

The response of *Fraxinus nigra* forest ground-layer vegetation to emulated emerald ash borer mortality and management strategies in northern Minnesota, USA



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ABSTRACT

When an invasive organism targets a dominant tree species, it can trigger unprecedented shifts in forest plant communities. Emerald ash borer (EAB; *Agrilus planipennis* Fairmaire), an invasive insect that kills by girdling trees, represents a significant threat to North American *Fraxinus* (ash) species. EAB has already decimated many *Fraxinus* populations and threatens loss of overstory cover in Great Lakes region wetland forests dominated by *Fraxinus nigra* (black ash). Canopy treatments, such as clearcutting and group selection, are being evaluated to promote regeneration of non-EAB-host tree species. Studies suggest clearcutting may raise water tables, lower tree regeneration, and shift the composition of woody and herbaceous ground-layer plant communities. However, no empirical research to date has examined the effects of canopy treatments on ground-layer plant communities in *F. nigra* wetlands. We used a large-scale field experiment in northern Minnesota *F. nigra* wetlands to examine the response of the woody and herbaceous ground-layer to four overstory treatments: clearcutting, group selection, *F. nigra* girdling, and unharvested forest. Our objectives were to determine: (1) to what extent established regeneration of associated tree species could be expected to contribute to overstory maintenance under EAB- and management-induced canopy changes; (2) the impact of canopy changes on the composition of the overall woody ground-layer; and (3) the effect of canopy treatments on the herbaceous layer. We found density of established tree regeneration was significantly higher in the clearcut treatment than in the group selection, girdle, and control. *Fraxinus nigra* had the highest seedling density in all treatments, while *Ulmus americana* (American elm) was the most abundant non-EAB-host tree species across treatments. Regeneration density of associated tree species varied by treatment and fell short of seedling stocking guidelines. Background variation in experimental blocks exerted a greater influence than treatment on overall woody community composition. Treatment influenced herbaceous layer height, but did not significantly impact total cover. Herbaceous species richness and diversity increased in all treatments, with the clearcut and group selection moving toward greater graminoid cover, while the control and girdling treatment increased in wetland indicator species. Our findings suggest artificial regeneration, combined with herbaceous and shrub competition control treatments, will be necessary to restock *F. nigra* forests following EAB invasion. Sites with lower abundance of shrub species and higher established tree regeneration should be prioritized for management activities.

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1. Introduction

When an invasive organism targets a dominant tree species, it can trigger unprecedented shifts in forest plant communities,

resulting in drastically altered ecosystem services and disturbance regimes (Orwig, 2002). In North American forests, non-native insects and diseases have functionally eliminated dominant tree species, such as *Castanea dentata* (Marshall) Borkh. (American chestnut) and *Tsuga canadensis* (L.) Carrière (eastern hemlock), from all or part of their range, resulting in dramatic shifts in ecosystem composition, structure and function (Ellison et al., 2005). Due to their unique influence on resource dynamics, litter

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quality, and understory communities (Preisser et al., 2014), the loss of such once-dominant canopy species can result in ecosystem conditions that lack contemporary analogs, posing a challenge to long-term conservation and management (Ellison et al., 2005).

The invasive insect, emerald ash borer (EAB; *Agrilus planipennis* Fairmaire) represents a significant threat to North American *Fraxinus* (ash) species (Herms and McCullough, 2014). EAB causes lethal girdling damage as its larvae feed on the phloem and cambium of North American *Fraxinus* trees, which lack resistance to the insect (Gandhi and Herms, 2010). Less than a decade after EAB was first identified in southern Michigan, *Fraxinus* spp. trees greater than 2.5 cm in diameter experienced greater than 99% mortality (Herms and McCullough, 2014), and viable *Fraxinus* seeds were negligible to non-existent on the most heavily infested sites (Klooster et al., 2014). While the growth of associated tree species was enhanced by the loss of *Fraxinus* spp. to EAB in mixed-species upland forests (Flower et al., 2013), advance regeneration and canopy-level individuals of associated tree species are much lower in wetland forests dominated by *Fraxinus nigra* Marsh. (black ash; Palik et al., 2012). Consequently, the continued spread of EAB could potentially result in loss of overstory cover and dramatic changes in ecosystem function in *F. nigra* forested wetlands (Iverson et al., 2016; Looney et al., 2015), which range from the western Great Lakes region (especially Minnesota) in the U.S. to southeastern Canada (Erdmann et al., 1987; Scott, 1995).

Our previous work evaluated the use of silvicultural treatments to promote artificial regeneration of non-EAB-host tree species to maintain ecosystem function following EAB invasion of *F. nigra* wetland forests (Looney et al., 2015). In many forested systems, harvest treatments can greatly enhance the potential for regeneration success (Smith et al., 1996). For example, clearcuts can aid the establishment of shade-intolerant species by opening the forest floor to sunlight (Smith et al., 1996), while group selection treatments can both improve light availability and ameliorate harsh microclimate effects (Smith et al., 1996), favoring a range of species tolerances. In *F. nigra* forests, the use of clearcutting may be problematic, as previous research suggests the loss of the *F. nigra* overstory may alter site hydrology and adversely impact the composition of both the woody and herbaceous understory plant communities (Erdmann et al., 1987; Slesak et al., 2014).

Woody plant regeneration appears to be strongly influenced by site hydrology in *F. nigra*-dominated stands, which occur on sites with heavily inundated soils and seasonal ponding (Erdmann et al., 1987; Slesak et al., 2014). In these wetland systems, *F. nigra* plays an integral role in regulating hydrology by lowering the water table through evapotranspiration during the summer growing season, in this way aiding the survival of less moisture-tolerant plant species (Telander et al., 2015). An empirical study found loss of the *F. nigra* overstory to clearcutting and EAB (as emulated by tree girdling) resulted in a multi-year rise in the water table (Slesak et al., 2014), which observational harvesting studies suggest could favor shrubs in the absence of sufficient advance tree regeneration (Erdmann et al., 1987). In a related study that examined artificial regeneration of *F. nigra* replacement species with different canopy treatments, we found significantly lower overall seedling survival in clearcuts compared to unharvested controls, group selection, and girdling treatments (Looney et al., 2015). Survival in the girdling treatment was comparable to that in the control and group selection, despite complete senescence of the girdled trees, suggesting that slower, multi-year mortality from EAB may provide a short-term shelterwood effect (Looney et al., 2015). It is unclear whether natural tree regeneration would also benefit from this effect, as no studies to date have examined the effects of EAB- or management-induced canopy changes on natural woody plant regeneration in *F. nigra* wetlands.

Changes to the overstory can also have an impact on the composition of the herbaceous plant community (Gandhi and Herms, 2010), which may further influence tree regeneration through altered competitive dynamics and/or changing ground layer environmental conditions (Royo and Carson, 2006). For example, in North American boreal forests, clearcutting is associated with aggressive growth of the grass species, *Calamagrostis canadensis* (Michx.) P. Beauv. (bluejoint), which suppresses tree regeneration through competition and by indirectly increasing soil freezing (Liefvers et al., 1993). Moreover, in high-latitude forests, the herbaceous layer often accounts for the majority of biodiversity (Gilliam, 2007), while contributing to aboveground net primary productivity (Nilsson and Wardle, 2005). Harvesting may threaten herbaceous layer biodiversity by both removing most of the understory and causing greater soil disturbance than natural processes (Roberts, 2004). Past experience suggests clearcutting in *F. nigra* forests could shift the composition of the herbaceous plant layer toward graminoids from its present mix of facultative and obligate wetland herbaceous species (Erdmann et al., 1987; MNDNR, 2003). Work in northwest Ohio examining mixed species forests, in which *Fraxinus pennsylvanica* Marsh. (green ash) made up 60% of the canopy trees, found both clearcutting from preemptive salvage logging and multi-year EAB-induced mortality increased the overall abundance of herbaceous plants, with clearcutting associated with more rapid environmental changes and an increase in invasive plant species (Hausman et al., 2010). In wetland forests where the *F. nigra* component often accounts for 75–90% of all tree species (MNDNR, 2003), no empirical studies have assessed the response of the herbaceous plant community to canopy changes from EAB mortality or silvicultural management.

