).

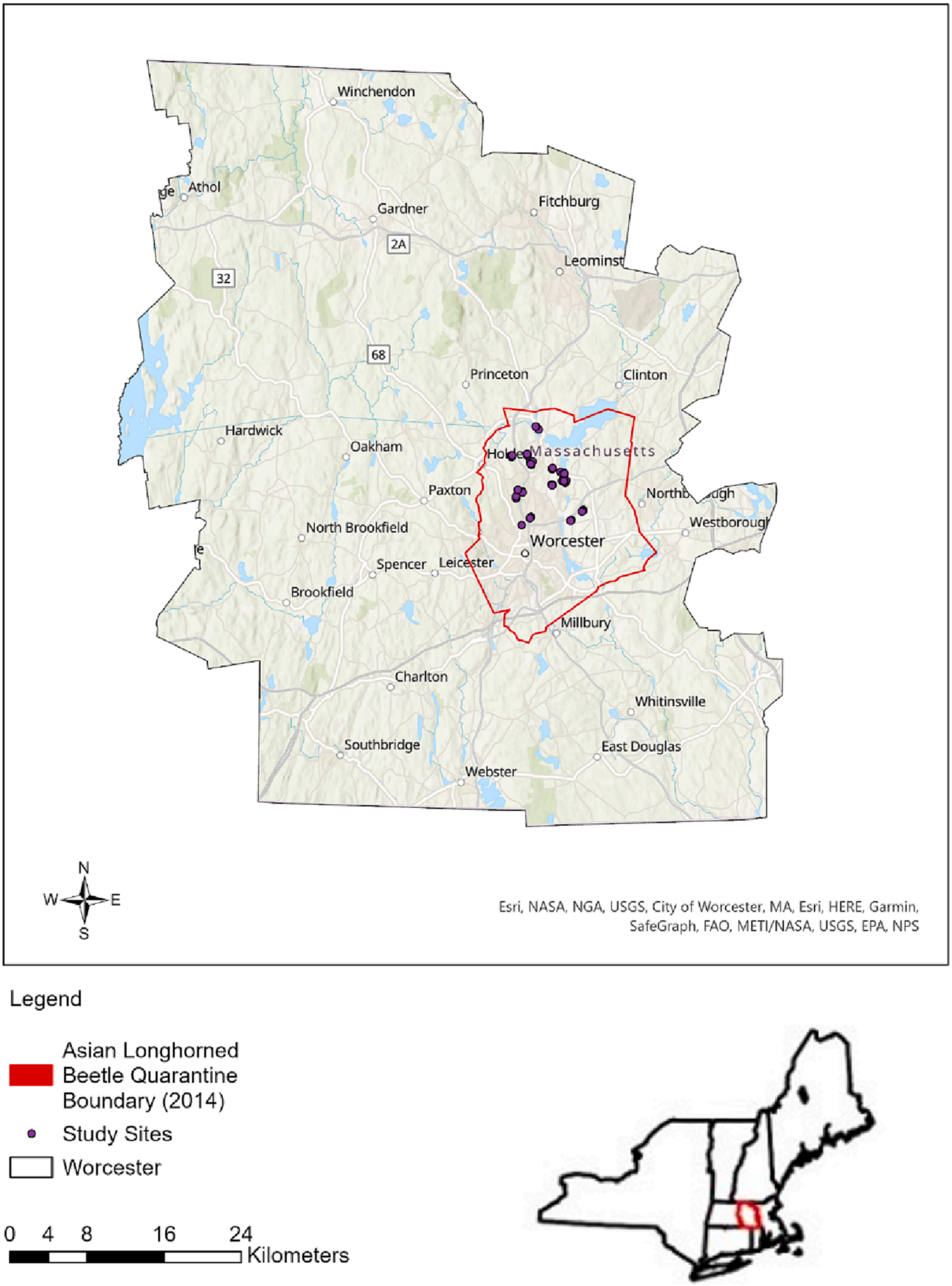

Fig. 1. Map of the study area, including Asian longhorned beetle quarantine boundary in Worcester County, MA USA with designated study sites.

Table 1
Sites in Worcester County, MA by treatment. All sites had a full-host removal, additional treatments are noted in the treatment column. Site codes are as follows: Full Host = FH, Stumps Ground = SG, Herbicide = H, and Control = C.

Treatment	Description	Treatment sample size (n)	Forest Type	Forest Type sample size (n)
Full Host Removal	All host species (primarily *Acer* spp.) were removed above 2.54 cm DBH.	4	Oak Hardwood	5
Herbicide	All host species (primarily *Acer* spp.) were removed above 2.54 cm DBH. Garlon 4 Ultra and Triclopyr was applied to stumps.	4	Red Maple Hardwood	5
Stumps Ground	All host species (primarily *Acer* spp.) were removed above 2.54 cm DBH. Stumps were then ground and chips were moved and disposed offsite.	4	White Pine Hardwood	5
Control	Sites not treated for Asian longhorned beetle, located adjacent to quarantine boundary in similar forest types.	3		

Species were identified when possible and the presence or absence of non-native, invasive species was also recorded in these plots.

Coarse woody material (CWM) was measured along three, 11.3 m transects originating from the center of each plot at azimuths of 0°, 120°, and 240° (CWM ≥7.6 cm and ≥1 m in length) following the line intercept method (Harmon and Sexton 1996). Species, intercept diameter, and decay class was recorded for each piece using a five-class system (Maser et al., 1979), with 1 being recently fallen and intact and 5 being highly decayed. When a specific species could not be identified, it was categorized as either "hardwood" or "softwood" based on wood anatomical features.

2.3. Statistical analysis

The influence of ALB eradication treatments, forest type, and their interaction on sapling and seedling regeneration density, CWM volume, and herbaceous plant community density were evaluated using generalized linear mixed model (GLM) analysis of variance (ANOVA) in R using the GLM package (R Core Team, 2018). For these ANOVAs, treatment and forest type were treated as fixed effects and site was treated as a random effect. Response variables tested included: average percent cover by life form (Percent cover classes, midpoint of the classes, were averaged), richness and diversity of the herbaceous layer, species composition and abundance of saplings and seedlings, the presence of stump sprouting, and volume of coarse woody material.

The presence of invasive plant species used a binomial distribution with a logit link, where the presence of an invasive species was indicated by a "1″ and the absence was indicated by a "0". The presence of stump sprouting also used a binomial distribution with a logit link and the same presence and absence system. Overstory basal area was averaged by site and a mixed model ANOVA was used to test for differences by treatment and forest type. The shape of diameter class distribution of trees (DBH >10.1 cm) by each treatment type was classified according to the methods used in Janowiak et al., (2008).

