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ARTICLE

Vegetation responses to simulated emerald ash borer infestation in *Fraxinus nigra* dominated wetlands of Upper Michigan, USA

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Abstract: The invasive emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae)) is a significant threat to biodiversity and ecosystem processes in North American forests. Of particular concern is the fate of *Fraxinus nigra* (black ash), which is frequently a dominant canopy species across much of its range. To investigate the potential vegetation response to the loss of this foundation species, EAB-induced mortality was simulated in *F. nigra* dominated wetlands of Upper Michigan, USA. No growth response of residual overstory species occurred over the course of three growing seasons, which may in part be attributed to negative effects of post-treatment growing conditions, including prolonged inundation. A significant increase in non-*Fraxinus* sapling growth rate was observed, however. Mortality of *F. nigra* did not impact overall stem recruitment or regeneration, although species composition is shifting towards *Acer rubrum* (red maple) and *Betula alleghaniensis* (yellow birch) in the seedling layer. The herbaceous community exhibited the greatest response, nearly doubling in areal cover by the end of the study. Importantly, this expanded cover was not associated with decreased establishment of new woody seedlings, suggesting that increased competition between these functional groups has not yet impacted the potential for future recovery of woody vegetation in these forests.

Key words: invasive species, disturbance impacts, gap dynamics, competition, forested wetlands.

Résumé : L'agrile du frêne (*Agrilus planipennis* Fairmaire (Coléoptère : Buprestidés)) est un insecte invasif qui constitue une menace importante pour la biodiversité et les processus de l'écosystème dans les forêts nord-américaines. Le sort du *Fraxinus nigra* Marshall (frêne noir), une espèce du couvert forestier souvent dominante dans la majeure partie de son aire de répartition, est particulièrement inquiétant. Pour étudier la réaction potentielle de la végétation à la perte de cette espèce fondatrice, la mortalité causée par l'agrile du frêne a été simulée dans les milieux humides du haut Michigan dominés par *F. nigra*, aux É.-U. La croissance des espèces résiduelles de l'étage dominant n'a montré aucune réaction au cours de trois saisons de croissance, ce qui peut en partie être attribué aux effets néfastes des conditions de croissance suivant le traitement, incluant une inondation prolongée. Une augmentation importante du taux de croissance des gaules des espèces autres que *Fraxinus* a cependant été observée. La mortalité du *F. nigra* n'a globalement pas eu d'impact sur le recrutement ou la régénération, bien que la composition en espèces soit en train d'évoluer vers *Acer rubrum* (érable rouge) et *Betula alleghaniensis* (bouleau jaune) dans la strate des semis. La végétation herbacée a eu la plus forte réaction, son couvert ayant presque doublé en superficie à la fin de l'étude. Il est important de noter que l'expansion du couvert herbacé n'était pas associée à une réduction de l'établissement de nouveaux semis ligneux, indiquant que la compétition accrue entre ces deux groupes fonctionnels n'a pas encore eu d'impact sur la possibilité d'une récupération future de la végétation ligneuse dans ces forêts. [Traduit par la Rédaction]

Mots-clés : espèce invasive, impacts des perturbations, dynamique des trouées, compétition, milieux humides boisés.

Introduction

Invasive insects are a serious threat to forests across North America (Lovett et al. 2006). The effects of introduced insects and associated pathogens have resulted in widespread alteration to the structure of these forests and ecosystem processes (Gandhi and Herms 2010). In addition to these ecological consequences, the estimated economic costs associated with control and mitigation of the negative effects of invasive insects alone range into the billions of US dollars (Pimentel et al. 2005).

Among the recently discovered invasive insects in North America, the emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae)) has received considerable attention for the breadth, depth, and severity of its potential impacts (Herms and McCullough 2014). First collected near Detroit, Michigan, in 2002 (Haack et al. 2002), this invasive wood-boring beetle has likely been present in the United States since the early- to mid-1990s (Siegert et al. 2014). Despite efforts to control the rate and extent of dispersal (Cappaert et al. 2005; Herms and McCullough 2014), EAB has since been discovered in 27 US states and two Canadian provinces (Emerald Ash Borer Information Network 2016). All eastern North American ash (genus *Fraxinus*) species are considered to be potential hosts (Rebek et al. 2008). Infestations occur in stems as small as 2.5 cm in diameter, with mortality of individual stems occurring as rapidly as 3–4 years following the initial infestation, as the phloem-feeding larvae effectively girdle the host tree (Cappaert et al. 2005; Herms and McCullough 2014). Mortality

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of *Fraxinus* trees in infested stands may rapidly exceed 99% (Klooster et al. 2014; Herms and McCullough 2014) although the rate of stand-level mortality may be affected by a number of factors, including the density of ash trees within the stand (Knight et al. 2013; Kashian 2016) and rate of EAB larval development, which may extend to 2 years in low-density infestations (Siegert et al. 2010; Mercader et al. 2011) or in northern regions (Wei et al. 2007; Orlova-Bienkowskaja and Bieńkowski 2016).