To provide a more complete scientific basis for efforts to mitigate the effects of EAB in *F. nigra* wetland forests, we investigated the response of ground-layer vegetation to four overstory treatments: clearcut; group selection; *Fraxinus* spp. girdling; and unharvested control. Our objectives were to determine: (1) to what extent established regeneration of associated tree species can be expected to contribute to future forest cover under the various canopy treatments; (2) the impact of EAB- and management-induced canopy changes on the overall composition of the woody vegetation community; and (3) the effect of canopy treatments on the structure and compositions of the herbaceous plant layer, which in turn may feedback to influence tree regeneration.

2. Materials and methods

2.1. Site description

Our study took place in sites established as part of a large-scale *F. nigra* wetland study on the Chippewa National Forest of northern MN, USA (Looney et al., 2015). Climate is continental, with 1981–2010 mean temperatures averaging -13.7 and 16.5 °C for January and July, respectively (PRISM Climate Group, 2015). Mean precipitation was 742 mm yr⁻¹, with the majority occurring during the May through September growing season (PRISM Climate Group, 2015). The sites are classified as WFn55 (northern wet *Fraxinus* swamp) grading into WFn64 (northern very wet *Fraxinus* swamp) based on the native plant community classification system developed for northern Minnesota (MNDNR, 2003). The predominant overstory species is *F. nigra*, which comprises 91% of basal area, with minor components of *Ulmus americana* L. (American elm), *Tilia americana* L. (American basswood), *Abies balsamea* L. (balsam fir), *Populus tremuloides* Michx. (quaking aspen), and *Quercus macrocarpa* Michx. (bur oak) (Looney et al., 2015). Soils are typed as Morph Series: Fine-loamy, mixed, superactive, frigid Typic Glos-saqualfs and Wildwood Series: Very-fine, smectitic, nonacid, frigid

Histic Humaquepts (Soil Survey, 2016). Drainage is poor due to flat topography and a confining clay layer (Slesak et al., 2014). Ponding occurs early in the spring-summer growing season, with water tables typically receding below the surface by mid-July (Slesak et al., 2014).

2.2. Overstory treatments

The study area was divided into 8 experimental blocks. Most stands in blocks 1–6 were predominantly even-aged, while blocks 7 and 8 had multi-aged structures (A.W. D'Amato and M.R. Reinikainen, unpublished data). Within each block, four 1.62 ha (71.8 m-radius) circular stands were established, each of which received one of four treatments: (1) clearcut, involving the removal of all standing living and dead trees above 6 cm diameter at breast height (DBH); (2) group selection, consisting of eight 0.04 ha (400 m²) circular gaps totaling approximately 20% of the plot; (3) girdling of all *Fraxinus* spp. trees ≥ 6 cm DBH to emulate multi-year EAB-induced mortality; and (4) control, consisting of unharvested forest. All treatments were implemented in winter 2011–2012 under frozen ground conditions (Looney et al., 2015). Girdling was repeated during winter 2012–2013 for trees where the original treatment was ineffective to guarantee mortality.

2.3. Data collection

2.3.1. Woody vegetation

We randomly installed six 11.3 m-radius (400 m²) plots within each treatment replicate, for a total of 48 plots per treatment. Plot centers were buffered 10 m from treatment edges to avoid sampling untreated forest. Within each group selection replicate, 4 plots were located in harvested gaps and 2 in unharvested matrix. Within each plot, we established three 7 m² subplots for vegetation sampling 5.5 m from plot center, at 0, 120, and 240 degrees. Large woody stems (≥ 0.5 m height but ≤ 2.54 cm basal diameter) were tallied within each subplot. Medium-sized woody stems (height ≥ 15 cm ≤ 50 cm) and small woody stems (≤ 15 cm height) were tallied separately within a nested 1 m² plot centered on the subplot. We distinguished between seed-origin regeneration and vegetative reproduction. Preliminary measurements found overwhelming numbers of stump-origin sprouts for species such as *F. nigra* and *Acer spicatum* Lam. (mountain maple) that made accurate tallies impractical. As a result, we recorded dense clusters of stump sprouts separately from isolated vegetative reproduction. Post-treatment woody vegetation was sampled annually in summer from 2012 to 2015.

2.3.2. Herbaceous layer vegetation

We assessed cover of herbaceous vegetation in 2013 and 2015. We sampled each treatment replicate once in each measurement year between leaf-out in late June and mid-August. We sampled herbaceous vegetation in four 0.25 m² quadrats systematically arrayed around the woody vegetation subplots within each 400 m² plot. As with the woody regeneration subplots, herbaceous plots were arrayed at 0°, 120°, and 240°, but were spaced 3.7 and 7.4 m from plot centers to avoid measuring herbaceous vegetation that had been disturbed during woody regeneration tallies. Herbaceous cover was assessed to the species level; due to overlapping strata of foliage, cover could potentially exceed 100% within quadrats.

In September 2015, we assessed the maximum height of the herbaceous layer for the growing season to help infer to what extent the herbaceous layer may shade tree seedlings. Height was assessed at the center of each 400 m² plot, for a total of six points per treatment replicate. We measured height with a meter stick from ground level to the top of the continuous herbaceous

layer; isolated taller vegetation, such as a graminoid inflorescence, was ignored.

2.4. Statistical analysis

We used generalized linear mixed modeling to examine the influence of canopy treatment on tree seedling density, herbaceous height, and herbaceous cover. We created Poisson models to test for differences in counts of established (≥ 15 cm height) regeneration among treatments for species with the potential to achieve tree stature (>10 m). Predictors included treatment, species, and their interaction, while blocks were treated as random effects. Combined counts of clustered and singly occurring vegetative as well as seed-origin sprouts within individual plots and subplots were aggregated to the level of treatment replicates, which served as sample units. Species not occurring in all blocks were eliminated from the Poisson models to achieve convergence and avoid over-dispersion. These species included *F. pennsylvanica*, *Acer rubrum* L. (red maple), *Picea glauca* (Moench) Voss (white spruce), and *Acer negundo* L. (box elder), which had mean regeneration densities of 101.4 (± 30.4), 44.9 (± 17.6), 7.5 (± 4.3), and 36.5 (± 4.3) stems ha⁻¹, respectively. These species were included in all other analyses. For the Poisson models, we assessed model fit using Poissonness plots and comparisons with zero-inflated models in the case of over-dispersion. For herbaceous height and cover, we used Gaussian models to evaluate treatment effects. For both sets of models, we examined plots of residuals vs. fitted values to assess model fit. The lme4 package (Bates et al., 2014) for R (R Core Team, 2013) was used for all analyses. Post-hoc comparisons using Tukey's HSD were used to examine differences between individual treatment levels or species in the event of a significant test result in both woody and herbaceous models. In the event of significant interactions between treatment and species in the analysis of tree seedling density, we used the lsmeans package (Lenth, 2016) to compare treatments within species.

We graphically examined gradients of woody and herbaceous community composition among treatments and over time using nonmetric multidimensional scaling ordination (Kruskal, 1964). We examined woody and herbaceous community matrices separately. The community matrix for woody vegetation included data measured annually from 2012 to 2015, while the herbaceous vegetation matrix included data from both the 2013 and 2015 measurements. For woody vegetation, vegetative sprouts (including stump sprout clusters), and seed-origin stems of species were treated as separate variables, due to potential differences in regeneration niche between these classes (Tardif and Bergeron, 1999). We also treated the size classes of a single species (large ≥ 0.5 m height and ≤ 2.54 cm basal diameter; medium ≥ 15 cm ≤ 5 m height; small ≤ 15 cm height) as separate variables due to ontogenetic changes in species/habitat relationships (Shipley et al., 1989).