To examine gradients in herbaceous and woody plant composition in response to treatments and across forest types, Nonmetric Multidimensional scaling (NMS) was used in PC-Ord version 7 (McCune and Medford, 2011). Specifically, a matrix of species density was created for the sapling community. Species that were rare (two occurrences or less) were excluded from the matrix. For the herbaceous plant community, a primary matrix of percent cover averaged by plot was used. Rare species (one occurrence) were excluded from the herbaceous primary matrix. A secondary matrix was created for sites by forest type and treatment for both the sapling and herbaceous plant communities. A general relativization was done to equalize the contribution of species to the overall ordination solution. NMS was run on autopilot and slow and through conditions to determine the axes with the lowest stress that explained the most variation. Axes that described the most variation in the final ordination solution were displayed, and the correlations between axes

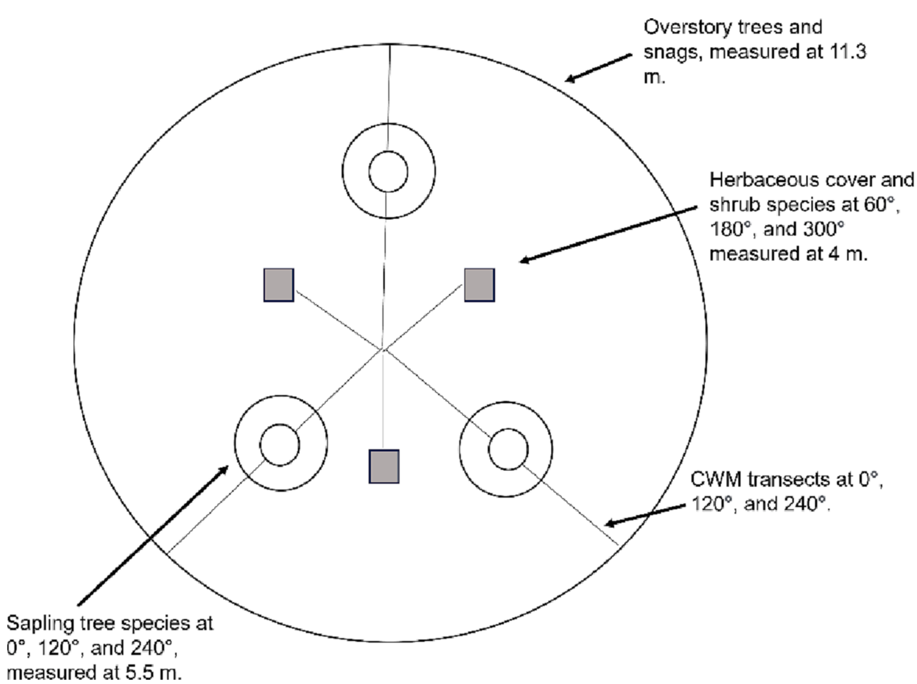

Fig. 2. A schematic of the field sampling plots and sub-plots, using Forest Health Monitoring protocol.

and species abundance were analyzed using Kendall's tau. Permutational multivariate analysis of variance tests (perMANOVA) were used to test for differences between treatment groups in terms of community composition. Finally, an indicator species analysis was used to identify species associated with treatments or forest types based upon frequency and abundance. An alpha = 0.05 was used for determining significance across all tests.

3. Results

3.1. Overstory structure and composition

Overstory tree basal area and composition varied across treatment and forest type, but there were not significant differences between treatments. White pine (*Pinus strobus*. 35.0% of total basal area) accounted for the largest percentage of basal area across sites, followed by red oak (*Quercus rubra*, 29.3%). Other hardwood species, including red maple (11.2%), white oak (*Quercus alba*, 10%), and hickory (*Carya ovata*, 3.3%), accounted for a lower percentage. White pine (42.6%) and *Quercus spp*. (40.8%) accounted for the most basal area of overstory trees in the full host (FH) treatments while *Quercus spp* (79.0%) and red maple (10.7%) accounted for the most basal area in herbicide (H) treatments. In stumps ground (SG) treatments, red oak (46.2%), and white oak (20.0%) accounted for the majority of basal area, followed by white pine (19.7%). In the control plots, red oak (33.1%) and white pine (32.9%) contributed most to average basal area. There was no difference between total basal area by treatment (f = 0.14, P = 0.93) or across forest types (f = 1.66, P = 0.27, Table 2).

Live-tree size distributions in the FH, H, and SG treatments all had negative exponential curve forms (Fig. 3). There was no significant difference between treatments or forest type in terms of quadratic mean diameter (f = 0.65, P = 0.60; f = 0.85, P = 0.45, for ALB treatment and forest type, respectively).

Non-host species accounted for most of the basal area in all treatments (30.2±0.03 m^2/ha; 88.8%) relative to host species (1.3±0.2 m^2/ha; 11.2%). There were no significant differences between total host basal area by treatment or by forest type (f = 1.95, p = 0.18; f = 0.52, P = 0.61). Average host basal area was the greatest in the H treatments (11.4±1.15 m^2/ha), and three out of four sites had host species present in the overstory. However, FH and SG treatments had only one site with host species present in the overstory. While there was not a significant difference between overstory host basal area by forest type, all of the treated sites in the oak hardwood forest type did not contain any overstory host species.

3.2. Coarse woody material and snags

There was no significant difference in volume of coarse woody material (CWM) among treatments (f = 0.21, P = 0.88) or forest type (f = 1.13, P = 0.36, Fig. 4) or biomass by treatment (f = 0.11, P = 0.95) or forest type (f = 0.87, P = 0.44). All decay classes were present in FH and SG plots, while H and control plots did not have any CWM in decay class 1. Snag volume and basal area did not vary significantly by treatment (f = 0.04, P = 0.99) or forest type (f = 0.03, P = 0.97, Table 2).

3.3. Regeneration

Total seedling density was not significantly influenced by treatment, but patterns emerged on a species-specific basis (Fig. 5). Red maple seedlings were the most abundant seedling counted across all treated sites (1650±40 stems/ha and 37.1% of all seedlings), followed by black birch and red oak at 1275±99 stems/ha (30.4%) and 450±21 stems/ha (10%), respectively. Host species (Acer spp. and Betula spp.) accounted for 26.8% of the total seedling count and were present across each treatment type. Host species density was greater in the treated sites versus the control sites, but there was not a significant difference in densities between treated and control sites.

The density of black birch seedlings was significantly impacted by treatment, with FH (P = 0.0004), H (P = 0.002), and SG treatments (P = 0.027) all having significantly different densities of this species. FH treatment had the greatest density of black birch seedlings (550±177 seedlings per hectare) followed by H (525±133) and SG (275±0; only one value). Similarly, densities of yellow birch were impacted by treatment with significantly greater densities of this species in the FH treatments (p = 0.04) relative to other treatments. Additionally, several species of seedlings had significantly higher densities by forest type, including black birch (P = 0.001) and hickory (P = 0.003) in oak hardwood forests, black birch in red maple mixed hardwood forests (P = 0.005), and white oak in white pine hardwood (P = 0.02).

3.4. Saplings

There were no significant differences in sapling density among treatments (P = 0.19) or forest type (P = 0.16). There was, however, some variation across treatment and forest type, with the most host species recorded in FH treatments, followed by H (Fig. 6). The SG treatment had the fewest host species recorded. Stump sprouting, noted qualitatively, occurred at approximately 60% of sites and was noted across treatment and forest type. There was no significant relationship between the presence of red maple stump sprouts by treatment (P = 0.59) or forest type (P = 0.92).

As with seedling count totals, red maple was the most abundant sapling species totaling 15,250±454 stems/ha (43.4% of all stems) across all treatments. The density of red maple did not vary across treatments (P = 0.56). White pine and black cherry were the next most abundant saplings counted at 7525±162 stems/ha (19.5%) and 2850 ±146 stems/ha (8.1%), respectively.