Concerns over the potentially profound effects of EAB on forest composition and ecosystem processes stem from the ubiquity of the genus *Fraxinus* across central and eastern North America (Cappaert et al. 2005). Members of the genus are widespread and common in a variety of forest types throughout the region as well as in urban environments (MacFarlane and Meyer 2005). Dramatic economic losses and expenditures related to EAB across such a wide geographic range and diversity of habitats have made EAB the most costly invasive species in the US to date (Aukema et al. 2011), and these costs may soon total in excess of 10 billion US dollars (Kovacs et al. 2010).

The potential fate of *Fraxinus nigra* Marshall (black ash) is of particular concern (Poland and McCullough 2006; Kashian and Witter 2011). *Fraxinus* species range from minor to major canopy components in a number of ecosystem types (MacFarlane and Meyer 2005; Pugh et al. 2011) and may be locally abundant (e.g., Baker and Wiley 2004; Hausman et al. 2010; Smith et al. 2015; Kashian 2016), although the most common North American species, *Fraxinus americana* L. (white ash). is less commonly the sole dominant canopy species (Schlesinger 1990). By comparison, *F. nigra* is frequently a major component of deciduous and deciduous–conifer forested wetlands (Wright and Rauscher 1990) and occurs in nearly pure stands in portions of the range (Erdmann et al. 1987). In the Upper Peninsula of Michigan, the *F. nigra* – *Ulmus americana* L. (American elm) – *Acer rubrum* L. (red maple) forest type tends to be dominated by *F. nigra*, particularly in areas with very poor drainage and organic soils (Erdmann et al. 1987). Additionally, of native North American *Fraxinus* species, *F. nigra* is among the preferred EAB hosts (Pureswaran and Poland 2009; Rigsby et al. 2014; Tanis and McCullough 2015, but see Chen and Poland 2010) and exhibits low resistance to infestation (Whitehill et al. 2012; Rigsby et al. 2015), which may lead to more rapid stand-level mortality (Smith et al. 2015).

The EAB-induced mortality of a substantial proportion of both the overstory and the understory within these forests may have extensive impacts on successional dynamics (Looney et al. 2015). Disturbance resulting from invasive phytophagous insects and other agents alters the forest environment in many ways, resulting in both positive and negative impacts on surviving individuals and co-occurring species (Gandhi and Herms 2010). The removal of overstory vegetation is generally assumed to have a positive and relatively immediate effect on growth rates of remaining overstory vegetation, presumably due to reduced competition (Lorimer and Frelich 1989; Nowacki and Abrams 1997). Both natural mortality processes and insect invasions can create gaps that have positive effects on growth rates of surviving overstory stems (Pedersen and Howard 2004; Nuckolls et al. 2009), which frequently extend to subcanopy layers (Poage and Peart 1993). In the understory, canopy openings may also play an important role in the process of forest regeneration (Runkle 1982; Bormann and Likens 1994), with gap creation frequently resulting in increased seedling establishment in a number of forest types (Chen et al. 1992; Beckage et al. 2000; Coates 2002).

However, the effect of overstory mortality is not uniformly positive. Gap creation can result in increased mortality of overstory stems near the affected area (Sprugel and Bormann 1981), resulting from changing environmental conditions that increase stress on remaining individuals. Reductions in growth rates of residual trees, termed "thinning shock", can also occur following sudden exposure and may persist for more than a decade (Harrington and Reukema 1983). Additionally, positive effects may not be exhibited equally across all stem sizes or classes, potentially resulting in little to no response from dominant overstory trees (Poage and Peart 1993; Latham and Tappeiner 2002) and stronger responses in subdominant stems (Jones and Thomas 2004; Sharma et al. 2006).

The potential for negative effects of gap creation may extend to regeneration and recruitment of understory stems. Recently, the importance of the herbaceous layer has received increased attention for the role it plays in the establishment, growth, and survival of woody plant species. The density of herbaceous layer cover may increase following disturbance (Roberts 2004; Elliott et al. 2015), resulting in competition with woody plant species that may diminish regenerative capacity, thus altering successional dynamics (Royo and Carson 2006; Gilliam 2007).

The type of mortality that results from EAB and other phytophagous insects differs fundamentally from other types of disturbance, in that mortality is generally slower and standing dead trees may persist in these forests for many years (Krasny and DiGregorio 2001; Gandhi and Herms 2010). The canopy gaps that occur following EAB-induced mortality may thus be termed "gradual" gaps, in which standing dead trees persist in the overstory, as opposed to the "sudden" gaps that result from windthrow or logging (Krasny and Whitmore 1992) that are likely to cause more rapid changes in microclimate and disruption to the forest floor, exposing mineral soil. As a consequence, gradual gaps may induce a vegetation response that differs from that expected following sudden gap creation (Kneeshaw and Bergeron 1998; Beckage et al. 2000).