For both woody and herbaceous species matrices, rows consisted of treatment replicates, which served as sample units, while columns consisted of individual species and regeneration classes. Due to sparsity of species within subplots, data were aggregated to the level of treatment replicates as per the analysis of tree seedling density. We relativized data by column totals to examine both rare and common species on a more comparable basis (McCune et al., 2002; Peck, 2010). Initial ordination runs with all species had high stress and instability. Therefore, to reduce noise, we eliminated woody species regeneration classes and herbaceous plant species that occurred in less than 5% of sample units (McCune et al., 2002). Under this criterion, 10 regeneration classes of woody species, representing a mean of 263.8 (± 53.5) stems ha⁻¹ or 0.3% (± 0.00) of total stem density, and 28 herbaceous species, together averaging 3.5% (± 0.03) of total cover, were eliminated prior to analysis. Matrices with these species omitted were also used for

PERMANOVA and indicator species analysis. We used Bray-Curtis distances for all ordinations, with 250 iterations and a stress improvement criterion of 5 for selecting axis number in Autopilot mode in PC-ORD v. 6.0 (McCune and Medford, 2011). We used Monte Carlo tests with 250 runs to evaluate axis significance ($\alpha = 0.05$). After verifying stability, dimensionality, and significance, we reran ordinations using 500 runs with real data (McCune et al., 2002). Ordinations were rotated to orthogonal principle axes (Peck, 2010). We examined relationships between ordination axes, individual species, and species traits using biplot overlays with a cutoff R^2 of 0.2 (McCune et al., 2002).

To aid in interpreting ordinations, we investigated additional explanatory and descriptive variables using biplots. We calculated species richness, evenness, and diversity (Shannon's H') of both woody regeneration and the herbaceous layer. Vegetative and seed-origin seedlings were combined for diversity calculations. In addition, we summarized species responses by categorizing individual species into non-exclusive groups based on soft traits (Lavorel and Garnier, 2002). Woody species traits included shade tolerance (0–5 scale), waterlogging tolerance (0–5 scale), drought tolerance (0–5 scale), and wetland indicator status (0–3 scale; Lichvar et al., 2016; Niinemets and Valladares, 2006). Herbaceous traits included life form (forb, graminoid, fern, horehound, or vine; "The PLANTS database," 2016), wetland indicator status (Lichvar et al., 2016), and shade tolerance ("Minnesota Wildflowers," 2016, "Native Plant Information Network," 2016; "The PLANTS database," 2016). We simplified herbaceous shade tolerance ratings to a 1–3 scale, given the lack of detailed information for many species. Species listed as growing under both sun and shade were classified as intermediate (score of 2). Average trait values were calculated based on weighted averages combining species' trait values with their relative abundance. We used overlays to plot mean treatment and block positions (\pm S.E.) in ordination space, in order to assess the effects of these factors. For woody species, data for 2012–2015 were pooled to calculate a single periodic mean for each treatment level or block number. We also calculated interannual treatment means in order to create successional trajectories of woody communities across time. For herbaceous data, treatments and blocks were calculated separately for the 2013 and 2015 datasets. Species richness, evenness, and diversity were calculated based on all species in the woody and herbaceous community datasets, prior to deletion of rare species. To restrict inferences based on species traits to the species used in the multivariate analyses, mean trait values were calculated after deletion of species occurring in less than 5% of sample units.

We used permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) to test for treatment effects on woody and herbaceous communities in 2015. This procedure permits the use of linear modeling of community distance matrices. We performed PERMANOVA in PC-ORD version 6.0 (McCune and Medford, 2011). In the event of a significant treatment effect, we performed post-hoc pairwise comparisons with Bonferroni corrections. Distance matrices were prepared identically to those used in ordinations, although restricted to species present in 2015. Permutational significance tests were based on 4999 iterations.

As a follow-up analysis, we performed blocked indicator species analysis (ISA) of both the woody and herbaceous communities in PC-ORD version 6.0 (McCune and Medford, 2011). This analysis calculates indicator values based on proportional representation of a species within a single group, compared to a species' prevalence across all groups (McCune et al., 2002). Indicator values potentially range from 0 (no treatment association) to 100 (perfect treatment association). Observed indicator values are compared to expected values derived from random permutations ($n = 4999$) to test significance. This analysis was performed for 2015 only, using the same species matrices as for PERMANOVA.

3. Results

3.1. Woody vegetation

3.1.1. Established tree regeneration: Treatment effect

In the analysis of 2015 established tree regeneration, there was a significant main effect for treatment ($F = 839.83$, $p < 0.001$) on total seedling density. For all six species combined, mean total seedling density in the clearcut was significantly higher than in other treatments (Table 1), followed by the group selection and control treatments, which had total densities that were not significantly different from each other. The girdling treatment had the lowest overall density, which was significantly lower than the clearcut and group selection but not the control.

3.1.2. Established tree regeneration: Species effect

Density of tree seedlings ≥ 15 cm in height also varied significantly by species ($F = 924.3$, $p < 0.001$). Mean density of *F. nigra* was significantly higher than any other species (Table 1), followed by *U. americana*, which was significantly more abundant than any species other than *F. nigra*. We found moderate seedling density for *Q. macrocarpa*. There was no significant difference between *Populus balsamifera* L. (balsam poplar), *T. americana*, and *P. tremuloides*, the three species with the lowest seedling density.

3.1.3. Established tree regeneration: Treatment \times species effect

There was also a significant species by treatment interaction effect ($F = 31.66$, $p < 0.001$, Table 1). The three species with highest overall abundance, *F. nigra*, *U. americana*, and *Q. macrocarpa*, exhibited different patterns of abundance across treatments. *Fraxinus nigra* seedling density was highest in the clearcut treatment, followed by the group selection, control, and girdle. All treatments had significantly different *F. nigra* densities in pairwise comparisons (Table 1). In contrast, *U. americana* densities were not significantly different across treatments. *Quercus macrocarpa* seedling density was significantly higher in the control than in the group selection and girdle treatments, which were also significantly different from each other in pairwise comparisons. *Quercus macrocarpa* had its second highest seedling density in the clearcut treatment, which was not significantly different from the control and group selection.

The less abundant species, *P. balsamifera*, *T. americana*, and *P. tremuloides*, also differed in their patterns of abundance across treatments. *Populus balsamifera* density in the control was not significantly different from the group selection but was significantly higher than in the girdling treatment. *Tilia americana* density was significantly higher in the group selection than in the clearcut, girdling, and control treatments, which were not significantly different from one another in pairwise comparisons. Finally, *P. tremuloides* seedling density was equivalent in the clearcut and girdle treatment which were, in turn, significantly higher than both the control or group selection treatment.

3.1.4. Woody vegetation community ordination

For shrub and tree communities with stems ≤ 15 cm in height included (measured annually post-treatment in 2012–2015), the NMS ordination yielded a 3-dimensional solution (final stress = 19.01, 145 iterations, final instability < 0.001). *Cornus sericea* L. (redosier dogwood) and *Alnus incana* (L.) Moench subsp. *rugosa* (Du Roi) R.T. Clausen (speckled alder) were more abundant in the positive portion of the first axis (variance represented = 31.1%), while *Q. macrocarpa*, *Prunus virginiana* L. (chokecherry), *Corylus cornuta* Marshall (beaked hazelnut), and *T. americana* were more abundant in the negative portion (Fig. 1). The positive portion of axis 2 was associated with *F. nigra* stump

Table 1
Mean density (stems ha⁻¹) of regeneration of woody species by treatment with potential to reach tree stature on *F. nigra* wetland forest study sites in northern Minnesota, USA.