Negative binomial GLMs indicated that certain species of saplings

Table 2
Average stand characteristics (±standard error) by treatment and forest type. Average overstory basal area, trees per hectare, quadratic mean diameter, coarse woody material volume and biomass, and total snag basal area.

Variable	N	Overstory Basal Area (m^2/ha)	Trees per Hectare	QMD (cm)	CWM Volume (m^3/ha)	CWM Biomass (Mg/ha)	Snag Basal Area (m^2/ha)
Treatment							
Full Host	4	33.6±7.2	525±118	29.8±4.8	17.1±4.0	6.0±1.7	1.47±1.1
Stumps Ground	4	34.4±4.6	383±94	35.9±6.0	23.2±6.0	7.1±1.5	1.88±0.1
Herbicide	4	30.68±4.7	400±61	31.4±3.5	17.9±10.1	5.4±3.6	1.56±1.0
Control	3	29.9±5.2	556±139	26.7±2.6	16.2±4.4	5.5±1.6	1.87±1.1
Forest Type							
White Pine Hardwood	5	32.8±2.2	387±45	32.6±3.2	22.5±6.9	6.9±2.6	1.76±0.7
Oak Hardwood	5	33.1±5.2	407±84	33.9±5.0	19.7±4.7	7.1±1.5	1.60±0.9
Red Maple Mixed Hardwood	5	30.9±4.8	587±105	27.1±3.3	14.1±5.0	4.0±1.1	1.88±1.0

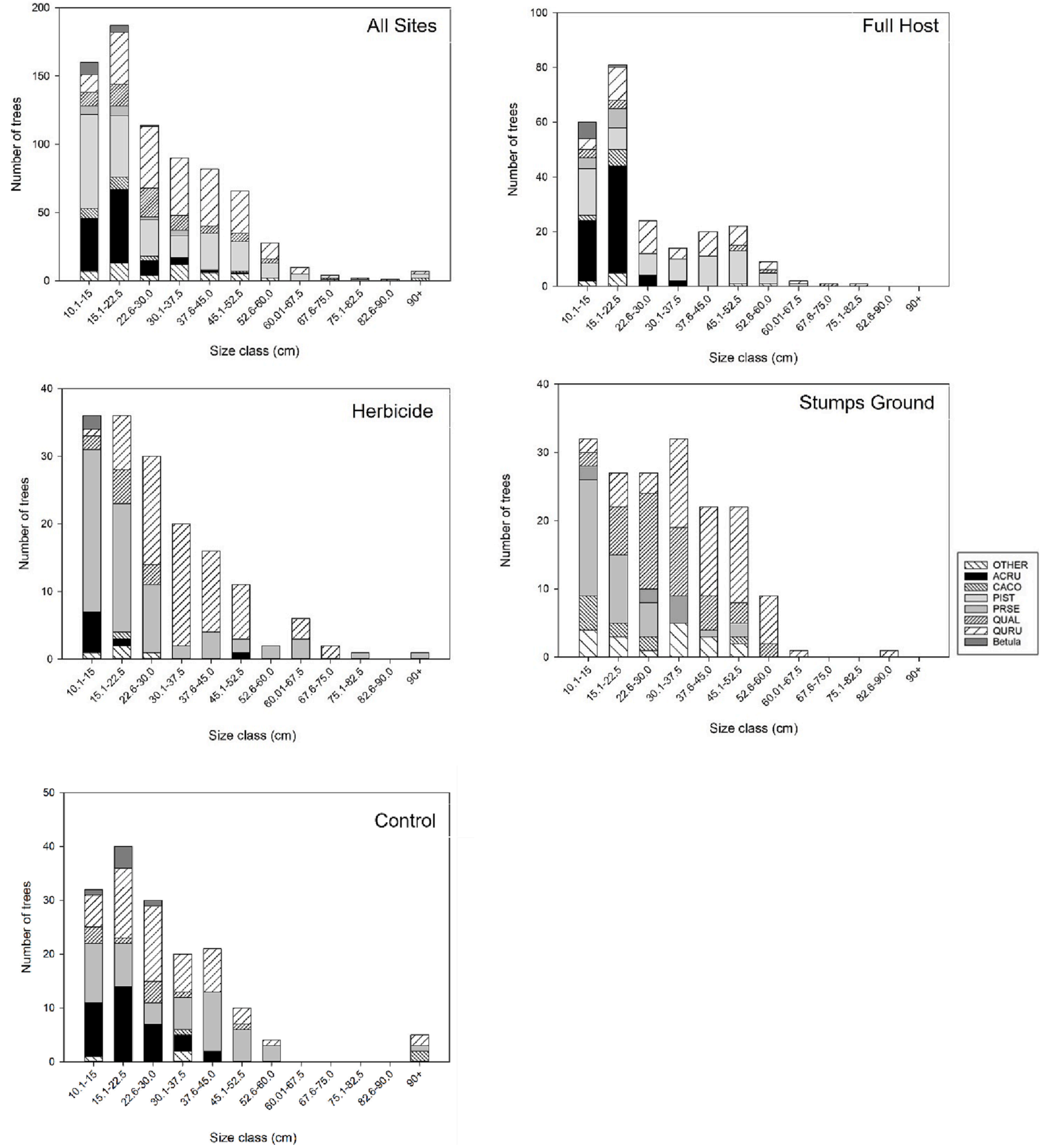

Fig. 3. Diameter at breast height (DBH) size class distributions by treatment and across all sites. Species are denoted by their four-letter codes: ACRU = red maple, CACO = shagbark hickory, PIST = white pine, PRSE = black cherry, QUAL = white oak, QURU = red oak, Betula = birch species, other = uncommon minor species, including basswood, hemlock, and red pine.

had greater densities in a given forest type or treatment. Red maple ($P = 0.04$) and eastern cottonwood ($P = 0.02$) had significantly higher densities in the SG treatment. The density of serviceberry was significantly greater in the red maple mixed hardwood forest type ($P = 0.04$).

3.5. Woody plant community composition

Woody plant species composition varied across treatments and forest types, as evidenced by the non-metric multidimensional scaling (NMS) ordination, which produced a three-dimensional solution explaining 69.2% of variation in the data (final stress = 9.94, p-value = 0.03,