Species	Clearcut	Treatment		Group	Species mean
		Control	Girdle		
FRNI	19980 ± 3871a	5788 ± 2930c	1806 ± 675d	10625 ± 1203b	9549 ± 1209a
ULAM	1429 ± 555a	1062 ± 340a	1448 ± 444a	1260 ± 356a	1300 ± 147b
QUMA	337 ± 221ab	566 ± 275a	129 ± 129c	319 ± 161b	337 ± 71c
POBA	526 ± 399a	169 ± 129b	40 ± 30c	119 ± 84bc	213 ± 215d
TIAM	79 ± 79b	20 ± 13b	40 ± 21b	476 ± 432a	153 ± 154d
POTR	169 ± 136a	30 ± 21b	169 ± 111a	20 ± 20b	97 ± 31d
Treatment Total	22520 ± 4351a	7629 ± 3054bc	3631 ± 700c	12818 ± 1629b	
Other	38 ± 46	83 ± 77	25 ± 33	46 ± 153	

Note: Abbreviations are as follows: FRNI=*Fraxinus nigra*, ULAM=*Ulmus americana*, QUMA=*Quercus macrocarpa*, POBA=*Populus balsamifera*, POTR=*Populus tremuloides*, TIAM=*Tilia americana*. Means and standard errors are provided for each species. Results of Tukey's post hoc comparisons for individual species across treatments (rows) are shown by the letters following each mean. Means with different letters are significantly different at the 95% confidence level. For the treatment × species interaction, pairwise comparisons of treatment are nested within each species. Treatment totals include the six common tree species and exclude species listed as Other. Other=*Acer rubrum*, *Acer negundo*, *Picea glauca*, and *Fraxinus pennsylvanica*, tree species not occurring on all 8 blocks and too rare to include in the analysis.

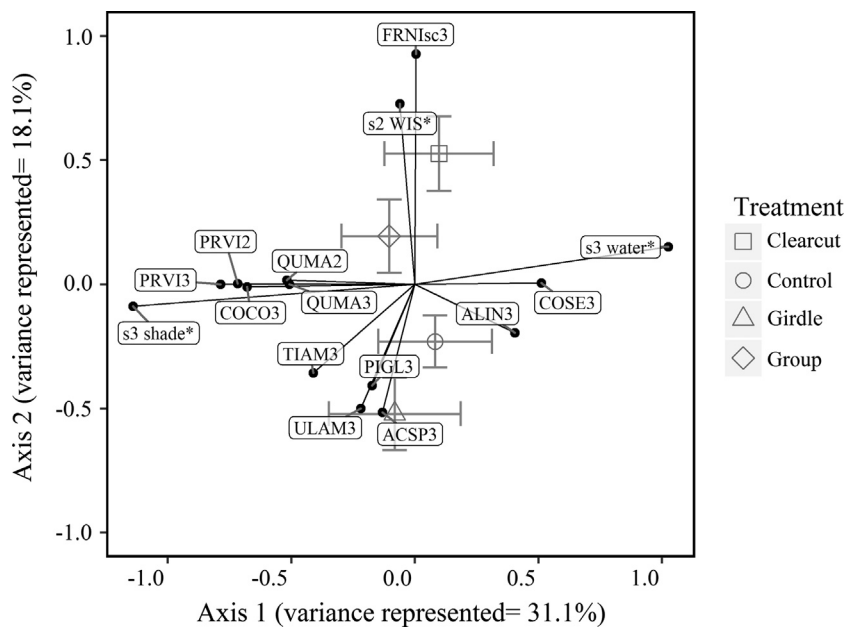


Fig. 1. Ordination plot of woody vegetation community structure based on post-treatment data collected annually from 2012 to 2015. Overlays of mean treatment position (\pm S.E.) in species space are averaged over the 2012–2015 period. The first and second-most important axes of the three-dimensional ordination are shown. Individual species and explanatory variables are included in the biplot. The biplot displays the strength and direction of relationships with the ordination axes with a minimum r^2 of 0.20. Explanatory variables are designated by *. Numbers designate shoot size and origin: 1 = small seedling, 2 = medium seedling, 3 = large seedling, s1 = small single vegetative sprout, s2 = medium single vegetative sprout, s3 = large single vegetative sprout, sc1 = small stump sprout cluster, sc2 = medium stump sprout cluster, sc3 = large stump sprout cluster. Abbreviations are as follows: WIS = wetland indicator status, COSE = *Cornus sericea*, water = waterlogging tolerance, ALIN = *Alnus incana*, QUMA = *Quercus macrocarpa*, PRVI = *Prunus virginiana*, COCO = *Corylus cornuta*, TIAM = *Tilia americana*, PIGL = *Picea glauca*, shade = shade tolerance.

sprouts clusters (variance represented = 18.1%), while seed-origin *T. americana* and *P. glauca* were more common in the negative portion of this axis. *Quercus macrocarpa* and *Acer spicatum* increased along the third axis (variance represented = 17.8%), while woody *Ribes* spp. declined (data not shown). Because this axis represented the least variance and was less interpretable, we focus only on the results for first two axes.

Biplot overlays suggested the positive portion of the first ordination axis was associated with large stems of species tolerant of flood-induced waterlogging, while the negative portion was associated with large stems of shade-tolerant species (Fig. 1). The mean position of each treatment, based on pooled 2012–2015 data, was distinct in ordination space (Fig. 1). The clearcut treatment was located in the positive portion of axis 2, which was associated with greater abundance of medium-sized stems of species with higher wetland indicator status. The girdling treatment was located in

the negative portion of axis 2, which was associated with large seed-origin regeneration of *P. glauca*, *T. americana*, and *U. americana*, as well as the shrub species, *Alnus incana* subsp. *rugosa* and *Acer spicatum*. The control and group selection treatments were located in the neutral portion of this axis.

The mean positions of blocks, based on pooled 2012–2015 data, were also frequently distinct in the ordination (Fig. 2). Blocks 4, 5, and 6 were located in the positive portion of axis 1, which was associated with large stems of waterlogging-tolerant species such as *A. incana* and *C. sericea*. Blocks 7 and 8 were located in the negative portion of axis 1, which was associated with large stems of shade-tolerant species such as *P. virginiana* and *C. cornuta*. Blocks 1, 2, and 3 were associated with the neutral portion of axis 1.

We also found distinct successional trajectories of treatments during the 2012–2015 post-treatment period (Fig. 3). Between 2012 and 2015, the girdle, group selection, and clearcut treatment

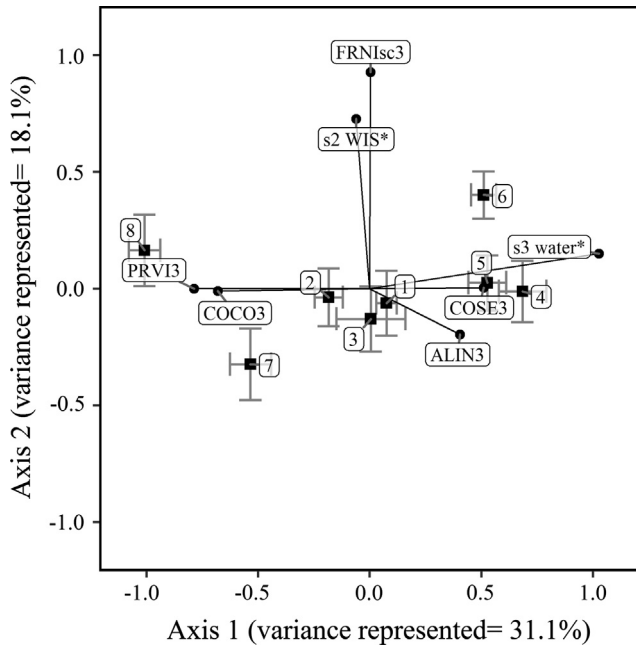


Fig. 2. Ordination plot of woody vegetation community structure, showing mean block positions (\pm S.E.) in species space. Overlays of block positions are based on data averaged over the 2012–2015 post-treatment period. Numbers next to blocks (filled square symbols) correspond with block number. The first and second-most important axes of the three-dimensional ordination are shown. For clarity, only explanatory variables from Fig. 1 (designated by *) are included in the biplot. The biplot displays the strength and direction of relationships with the ordination axes with a minimum r^2 of 0.20. Numbers adjacent to biplot variables (filled circle symbols) designate shoot size and origin: 1 = small seedling, 2 = medium seedling, 3 = large seedling, s1 = small single vegetative sprout, s2 = medium single vegetative sprout, s3 = large single vegetative sprout, sc1 = small stump sprout cluster, sc2 = medium stump sprout cluster, sc3 = large stump sprout cluster. Abbreviations are as follows: FRNI = *Fraxinus nigra*, COSE = *Cornus sericea*, ALIN = *Alnus incana*, PRVI = *Prunus virginiana*, COCO = *Corylus cornuta*, WIS = wetland indicator status, water = waterlogging tolerance, shade = shade tolerance.

became more closely associated with the positive portion of axis 1. This shift coincided with decreasing upland species density and increasing waterlogging-tolerant species, such as *Alnus incana* and *Cornus sericea*. The girdle, group selection, and clearcut treatments also shifted toward the negative end of axis 2, coinciding with greater abundance of bottomland tree species, including trees such as *P. glauca* and *T. americana*, and bottomland shrubs such as *Alnus incana* and *Acer spicatum*. The control showed minimal movement along either axis.

Based on PERMANOVA results, woody community composition differed significantly among treatments in 2015 ($F = 2.55$, $p = 0.001$). In Bonferroni-corrected pairwise comparisons (6 comparisons; critical p -value = 0.0083), woody community composition was significantly different only between clearcuts and girdles ($p = 0.0078$).

There were several woody species treatment indicators in 2015 (Table 2). Both large *F. nigra* stump-origin sprout clusters and large singly occurring vegetative sprouts were indicators of clearcuts ($IV = 62.3$, $p = 0.001$ and $IV = 66.0$, $p = 0.002$, respectively). Within the girdle treatment, large seed-origin *Acer spicatum* was a significant indicator ($IV = 49.4$, $p = 0.037$), while large seed-origin *F. nigra* ($IV = 39.6$, $p = 0.042$) was an indicator of group selections.

3.2. Herbaceous layer vegetation

3.2.1. Herbaceous layer height and cover

Treatment had a significant influence on 2015 herbaceous layer height ($F = 82.3$, $p < 0.001$), but did not significantly impact total cover ($F = 2.57$, $p = 0.08$, data not shown). The height of the herbaceous layer was significantly greater in the clearcut (95.2 ± 2.5 cm) than in the girdle ($76.4 \text{ cm} \pm 2.8$) or group selection treatment ($70.8 \text{ cm} \pm 3.1$). The control ($40.9 \text{ cm} \pm 1.5$) had the lowest mean herbaceous layer height of any treatment. Cover averaged $294\% \pm 20$ in the girdle, $235\% \pm 23$ in the control, $227\% \pm 20$ in the group selection, and $219\% \pm 22$ clearcut treatment.

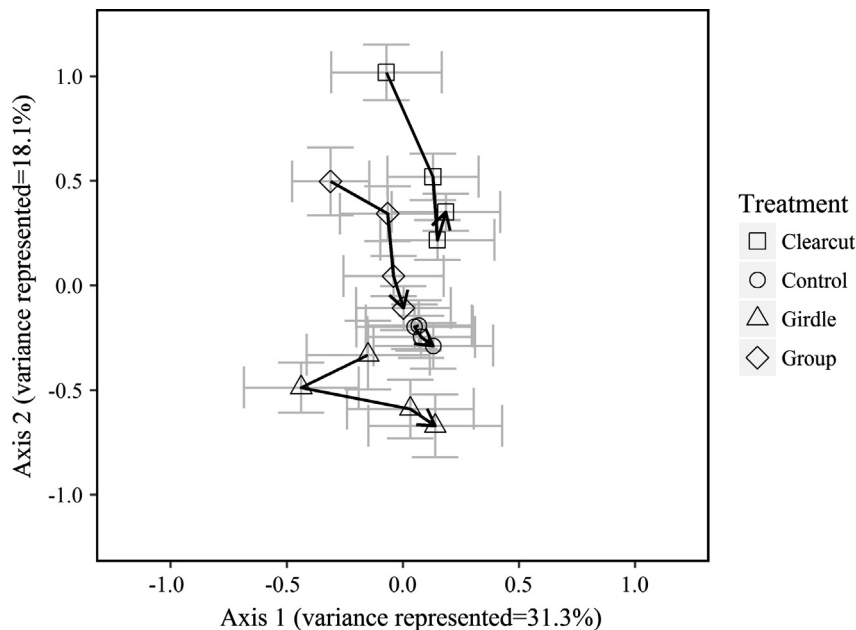


Fig. 3. Ordination plot of woody vegetation community structure, showing successional trajectories of mean treatment positions in species space. Mean treatment positions (\pm S.E.) are provided for each year from 2012 to 2015. Arrows indicate successional trajectories showing the annual movement of treatments beginning in 2012 and ending in 2015. For all treatments, the oldest (2012) point is in the leftmost position of axis 1, while the most recent (2015) is in the rightmost portion. The first and second-most important axes of the three-dimensional ordination are shown.

Table 2
Significant woody and herbaceous treatment indicator species on *F. nigra* forest study sites in northern Minnesota, USA.

Response	Treatment	Species	Indicator value	Significance
Woody vegetation	Clearcut	<i>F. nigra</i> stump sprout clusters (>50 cm)	62.3	0.002
Woody vegetation	Clearcut	<i>F. nigra</i> single vegetative sprouts (>50 cm)	66.0	0.001
Woody vegetation	Girdle	<i>Acer spicatum</i> (>50 cm)	49.4	0.037
Woody vegetation	Group	<i>F. nigra</i> seed-origin stems (>50 cm)	39.6	0.04
Herbaceous layer	Clearcut	<i>Calamagrostis canadensis</i>	50.4	0.001
Herbaceous layer	Control	<i>Geum rivale</i>	35.3	0.04
Herbaceous layer	Girdle	<i>Arisaema triphyllum</i>	52.3	0.01
Herbaceous layer	Girdle	<i>Carex radiata</i>	51.5	0.02
Herbaceous layer	Girdle	<i>Matteuccia struthiopteris</i>	39.6	0.04

Note: For woody vegetation, the origin (vegetative vs. seed) and size class are included. Potential indicator values ranged from 0 to 100, while the cutoff for significance was 0.05.

3.2.2. Herbaceous layer ordination

The NMS ordination of 2013 and 2015 herbaceous community measurements produced a 3-dimensional solution (Final stress = 17.43, 67 iterations, final instability < 0.001). The first axis represented the most variation (41.7%). The positive portion of axis 1 was associated with *Onoclea sensibilis* L. (sensitive fern), *Impatiens capensis* Merrb. (jewelweed), and *Carex lacustris* Willd. (hairy sedge), while species associated with the negative portion of this axis included *Equisetum pratense* Ehrh. (meadow horsetail), *Laportea canadensis* (L.) Weddell (Canadian woodnettle), *Dryopteris carthusiana* (Vill.) H.P. Fuchs (spinulose woodfern), *Mitella nuda* L. (naked miterwort), *Rubus pubescens* Raf. (dwarf raspberry), *Thalictrum dioicum* L. (early meadow-rue), *Fragaria virginiana* Duchesne (Virginia strawberry), *Asarum canadense* L. (Canadian wild ginger), and *Streptopus lanceolatus* (Aiton) Reveal var. *longipes* (Fernald) Reveal (twisted stalk; Fig. 4). The positive portion of axis 2 was associated with forb species, including *Solidago gigantea* Aiton (giant goldenrod), *Polygonum arifolium* L. (halberdleaf tearthumb), *Crepis tectorum* L. (narrowleaf hawksbeard), and *Athyrium filix-femina* L. Roth (common ladyfern), as well as the sedge, *Carex praegracilis* W. Boott (clustered field sedge; variance represented = 17.4%; Fig. 4). Only *Galium trifolium* Michx. (fragrant

bedstraw) was associated with the negative portion of axis 2. The third axis represented minor variation in species composition, with *Viola* spp. (violet) associated with the positive and *Caltha palustris* L. (yellow marsh marigold) associated with the negative portion of this axis (variance represented = 14.3%; data not shown).