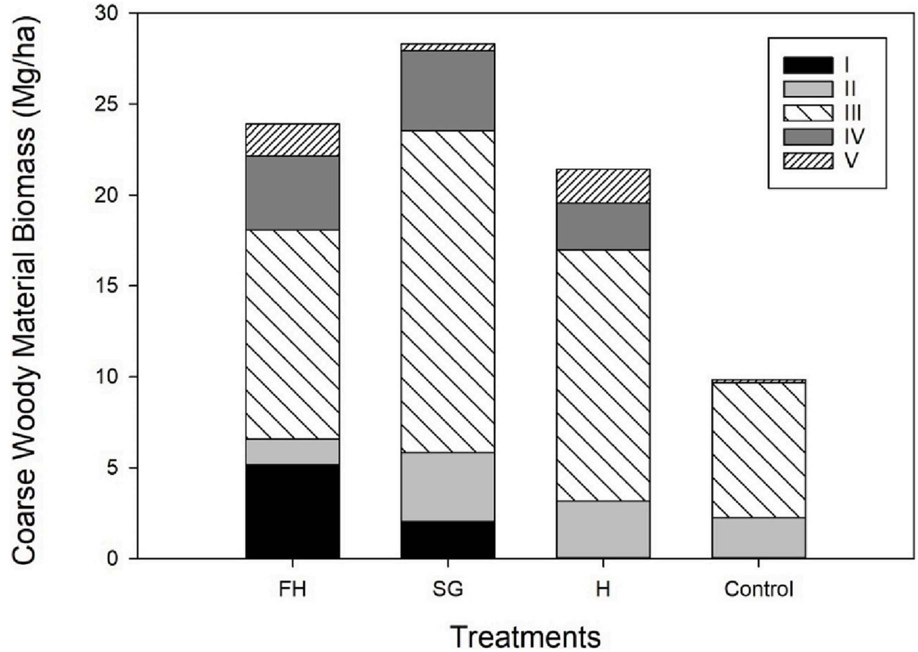

Fig. 4. Coarse woody material biomass by decay class across eradication treatments with decay class 1 = least decayed and decay class 5 = most decayed. FH = full-host removal, SG = stumps ground, and H = herbicide. Decay classes are according to Maser et al., 1979.

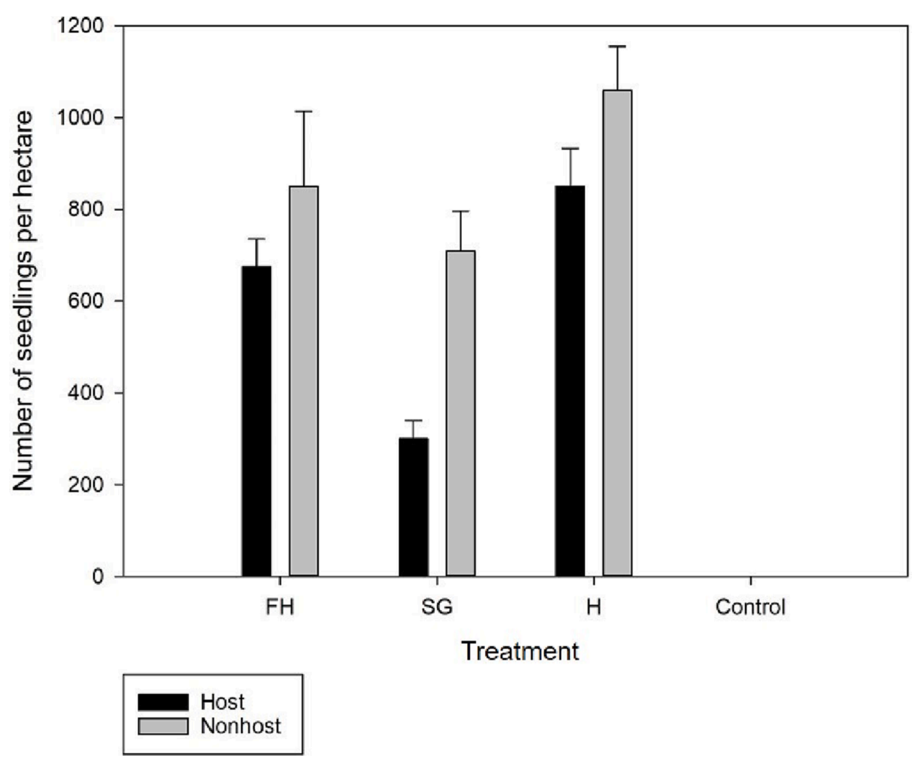

Fig. 5. Number of host and non-host seedlings by hectare categorized by treatment type (Stems ± SE). There were no significant differences between treatments and no seedlings present in control plots.

instability = 0; Fig. 7).

Axis 1 explained 54.7% of the variation and ranged from C and FH treatments in the negative portions to SG treatments in the positive portions. Axis 1 included H sites in the negative portion of the axis. This axis was positively correlated with yellow birch ($\tau = 0.547$) and hickory ($\tau = 0.541$) and negatively correlated with white pine ($\tau = -0.522$) and red maple ($\tau = -0.604$) (Table 3). Axis 2 largely contained plots from the H treatment and FH in the positive portion of the axis. Axis 2 explained a cumulative 14.5 % of the variation and was positively correlated with black birch ($\tau = 0.445$) and American beech ($\tau = 0.642$) and negatively associated with eastern cottonwood ($\tau = -0.552$) and red oak ($\tau = -0.545$). A final PerMANOVA analysis indicated that there was no significant difference in woody species community composition between treatments ($f = 1.59$, $P = 0.13$) or forest type ($f = 1.30$, $P =$

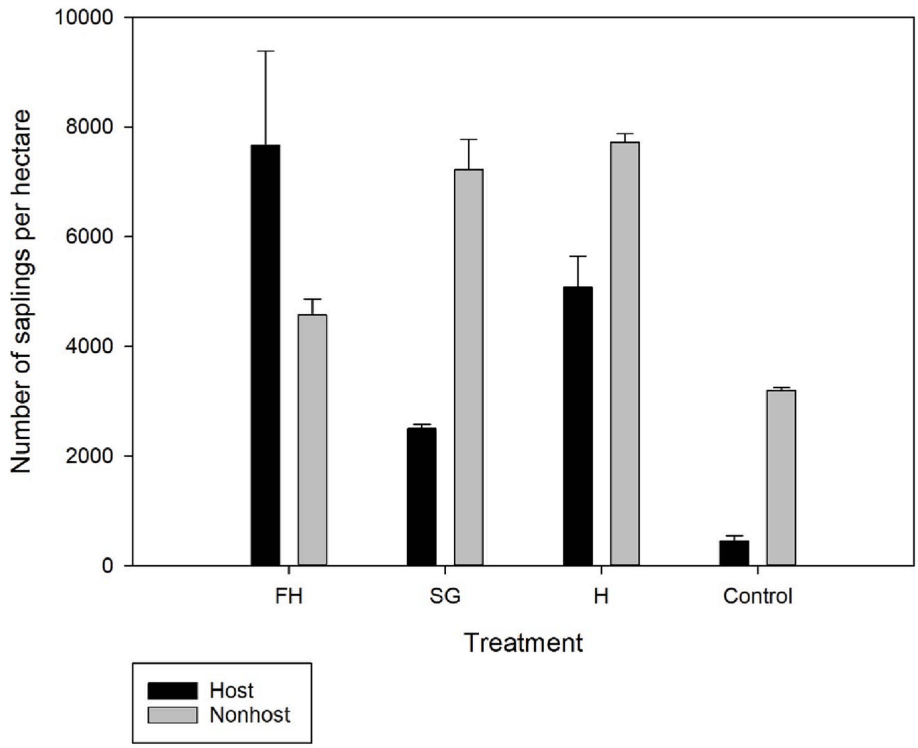

Fig. 6. Number of host and non-host saplings by treatment type (Stems ± SE). There were no significant differences between treatments.