In ordination biplot overlays, the positive portion of axis 1 was associated with greater abundance of graminoid cover, while the negative portion was associated with wetland indicator species, horsetails, and ferns (Fig. 4). The group selection and clearcut treatments were associated with the positive portion of this axis in both 2013 and 2015. The control and girdle treatments were associated with the negative portion of axis 1 in 2013, becoming more neutral in 2015. Forb cover was associated with the positive portion of axis 2, while other species groups showed no consistent trends. Between 2013 and 2015, all treatments shifted from the negative to the positive portion of axis 2, indicating a general increase in species richness, species diversity, and graminoid cover, with specific increases in *Athyrium filix-femina*, *Crepis tectorum*, and *Carex praegracilis*. Blocks did not show a relationship with either ordination axis.

In 2015, treatment had a significant effect on herbaceous composition in PERMANOVA ($F = 2.05$, $p < 0.001$). In pairwise

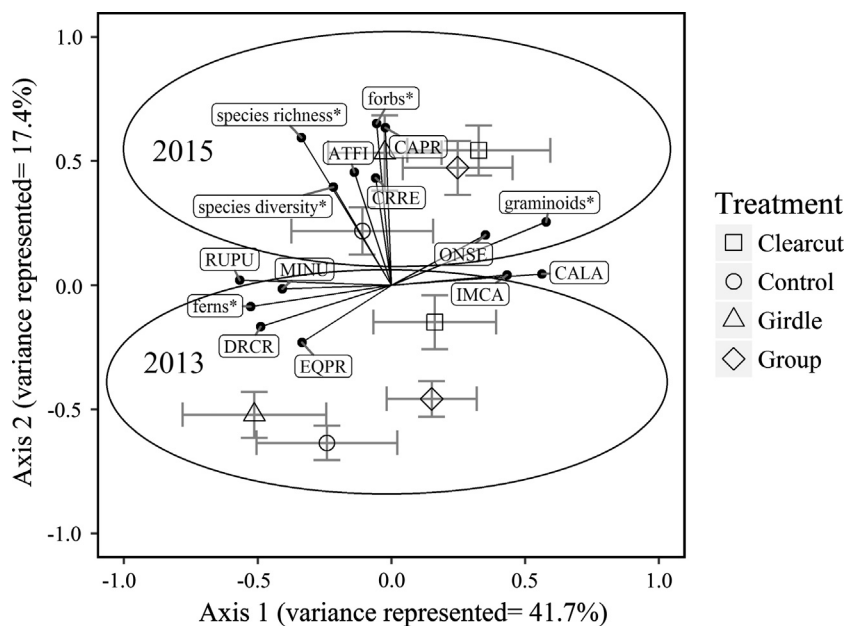


Fig. 4. Ordination plot of herbaceous layer community structure, showing mean treatment positions (\pm S.E.) in species space for 2013 and 2015. The first and second most important axes of the three-dimensional ordination are shown. Individual species and explanatory variables are included in the biplot. The biplot displays the strength and direction of the relationship with the ordination axes of species with a minimum r^2 of 0.25. See text for additional, weaker relationships. * indicates explanatory variables. Abbreviations are as follows: ONSE = *Onoclea sensibilis*, CALA = *Carex lacustris*, IMCA = *Impatiens capensis*, EQPR = *Equisetum pratense*, DRMA = *Dryopteris carthusiana*, WIS = wetland indicator status, MINU = *Mitella nuda*, RUPU = *Rubus pubescens*, ATFI = *Athyrium filix-femina*, CAPR = *Carex praegracilis*, CRTE = *Crepis tectorum*.

comparisons, the clearcut was significantly different from the control ($p = 0.007$) and girdle ($p = 0.008$) treatments, but not significantly different from the group selection treatment. No other pairwise comparisons were significant with Bonferroni corrections (6 comparisons; critical p -value = 0.0083).

In 2015, there were several significant herbaceous treatment indicator species (Table 2). The grass, *Calamagrostis canadensis* (IV = 50.4, $p = 0.001$), was an indicator of the clearcut, while the forb, *Geum rivale* L. (purple avens; IV = 35.3, $p = 0.04$), was a significant indicator of control treatment. Three species were indicators of the girdle treatment: *Arisaema triphyllum* (L.) Schott (Jack in the pulpit; IV = 52.3 $p = 0.01$), *Carex radiata* (Wahlenb.) Small (eastern star sedge; IV = 51.5, $p = 0.02$), and *Matteuccia struthiopteris* (L.) Todaro (ostrich fern; IV = 39.6, $p = 0.04$). There were no significant indicators for the group selection treatment.

4. Discussion

The loss of a dominant tree species to invasive organisms may result in rapid shifts in function, structure, and biological diversity, particularly in ecosystems with low canopy tree diversity (Ellison et al., 2005). While silvicultural management can be used to guide succession and influence the direction of these shifts (Waring and O'Hara, 2005), management strategies can nonetheless have unintended and potentially adverse consequences on other ecosystem components, including ground layer communities. Thus far, strategies to manage the effects of EAB in *F. nigra* wetland forests have focused on promoting regeneration of associated tree species to maintain tree cover (Looney et al., 2015). We discuss below the complex changes observed in *F. nigra* forest ground-layer plant communities from harvesting and simulated EAB mortality, changes which highlight the importance of taking into consideration not only the impacts of EAB, but also the ecosystem-wide effects of associated management strategies designed to address overstory impacts.

4.1. Woody vegetation

4.1.1. Established tree regeneration

Based on seedling density, established tree regeneration in the *F. nigra* wetland forests examined was confined to six major species: *F. nigra*, *U. americana*, *Q. macrocarpa*, *P. balsamifera*, *P. tremuloides*, and *T. americana*. The limited regeneration density of tree species besides *F. nigra* is consistent with previous research on regional *F. nigra* forests (Palik et al., 2012). While Erdmann et al. (1987) recommended at least 12,500 *F. nigra* seedlings ha^{-1} to guarantee restocking of harvested stands, the combined density of alternate species fell far short of this figure regardless of treatment, suggesting that these other species will not readily fill growing space vacated by *F. nigra*.

The clearcut supported significantly higher mean total regeneration densities than other treatments. While lower than the clearcut treatment, total seedling densities in the group selection were also significantly higher than the girdle treatment, but not significantly different from the control. Seedling densities in both the clearcut and group selection treatments were largely driven by the regeneration response of *F. nigra*, which had the highest seedling density of any species in this study. High *F. nigra* seedling density in the two harvesting treatments reflected the vigorous post-harvesting sprouting response reported in previous studies of *F. nigra* regeneration (Erdmann et al., 1987). *Fraxinus nigra* showed lower but still relatively abundant established regeneration in the undisturbed control treatment, and much lower established regeneration in the girdle treatment, despite the complete mortal-

ity of the ash overstory by 2014 (Slesak et al., 2014). Kashian and Witter (2011) found *Fraxinus* spp. regeneration declined across multiple sites in southern Michigan mixed species forests following EAB invasion, while Klooster et al. (2014) found newly germinated *Fraxinus* seedlings almost non-existent in heavily infested Michigan and Ohio mixed *Fraxinus* stands. Both studies attributed the decline in *Fraxinus* regeneration to depletion of the seed bank following overstory mortality (Kashian and Witter, 2011; Klooster et al., 2014).

Ulmus americana was the second most abundant species after *F. nigra* across all treatments. Formerly a common species of regional wetland hardwood forests, *U. americana* may still grow to reproductive size but typically succumbs to Dutch Elm disease (*Ophiostoma novo-ulmi* Brasier) prior to reaching the overstory (Barnes, 1976). The fact that *U. americana* seedling density did not vary significantly across treatments and nearly equaled that of *F. nigra* in the girdling treatment suggests *U. americana* could be relatively more versatile than other species in the aftermath of EAB.

Seedling density of the third most abundant species, *Q. macrocarpa*, was highest in the control and lowest in the girdling treatment, while density in the clearcut treatment overlapped statistically with both that of the slightly higher control and slightly lower group selection treatment. In the northeastern U.S., overstory cover may promote the initial survival of *Quercus* species, although subsequent removal of the overstory may be necessary for sapling recruitment (Dey et al., 2008). The variation in *Q. macrocarpa* seedling density among treatments suggests advance regeneration, which is often critical to successful regeneration of *Quercus* species (Hannah, 1987), may influence *Q. macrocarpa* persistence in *F. nigra* forests. Seedling density of *Q. macrocarpa* was significantly lower in the girdling treatment than in the control or clearcut treatment, negating the hypothesis in our previous study that girdling may produce a short-term shelterwood effect that promotes seedling survival (Looney et al., 2015). A combination of water table rise and invigorated shrub and herbaceous competition may have contributed to lower *Q. macrocarpa* density in this treatment. Regionally, shelterwood harvests may fail to stimulate tree regeneration as a result of increased shrub growth (Hannah, 1988).

Populus balsamifera, *T. americana* and *P. tremuloides* were statistically similar and had the lowest established seedling density. *Tilia americana* achieved high mean seedling density only in the group selection treatment, perhaps aided by a combination of shade tolerance (Niinemets and Valladares, 2006) and vigorous stump sprouting response (Tredici, 2001). The large, immobile seed of *T. americana* (Cowell et al., 2010) may have limited its dispersal into the clearcuts. Established seedling density of *P. balsamifera* was significantly higher in the clearcut than in any other treatment, while *P. tremuloides* had the highest established seedling density in the clearcut and girdling treatments. Previous work in these systems indicated LAI values for the clearcut, girdling and group selection treatments were 11%, 69%, and 82% of controls, respectively (Looney et al., 2016). The suckering response of the two shade-intolerant *Populus* species appears to be stimulated by increased solar heating of the soil, as well as lack of hormonal suppression from adult trees (Doucet, 1989; Zasada et al., 1981). Neither *P. tremuloides* nor *P. balsamifera* showed high regeneration density in the group selection, where suckering may have been inhibited by unharvested edge trees (Doucet, 1989), given the relatively small size (400 m^2) of the gaps. While group selection may potentially reduce growing season length through the formation of cold air sinks (McDonald and Abbott, 1994), data on 2015 minimum temperatures indicated that only the clearcuts were significantly colder than other treatments (R.A. Slesak, unpublished data).

4.1.2. Woody vegetation community

The main gradient of variation in the woody ground-layer community, which included all size classes (<1.5 cm height to >0.5 m but <2.5 cm basal diameter) of trees and shrubs, appeared to be driven by differences between experimental blocks rather than overstory treatment. Based on plant wetland indicator status, the differences among blocks appeared to reflect variation in site hydrology and stand history. Blocks 7 and 8 were associated with species with lower tolerance to waterlogging and higher shade tolerance, such as *Prunus virginiana*. These blocks were characterized by shorter duration of seasonal ponding compared to the other study sites (R.A. Slesak, unpublished data). In contrast, we observed standing water as late as August in blocks 4, 5 and 6 (C. E. Looney, personal observation), which were associated with species with higher waterlogging tolerance, principally the shrubs, *Alnus incana* and *Cornus sericia*. This finding is in agreement with Keddy and MacLellan's (1990) centrifugal forest composition model, which suggests that increasing waterlogging stress and disturbance cause *F. nigra* community composition to shift from shade-tolerant, upland species to less productive, shrub-dominated systems. Heinselman (1963) described a similar transition in regional minerotrophic swamps, with topographic transitions from uplands to peatlands corresponding with the change of mixed forest to *Alnus incana*.

The second gradient of variation in the woody layer ground community was driven by overstory treatment, with the girdling treatment and control associated with bottomland shrubs, while the group selection and clearcut treatments were associated with high densities of resprouting *F. nigra*. Heinselman (1963) reported that harvested swamp forests in the region commonly convert to *Alnus incana* thickets, while silvicultural experience with *F. nigra* suggests increased site moisture from harvesting could lead to a compositional shift toward graminoid and shrub species (Erdmann et al., 1987). Slesak et al. (2014) found that water tables rose immediately after treatment in the clearcut, while the girdling treatment showed a similar response two years post-treatment.

Based on PERMANOVA results, the woody vegetation community in the control was not significantly different from that in the girdling treatment in 2015. EAB mortality and the girdling treatment that emulated it differ from the harvesting treatments both in the multi-year decline of the overstory (Klooster et al., 2014) and lack of incidental damage to shrubs from harvesting. In this respect, the short-term effects of EAB-girdling may be similar to wind disturbance or native insect defoliation, which also reduces the overstory canopy while preserving much of the shrub layer (Roberts, 2004). Girdling also appears to moderate changes in microclimate by lessening temperature fluctuations (Slesak et al., 2014). The ordination showed the girdling treatment had higher densities of large stems of the midstory shrub species, *Acer spicatum* and *Alnus incana*, compared to the control. In canopy gaps created by EAB mortality in upland mixed-species forests, midstory shrubs were also found to increase, which suppressed tree regeneration (Klooster, 2012).

Both the ordination and indicator species analysis showed the clearcut treatment was characterized by *F. nigra* stump sprouts. While Heinselman (1963) reported presettlement swamp forests, including those dominated by *F. nigra*, often converted to shrublands following harvest, most of the stands examined in this study were previously harvested in the early 1900s. The single treatment replicate that showed low sprouting response to clearcutting was part of block 7, an old-growth stand. The ability of trees to produce stump sprouts commonly declines with age (Tredici, 2001), so older stands may be at greater risk of water table rise and ecosystem conversion from overstory loss. The vigorous sprouting response in the clearcut treatment in this study may have moderated water table rise (Slesak et al., 2014). While sprouting ash will

likely not survive to reproductive size prior to EAB reinfestation (Aubin et al., 2015), sprouts may nevertheless aid post-EAB succession by moderating water table rise. PERMANOVA results for 2015 indicate the clearcut treatment did not significantly differ from the group selection treatment in terms of woody species composition. While the group selection treatment also supported *F. nigra* stump sprouts, densities were lower than in the clearcuts, perhaps reflecting that only four of the six sample plots in each treatment replicate were positioned in gaps.

Between 2012 and 2015, the clearcut and group selection treatments shifted from dominance by *F. nigra* stump sprouts to increased prevalence of seed-origin tree species, such as *U. americana*, *P. glauca*, and *T. americana*. The first year of this study, 2012, was exceptionally dry, while subsequent years had heavier precipitation (National Oceanic and Atmospheric Administration, 2015). The initial drought may have promoted seedling establishment by lowering water tables (Roy et al., 2000). However, clearcuts and group selections showed simultaneous increases in densities of the shrub species, *Alnus incana* and *Acer spicatum*, which may form dense cover following harvesting (Harvey and Bergeron, 1989) and hinder future tree regeneration in the mechanical treatments.