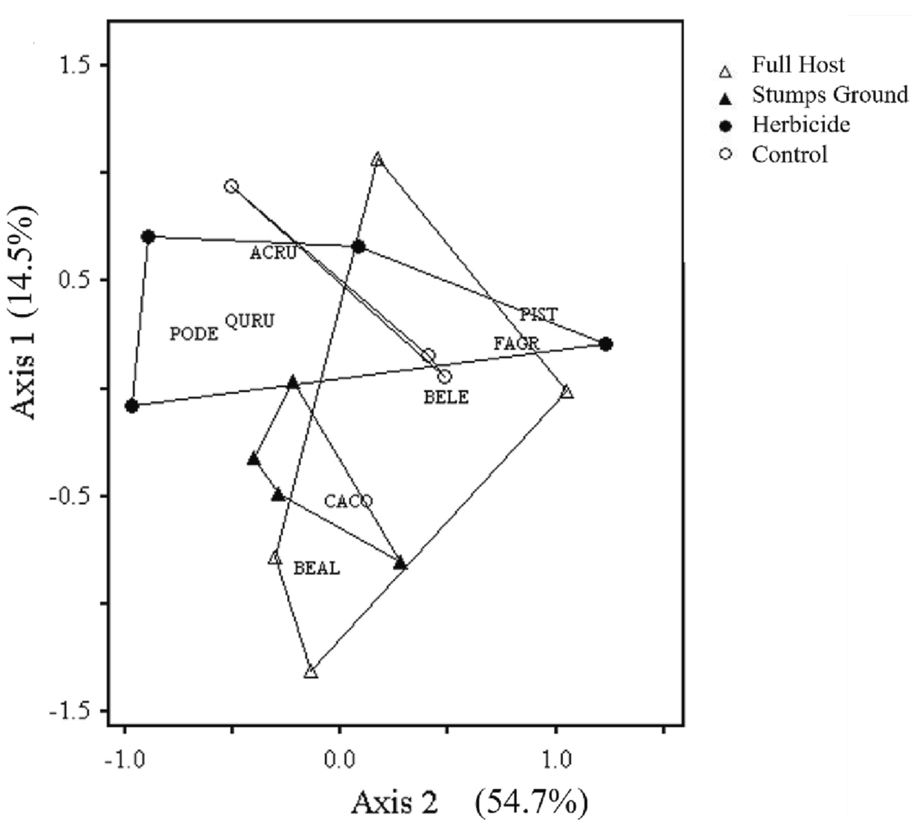

Fig. 7. Nonmetric multidimensional scaling (NMS) for sapling species by treatment. Species are denoted by their four-letter codes and are located on the axis according to their weighted average species score. Only species significantly correlated with either axis are shown.

0.25) or their interaction (f = 0.97, $P = 0.56$). Hickory ($P = 0.02$) and black cherry ($P = 0.03$) were significantly associated with the SG treatment based on indicator species analysis. No species were significantly associated with any forest type.

Table 3
Correlation between sapling species densities and NMS axis scores based on Kendall's tau. * P < 0.05, ** P < 0.01.

Species	Common Name	Axis 1	Axis 2	Axis 3
ACRU	Red Maple	−0.201	−0.604**	−0.179
ACRU.S	Red Maple (S. denotes stump sprout)	−0.067	0.358	0.269
BEAL	Yellow birch	−0.047	0.547*	−0.078
BELE	Black birch	0.445*	0.134	−0.217
BEPO	Gray Birch	0.158	0.063	0.570**
CACO	Hickory	−0.229	0.541**	−0.187
FAGR	American beech	0.642**	−0.237	0.237
PIST	White pine	0.116	−0.522**	0.155
PODE	Eastern cottonwood	−0.552*	0.110	0.166
PRSE	Black cherry	−0.381	0.313	0.045
QUAL	White oak	0.206	0.226	0.082
QURU	Red Oak	−0.545**	−0.248	0.367

3.6. Herbaceous and shrub community composition

There were 28 unique species recorded, four of which were invasive species, across all treatments and forest types (*Berberis* sp., *Microstegium* sp., *Rhamnus frangula*, *Celastrus orbiculatus*). Despite detecting these invasive species, they represented a small proportion of understory plants across all treatments and there was no significant difference between treatments in terms of their occurrence. Species richness ranged from 6 to 9 species in the FH treatment, 4–8 in the SG, 4–8 in H, and 3–6 in control plots (app endix). There was no significant difference between richness, evenness, or Shannon's index between treatments. Shannon's diversity was significantly different between forest types (p-value = p < 0.0005) with white pine hardwood have significantly lower understory plant diversity than oak-hardwood and red maple hardwood, which were not significantly different from one another.

As with woody plant communities, there was a high degree of variation within and across treatments in herbaceous and shrub communities, as illustrated by NMS. The NMS analysis produced a three-axis solution with a final stress value of 9.9943 ($P = 0.0319$, instability = 0). The solution accounted for 53.9% of variation in the data with axes 2 and 3 explaining the most variation in the data (Fig. 8). Axis 2 explained 35.7% of the variation and was positively associated with herbicide treatments and negatively correlated with barberry ($\tau = -0.468$) and stilt grass ($\tau = -0.5$). Axis 3 explained 28.2 % of the variation and was positively associated with SG plots, and negatively correlated with blueberry ($\tau = -0.41$) and starflower ($\tau = 0.48$) and positively correlated to bryophyte *spp.* ($\tau = 0.45$) and fern *spp.* ($\tau = 0.45$) (Table 4). Bryophyte *spp.* were significant indicator species for the stumps ground treatment, but no other species were significant by treatment (p = 0.0008). There were no significant differences between forest type, treatment, or their interaction in terms of understory species composition based on PerMANOVA. (f = 0.98, $P = 0.52$).

4. Discussion

Invasive pests are one of the most pressing threats to forest health in many regions of the globe. This study contributes to our understanding of the near-term effects of targeted eradication treatments designed to mitigate ALB in North American forests. Although short-term and observational in nature, this study is the first examination of forest development in natural forest settings following ALB eradication treatments, including full host removal, herbicide treatment of stumps after tree removal, and stump grinding after tree removal. Results from this work indicate that patterns of recovery are consistent with post-disturbance trajectories previously documented for mixed temperate hardwood forests in northeastern North America (Plotkin et al. 2013; Orwig et al., 1998, Taylor et al., 2017), including post-disturbance recruitment of ALB host species.

Our results suggest that ALB eradication efforts do not significantly

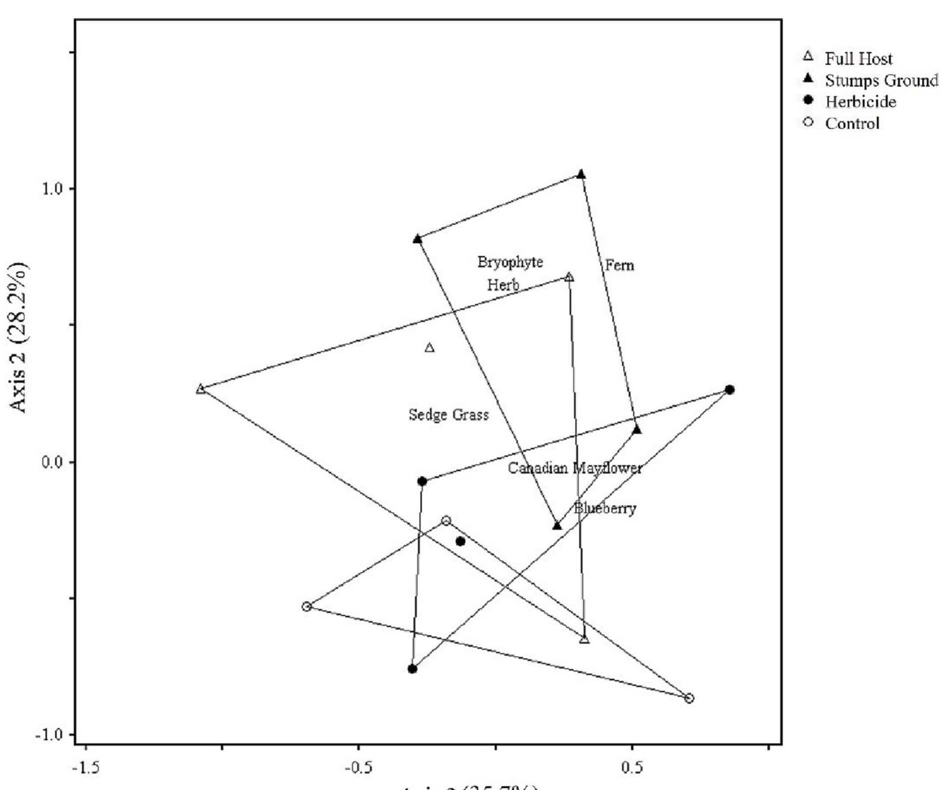

Fig. 8. Nonmetric multidimensional scaling (NMS) for understory plant communities by treatment. Axis 2 and 3 are presented given they explained the most variation in the data. Species location are based on weight average scores with only species significantly correlated with at least one axis displayed.

Table 4
Results of the understory species correlation species by each axis based on Kendall's tau. P < 0.05, ** P < 0.01.

Species	Common Name	Axis 1	Axis 2	Axis 3
Berberis vulgaris	Barberry	−0.169	−0.056	−0.470*
Microstegium vimineum	Stilt Grass	−0.500*	0.122	−0.278
Parthenocissus quinquefolia	Virginia Creeper	−0.282	0.432	−0.094
Toxicodendron radicans	Poison Ivy	−0.304	0.386	−0.414
Athyrium filix-femina	Lady Fern	−0.524*	−0.028	0.331
Dryopteris	Wood Fern	−0.247	−0.082	0.270
Cyanococcus	Blueberry	0.411*	−0.451*	−0.17
Maianthemum canadense	Canadian Mayflower	0.425*	−0.213	−0.97
Viburnum acerifolium	Maple Viburnum	−0.094	−0.169	0.319
Dendrolycopodium dendroideum	Prickly Clubmoss	−0.386	−0.304	0.110
Hamamelis	Witch Hazel	−0.244	−0.319	−0.094
Trientalis borealis	Starflower	−0.016	0.275*	0.016
Rubus	Raspberry	−0.234	0.016	−0.328
Dryopteris filix-mas	Male Fern	−0.169	0.131	−0.169
	Sedge/Grass Spp.	−0.411*	−0.050	−0.531**
	Herb Spp.	0.484*	0.391	0.141
	Bryophyte Spp.	0.149	0.447*	0.021
	Fern Spp.	−0.109	0.453*	0.328

impact understory herbaceous or woody plant community composition or the presence of invasive plant species in these stands. As expected, overstory basal area was primarily composed of non-host species across both treatment and forest types. There were no significant differences in total sapling density or plant abundance among ALB eradication treatments, but several understory plant and tree species were more commonly associated with certain treatments. In contrast, host species accounted for the greatest portion of sapling and seedling tree species (43.4%) in areas experiencing ALB eradication treatments, suggesting developmental trajectories towards future vulnerability of these sites to ALB. Overall, forest recovery reflects the resiliency mechanisms and recovery patterns common to temperate hardwood forests following a large-scale disturbance (Santoro and D'Amato, 2019), suggesting that despite generating significant changes to mature tree structure, the ALB eradication treatments maintain compositional conditions associated with these ecosystems.

4.1. Effects of host removals on forest composition

Nonnative invasive insects and fungal diseases can functionally eliminate host tree species from a forest and shift overstory species dominance, such as in the historical case of chestnut blight and the ongoing threat of emerald ash borer (Lovett et al. 2006, Herms et al. 2014). Pre-emptive salvage logging or sanitation harvests of host species can have a similar effect (Elliott and Swank, 2008; Herms and McCullough, 2014; Waring and O'Hara, 2005; Kizlinski et al., 2002). In the cases of ALB, host removals applied largely as sanitation harvests have been effective at containing invasions and eliminating populations of ALB in urban environments, namely in the Canadian and US cities of Toronto, Chicago, and Brooklyn, Islip, Staten Island, Manhattan, Queens, Boston, and Jersey City (APHIS, 2016; Haack et al., 2009, Liebhold and Kean, 2019) with concomitant impacts on shade trees. In the present study, the preemptive removal of host species, primarily *Acer* spp., from the overstory has not led to their functional elimination in stands, but instead increased their density in the seedling, sapling, and smaller diameter canopy tree classes. Nevertheless, the general shift toward non-host overstory species dominance that we documented was consistent with predictions from initial surveys of forest conditions in our study area that forecasted these forests would most likely shift to predominately oak and hickory species (Dodds and Orwig, 2011).

The maintenance of host species in these forests following sanitation harvests is in contrast to the results of model simulations of pre-emptive salvage harvests of *Fraxinus americana* in advance of emerald ash borer in New England forests, which led to significant reductions in host species abundance (MacLean et al., 2020). These differences may be related to the limited ability of *F. americana* to recruit in the partial canopy openings associated with its selective removal from mixed species forests (D'Amato et al. 2020) relative to the *Acer* spp. examined in the present study (see below).

The compositional conditions of the forests we examined were largely influenced by previous forest management and a history of post-agricultural abandonment prior to ALB infestation in the region. As such, the responses we observed are largely a reflection of the interaction of sanitation treatments with the stand structural and compositional conditions present in these systems (Dodds and Orwig, 2011; DCR, 2018; Foster et al., 1998). For example, diameter distributions for all treatments were characteristic of stratified, even-aged stands (reverse-J curve) (Janowiak et al., 2008; Oliver and Stephens, 1977). In addition, the overstory layer of many sites were dominated by white pine, *Quercus* spp., and *Carya* spp., all of which are common in areas with a historic legacy of clearing for agriculture (in the case of white pine) and harvesting of second-growth stands (*Quercus* spp. and Carya spp.; Foster, 1992). These three species were also in high abundance before ALB infestation in some previously studied sites as well (Dodds and Orwig, 2011). Furthermore, the presence of host species in the overstory in our study could be due to trees missed in the initial eradication treatments. This factors are important to consider when interpreting our findings of *Acer* species identified in the overstory. As such, the composition of these forests did not change dramatically after the host removals with conditions like many other areas experiencing historic, intensive land use in south-central New England (Foster et al. 1998).