4.2. Herbaceous community composition

Overstory treatment influenced both the height and composition of the herbaceous layer, with potential implications for tree seedling regeneration. Herbaceous layer height increased with decreasing overstory cover, which is consistent with the findings of Aubin et al. (2000) in southern boreal forests. Interception of available light, which is generally lower in the herbaceous layer than in the shrub layer, also increases as overstory cover decreases (Aubin et al., 2000). In the clearcut, girdle, and group selection treatments, mean herbaceous layer height exceeded the height of the small and medium woody vegetation size classes in this study. Mean total herbaceous cover averaged over 200% in all treatments, which suggests that microsites where tree seedlings could escape herbaceous competition were rare.

Results of the PERMANOVA analysis for 2015 indicated herbaceous community composition responded to overstory treatments. The control and girdling treatment were not statistically different from one another. The ordination showed both the control and girdling treatment were associated with diverse communities of obligate and facultative wetland plants, such as *Rubus pubescens*, *Geum rivale*, *Mitella nuda*, *Dryopteris carthusiana*, and *Equisetum pratense*. These species are characteristic of closed, mesic forests in the region (Rogers et al., 2008). *Arisaema triphyllum* and *Asarum canadense* were also associated with the girdle and control treatments and are typical of undisturbed, wet-mesic hardwood sites (Jenkins and Parker, 2000). High spring water levels in *F. nigra* forests create seasonal pools (Palik and Kastendick, 2010), which support diverse plant communities yet contain few endemic species (Palik et al., 2007).

Water table rise in the girdle treatment (Slesak et al., 2014) was reflected in increased relative cover of wetland indicator species. The short-term effects of girdling were limited to overstory removal, since neither understory vegetation nor soil was disturbed. In the conceptual model of Roberts (2004), disturbances with effects confined to the overstory are expected to stimulate species with aboveground vegetative reproduction, as well as those with seeds stored in the soil seed bank. In agreement with this model, we found the girdling treatment promoted two significant rhizomatous indicator species: the fern, *Matteuccia struthiopteris*, and the sedge, *Carex radiata*. Ferns may form dense layers which inhibit tree regeneration through a combination of shading, below-ground competition, and allelopathy (George and Bazzaz, 1999).

The significant girdling indicator species, *Arisaema triphyllum*, a shade-tolerant perennial characteristic of undisturbed wet/mesic forests (Jenkins and Parker, 2000), suggests shade from the herbaceous and woody vegetation layers has largely compensated for loss of the *F. nigra* overstory. The lower regeneration density of most tree species in this treatment may be linked to the dense herbaceous layer.

Group selections supported herbaceous communities that were compositionally intermediate of other treatments in both PERMANOVA and ordination analysis. Furthermore, we found no significant indicator species for this treatment. The lack of distinctive plant communities may reflect the sampling design, in which four of six sampling plots were located in harvested groups, while two plots were located in untreated matrix. Unfortunately, differences in sampling intensity within the group selection treatment prevented direct comparison between harvested groups and untreated matrix. However, a study of herbaceous communities following group selection harvest in Wisconsin found harvested groups supported greater abundances of disturbance-adapted species compared to untreated matrix (Shields and Webster, 2007). The relatively small 400 m² size of the group openings likely also limited the duration of direct sunlight at the high latitude of the study area (Canham et al., 1990). A study in Michigan *Betula alleghaniensis* Britton forest found harvested groups had increased importance of wetland indicator species, including *Arisaema triphyllum*, compared to untreated matrix (Shields and Webster, 2007). Palik and Kastendick (2010) found retaining a 15.3 m buffer of partially harvested forest around *F. nigra* and *P. tremuloides*-dominated seasonal pools mitigates increases in graminoid cover associated with clearcutting.

Our results support previous research that found clearcuts are associated with high relative *Carex* spp. and other graminoid cover (Slesak et al., 2014), including the grass, *Calamagrostis canadensis*, a significant indicator species for this treatment in 2015, and the sedge, *Carex lacustris*. Clearcutting of *F. nigra*/*P. tremuloides*-dominated seasonal pools was also associated with increased graminoid importance in an earlier study (Palik and Kastendick, 2010). *Calamagrostis canadensis* has been associated with regeneration failures in boreal forests following harvesting (Lieffers et al., 1993). In addition to competition from living plants, matted dead *Calamagrostis canadensis* vegetation increases soil freezing, reducing the growing season for tree species and suppressing the suckering response of *P. tremuloides* (Lieffers et al., 1996). While both *Calamagrostis canadensis* and *Carex lacustris* are obligate wetland species (Lichvar et al., 2016), clearcutting did not lead to an overall increase in obligate wetland species cover as we had anticipated. In contrast to the findings of Klooster (2012) in Michigan and Ohio mixed *Fraxinus* forests, invasive species were unimportant in our study area. We found low cover of the invasive forb, *Crepis tectorum*, which increased in all treatments in 2015. The invasive grass *Phalaris arundinacea* L. occurred sporadically in the clearcuts, but was too rare to be included in the multivariate analyses.

All treatments showed dramatic compositional changes between 2013 and 2015, indicative of increased species diversity and graminoid cover. A drought in 2012 (National Oceanic and Atmospheric Administration, 2015) likely influenced community composition in the following year. Reduced seasonal water levels may allow a greater variety of waterlogging-intolerant species to regenerate from the soil seedbank (Keddy and Reznicek, 1986). Changes in relative cover may also be more pronounced following drought's end, due to lagged effects on soil seedbanks (Stampfli and Zeiter, 2004). Greater 2012 water table rise in the clearcut treatments (Slesak et al., 2014) may have offset drought effects, rendering clearcut herbaceous communities more similar between sampling periods than other treatments.

5. Conclusions

Artificial regeneration in harvesting treatments, possibly combined with shrub and herbaceous layer control in EAB-girdled stands, may be necessary to restock *F. nigra* forests following EAB invasion. While *F. nigra* was the most abundant tree species, particularly in harvested areas, there is little likelihood this species could reach reproductive maturity before re-infestation in the event of heavy EAB invasion (Aubin et al., 2015). The second-most abundant species, *U. americana*, was widespread regardless of overstory treatment, but, while *U. americana* trees usually survive to reproductive age, they generally succumb to Dutch elm disease before reaching the overstory. *Quercus macrocarpa*, the third-most abundant species, had moderately high density in the control, clearcut, and group selection treatments, and could potentially aid in maintaining overstory cover provided advance regeneration is protected during harvesting. While clearcutting promoted the highest density of non-EAB-host species, including *P. balsamifera*, *P. tremuloides*, and *U. americana*, the number of seedlings fell far short of recommended regeneration density for *F. nigra* stands (Erdmann et al., 1987).

Background variation in experimental blocks, likely reflecting differences in hydrology, appears to be the main influence on the woody vegetation community regardless of treatment. The pre-existing composition of the woody vegetation community, therefore, heavily influences post-disturbance patterns. Sites with lower abundance of shrub species and higher established tree regeneration should be prioritized for management activities. While harvesting treatments reduced shrub competition, additional shrub removal may be necessary to aid tree regeneration in stands affected by EAB.

Herbaceous layer height was greater in treatments with reduced overstory cover. Thus, herbaceous growth may inhibit tree regeneration to a greater degree in harvested treatments than in unharvested controls. The clearcut treatment also appeared to foster competition from graminoids, notably *Calamagrostis canadensis*. Herbaceous plant communities in the girdling treatment were more similar to those in controls than in clearcuts, suggesting EAB mortality may not introduce novel changes to herbaceous communities relative to historic management practices in the short term. However, the girdling treatment was associated with an increase in the fern layer, which may suppress tree regeneration in unmanaged stands following EAB invasion. Our results suggest tree seedlings may require herbaceous competition control treatments under low canopy cover conditions.

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