4.2. Regeneration of seedlings and saplings

Post-disturbance regeneration patterns in the areas we sampled were more significantly influenced by forest type, site characteristics, and regeneration mechanisms of the constituent species than by the host treatments themselves, a pattern that aligns with previous studies from other temperate forests (Dodds and Orwig, 2011; Plotkin et al., 2013; Orwig et al., 1998, Taylor et al., 2017). Following disturbance, such as the eradication treatments we examined, the regeneration layer is not species rich, and species that can adapt readily and tolerate changes in the microclimate are most dominant (Lindenmayer and Ough, 2006). However, in our study, the understory sapling and herbaceous layer remained diverse with no indication of invasion by non-native woody species five years from the time of disturbance. Furthermore, there was no significant difference between the sapling and seedling composition or density by treatment or forest type. The majority of sapling species recorded were red maple, as well as several shade intolerant species, including *Carya* spp., black cherry, and gray birch. However, given the short-term nature of this study (5–7 years post-removal), other species may eventually dominate both the canopy and understory layers (e.g., Hoven et al. 2020; Zhu et al., 2014). For example, studies examining long-term forest recovery after windthrow and associated salvage logging treatments have demonstrated that initial differences in communities are reduced over time (Lang et al., 2010; Peterson and Leach, 2008). Nevertheless, the early patterns we observed are different than those observed following pre-salvage harvests in response to hemlock woolly adelgid (HWA), where post-harvest regeneration was dominated by native, intolerant tree species and invasive species favored by the levels of disturbance generated by host tree removals (Brooks, 2004; Foster and Orwig, 2006; Orwig et al., 1998). We did not record seedlings in the understory of control sites. The controls sampled were second-growth forests in the late stem exclusion stage and had limited regeneration. The lack of ruderal and introduced species in the sapling layer of the systems we examined may reflect a greater ability of current overstory species to regenerate in response to the disturbance levels generated by sanitation treatments (See below).

4.3. Host species recovery

Overall, our results indicate that the current composition of sapling and seedling species is more likely influenced by forest type and resilience mechanisms than by the different treatments employed (Plotkin et al., 2013; Peterson and Leach 2008; Palik and Kastendick, 2009). Many of the species seen in high abundance in the areas we sampled are species common to disturbed forests, such as white pine, black cherry, and white oak (Oliver and Stephens, 1977; Ellison et al., 2018). In our study sites, we found high amounts of host seedlings and saplings returning in the understory, suggesting that host species are recovering despite the application of treatments designed to reduce their presence in these systems. Red maple is a shade-tolerant generalist, a prolific sprouting species, and common in forests with disturbed soils (Abrams, 1998). Red maple and white pine, the most abundant saplings and seedlings found in our sites, are also commonly found in early seral and post-disturbance forests. Additionally, given these areas were prioritized for host-tree removal, including of red maple, we assume the presence of *Acer* spp. in the overstory before eradication efforts contributed to this regeneration response (Dodds and Orwig 2011, Dodds et al., 2014, Butler, 2017).

The size and severity of a disturbance and ability of preexisting vegetation to survive and colonize post-disturbance both have a strong influence on forest developmental patterns. (Oliver and Stephens, 1977; Cline and Spurr, 1942). The findings from this work argue for considering these mechanisms when evaluating the potential impacts of host removal treatments on future forest development. In our field sites, host species were present in high numbers across forest types and eradication treatments, particularly red maple, which was noted qualitatively as stump sprouts at our sites. While stump sprouts did not associate significantly with one treatment over the other, the prevalence of sprouting is worth noting given stump grinding and herbicide applications were designed to minimize stump sprouting of red maple and ultimately discourage future host material for ALB (Dodds and Orwig 2011). These patterns are consistent with those documented following a spruce budworm invasion in northern Minnesota, where recovery was most influenced by management, land history, and species composition, particularly in the immediate years. The species that returned post-spruce budworm aligned most strongly with previous management and disturbance history (Robert et al., 2012; Sturtevant et al., 2014). If the long-term goal for these forests is to continually suppress host species, further stand treatments should be applied to limit red maple sapling growth, and particularly low-quality growing stock such as stump sprouts. Preemptive harvesting in advance of an invasive species is designed to minimize the abundance of the host tree species that provide habitat for the invading insect. In the case of ALB eradication, trees over 2.5 cm DBH were targeted because they support beetle populations. Our results suggest that while sanitation harvests that targeted ALB tree habitat removed these trees and changed overstory stand structure and composition, they had only a transient effect on total host species abundance across strata.

4.4. Herbaceous plant and woody communities

Herbaceous community composition across sites was largely dominated by species tolerating sanitation treatments as opposed to invader species (Roberts, 2004, Fahey and Puettmann, 2007). The abundance and diversity of herbaceous plants and woody shrubs were not influenced by the treatments employed, suggesting that the composition was more influenced by the forest cover type, species abundance prior to treatment, life history traits, and the seedbank. As with woody plants, invasive species represented a small portion of the species recorded (14%), and while composition varied across treatments and forest type, there ultimately were no significant differences. Like other studies of forest harvesting impacts on understory plant communities, our results reflected the multidimensional effects of disturbance on understory plants as introduced by Roberts (2004), indicating that canopy removal alongside the effects of harvest were impacting patterns in community composition post-disturbance. While we cannot directly compare the composition before the eradication efforts to our findings, our results are consistent with the finding that vegetation communities rely on the species and conditions present before gap creation (Fahey and Puettmann, 2007). In addition, our results align with other studies conducted in similar forest types across Massachusetts. For example, past work has indicated that past intensive land use has led to the introduction of some invasive plants in upland, mesic sites, however this trend is also strongly influenced by soil characteristics and harvest regimes as well (McDonald et al., 2008). While land-use history is a driving factor in many of our results, the harvest regimes associated with ALB sanitation harvests do not appear to have increased invasive species.

5. Conclusions and management implications

Our study is the first examination of the response of natural forest communities to eradication treatments in response to ALB invasion. The observational nature of this work and associated variation across sites likely influenced our ability to detect significant difference between treatments; however, it is essential to continue to monitor and study the effectiveness of the long-term implications of ALB eradication treatments on natural forests. These results confirm that these forests are largely resilient to canopy disturbance at the levels encountered in this study targeting specific ALB host trees. As such, forests undergoing eradication methods will eventually be susceptible to ALB again due to the large portion of red maple in the understory and the presence of red maple in surrounding forests (Butler, 2017). However, given the success of ALB eradication efforts in North America and elsewhere, it is hoped that the beetle will not be an ongoing disturbance in these forests over time. Management for ALB should continue to consider the desired long-term forest composition and structure in these areas (Lovett et al., 2006). If the long-term goal is to reduce host abundance in treated stands, more deliberate actions should be taken to reduce maple regeneration, such as additional stump grinding or a second, delayed stand reentry targeting these species.

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.

Data availability

Data will be made available on request.

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References

Aukema, J.E., Leung, B., Kovacs, K., Chivers, C., Britton, K.O., 2011. Economic Impacts of Non-Native Forest Insects in the Continental United States. PLoS ONE 6 (9), e24587.

Brooks, R.T., 2004. Early regeneration following the presalvage cutting of hemlock from hemlock-dominated stands. Northern Journal of Applied Forestry 21 (1), 12–18.

Butler, B.J., 2017. Forests of Massachusetts, 2017. Resource Update FS-161. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, p. 3.

Carta, L.K., Handoo, Z.A., Li, S., Kantor, M., Bauchan, G., McCann, D., Gabriel, C.K., Yu, Q., Reed, S., Koch, J., Martin, D., Burke, D.J., Woodward, S., 2020. Beech leaf disease symptoms caused by newly recognized nematode subspecies Litylenchus crenatae mccannii (Anguinata) described from Fagus grandifolia in North America. For Path. 50 (2), e12580.

Cline A.C., Spurr S.H. 1942. The Virgin upland forest of central New England: A study of old growth stands in the Pisgah Mountain section of southwestern New Hampshire. In Harvard Forest Bulletin No. 21. (pp. 1–56).

Dodds, K.J., Orwig, D.A., 2011. An invasive urban forest pest invades natural environments — Asian longhorned beetle in northeastern US hardwood forests. Canadian Journal of Forest Research 41 (9), 1729–1742.

Dodds, K.J., Hull-Sanders, H.M., Siegert, N.W., Bohne, M.J., 2014. Colonization of three maple species by Asian longhorned beetle, Anoplophora glabripennis, in two mixed-hardwood forest stands. Insects. 5 (1), 105–119.

Elliott, K.J., Swank, W.T., 2008. Long-term changes in forest composition and diversity following early logging (1919–1923) and the decline of American chestnut (Castanea dentata). Plant Ecology 197 (2), 155–172.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N. L., Sobczak, W., v, Stinson, K. A., Stone, J. K., Swan, C. M., Thompson, J., von Holle, B., & Webster, J. R., 2018. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 9, 479–486.

Engelken, P.J., Benbow, M.E., McCullough, D.G., 2020. Legacy effects of emerald ash borer on riparian forest vegetation and structure. Forest Ecology and Management 457, 117684.

Forrester, J.A., Mcgee, G.G., Mitchell, M.J., 2003. Effects of Beech Bark Disease on Aboveground Biomass and Species Composition in a Mature Northern Hardwood Forest, 1985 to 2000. The Journal of the Torrey Botanical Society. 130 (2), 70–78.

Foster, D.R., 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, USA. Journal of Ecology 80, 753–772.

Foster, D.R., Orwig, D.A., 2006. Preemptive and salvage harvesting of New England forests: when doing nothing is a viable alternative. Conservation Biology 20 (4), 959–970.

Gao, R., Qin, X., Chen, D., Chen, W., 1993. A study on the damage to poplar caused by Anoplophora glabripennis. Forest Resources. 6, 189–193.

Haack R.A., Hérard F., Sun J., Turgeon J.J. 2009. Managing Invasive Populations of Asian Longhorned Beetle and Citrus Longhorned Beetle: A Worldwide Perspective. 55. 1. 521-546.

Haack, R.A., Law, K.R., Mastro, V.C., Ossenburgen, H., Sharon; Raimo, Bernard J., 1997. New York''s battle with the Asian long-horned beetle. Journal of Forestry. 95 (12), 11–15.

Heuss, M., D'amato, A.W., Dodds, K.J., 2018. Northward expansion of southern pine beetle generates significant alterations to forest structure and composition of globally rare Pinus rigida forests. Forest Ecology and Management 434, 119–130.

Hu, J., Angeli, S., Schuetz, S., Luo, Y., Hajek, A.E., 2009. Ecology and management of exotic and endemic Asian longhorned beetle Anoplophora glabripennis. In Agricultural and Forest Entomology. 11 (4), 359–375.

Hull-Sanders, H., Pepper, E., Davis, K., Trotter, R.T., Doucet, D., 2017. Description of an establishment event by the invasive Asian longhorned beetle (Anoplophora glabripennis) in a suburban landscape in the northeastern United States. PLoS ONE 12 (7), e0181655.

Janowiak, M.K., Nagel, L.M., Webster, C.R., 2008. Spatial scale and stand structure in northern hardwood forests: Implications for quantifying diameter distributions. Forest Science 54 (5), 497–506.

Kizlinski, M.L., Orwig, D.A., Cobb, R.C., Foster, D.R., 2002. Direct and indirect ecosystem consequences of an invasive pest on forests dominated by eastern hemlock. Journal of Biogeography 29 (10), 1489–1503.

Klooster, W.S., Gandhi, K.J.K., Long, L.C., Perry, K.I., Rice, K.B., Herms, D.A., 2018. Ecological impacts of emerald ash borer in forests at the epicenter of the invasion in North America. Forests 9 (5), 18–20.

Krist, F.J., Ellenwood, J.R., Woods, M.E., McMahan, A.J., Cowardin, J.P., Ryerson, D.E., Sapio, F.J., Zweifler, M.O., Romero, S.A., 2014. 2013–2027 National Insect and Disease Forest Risk Assessment. USDA Forest Service Forest Health Technology Enterprise Team, Fort Collins, Colorado, USA. FHTET 14–01.

Liebhold, A.M., Kean, J.M., 2019. Eradication and containment of non-native forest insects: successes and failures. Journal of Pest Science 92 (1), 83–91. https://doi.org/10.1007/s10340-018-1056-z.

Lindenmayer, D.B., Ough, K., 2006. Salvage logging in the montane ash eucalypt forests of the Central Highlands of Victoria and its potential impacts on biodiversity. Conservation Biology 20 (4), 1005–1015.

Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., Fitzhugh, R.D., 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. BioScience 56 (5), 395–405.

Lovett, G.M., Weiss, M., Liebhold, A.M., Holmes, T.P., Leung, B., Lambert, K.F., Orwig, D. A., Campbell, F.T., Rosenthal, J., McCullough, D.G., Wildova, R., Ayres, M.P., Canham, C.D., Foster, D.R., LaDeau, S.L., Weldy, T., 2016. Nonnative forest insects and pathogens in the United States: Impacts and policy options. Ecological Applications 26 (5), 1437–1455.

MacLean, M.G., Holt, J., Borsuk, M., Markowski-Lindsay, M., Butler, B.J., Kittredge, D.B., Duveneck, M.J., Laflower, D., Orwig, D.A., Foster, D.R., Thompson, J.R., 2020. Potential impacts of insect-induced harvests in the mixed forests of new England. Forests 11 (5), 498.

Nowak, D.J., Pasek, J.E., Sequeira, R.A., Crane, D.E., Mastro, V.C., 2001. Potential effect of Anoplophora glabripennis (Coleoptera: Cerambycidae) on urban trees in the United States. Journal of Economic Entomology. 94 (1), 116–122.

Oliver, C.D., Stephens, E.P., 1977. Reconstruction of a Mixed-Species Forest in Central New England. Ecology 58 (3), 562–572. https://doi.org/10.2307/1939005.

Orwig, D.A., Foster, D.R., Foster, D.R., 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. In Journal of the Torrey Botanical Society. 125 (1), 60–73.

Plotkin, A.B., Foster, D., Carlson, J., Magill, A., 2013. Survivors, not invaders, control forest development following simulated hurricane. Ecology 94 (2), 414–423.

Roberts, M.R., 2004. Response of the herbaceous layer to natural disturbance in North American forests. Canadian Journal of Botany 82 (9), 1273–1283.

Santoro, J.A., D'Amato, A.W., 2019. Structural, compositional, and functional responses to tornado and salvage logging disturbance in southern New England hemlock-hardwood forests. Forest Ecology and Management 444, 138–150.

United States Department of Agriculture. 2018. Asian Longhorned Beetle (ALB). USDA APHIS | Asian Longhorned Beetle (ALB). https://www.aphis.usda.gov/aphis/resources/pests-diseases/asian-longhorned-beetle. Accessed June 2018.