In *F. nigra* dominated wetlands, the potential hydrologic response is a further consequence of EAB-induced mortality that must be considered. Removal of significant proportions of woody vegetation may result in increased discharge from streams draining affected areas (Bosch and Hewlett 1982) or rising water tables (Riekerk 1983; Slesak et al. 2014) and increased overland flow (Beasley and Granillo 1988) in forests with poorly drained soils. Flooding has the potential to impact woody plants at nearly all life stages, resulting in a multitude of deleterious effects (Kozlowski 1997). Erdmann et al. (1987) reported increased water table height following clearcutting of *F. nigra* dominated wetlands in the Great Lakes region, which was associated with increased herbaceous layer growth and decreased tree regeneration.

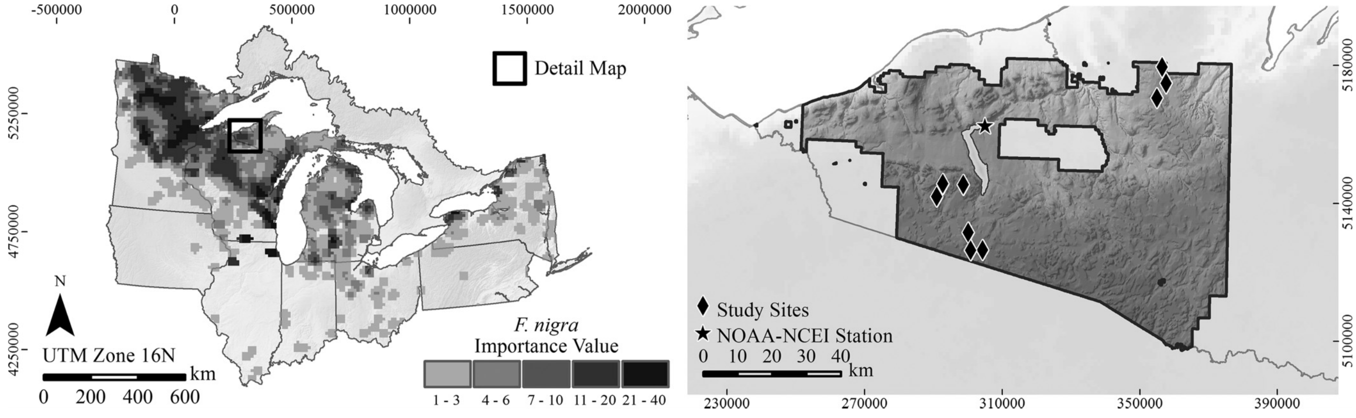
To assess these potential interactive effects on *F. nigra* dominated wetlands, a multiyear manipulative study was established on the Ottawa National Forest (ONF), Michigan, USA. Emerald ash borer induced mortality of *F. nigra* was simulated across a series of stands to emulate the effects of short- and long-term changes in site conditions following EAB infestation on growth and survival of co-occurring species, woody regeneration and recruitment, and herbaceous layer cover. Our objective was to determine the effects of *F. nigra* mortality on successional dynamics to understand how the loss of the dominant overstory species will affect the future species composition and fate of these stands. Additionally, the differential response of residual vegetation to these two simulations may provide insight into the responses of vegetation to sudden and gradual gaps within this forest type.

Materials and methods

Study site description

Study sites were located on the ONF in the western Upper Peninsula of Michigan, USA (Fig. 1). The regional climate is continental, with average monthly temperatures ranging from a minimum of –11.3 °C in January to a maximum of 18.2 °C in July (1981–2010 normals data from the Bergland Dam, Michigan station, UTM Zone 16N 304840 5162412 (Arguez et al. 2010)). Over the same period, mean annual precipitation was 1010 mm·year^{-1}, with the majority occurring from June through November (Arguez et al. 2010). During this study, surface water in these wetlands typically

Fig. 1. Regional map (left) with Forest Inventory and Analysis importance value (Prasad and Iverson 2003) and detail map of the Ottawa National Forest in western Upper Michigan (right) with study site locations (diamonds).



persisted from the onset of snowmelt until midsummer and remained near the soil surface throughout the growing season (Van Grinsven 2015). Surface soils consisted of woody peat histosols ranging in depth from 40 to greater than 690 cm, typically underlain by a layer of clay or clay loam.

Nine wetlands were selected based upon overstory composition, size, and landscape position. All nine study sites contained *F. nigra* as the most abundant overstory species, ranged in size from 0.23 to 1.19 ha, and were located in isolated depressions within first-order watersheds. This size range is typical of the *F. nigra* dominated forests encountered during site selection surveys. Study sites were divided into three blocks based upon geographical location, in which a "greedy" algorithm was used to create blocks with minimized in-block spatial variation using the blockTools package (Moore 2011) for the R statistical environment (R Core Team 2015). This method assigns sites to blocks by iteratively selecting three sites with the smallest distance between them. To assign treatments within each block, a custom optimizing algorithm was used that minimized among-treatment variability in percent *F. nigra* basal area (BA), depth of organic soil, and site area. Basal area percentage was taken from three variable-radius plots (10 BA factor) collected while evaluating potential study sites in 2011. Depth of organic soil was calculated as the mean depth of organic material in three soil cores per study site, and site area was taken from field mapping of the characteristically narrow ecotone separating these isolated wetlands from surrounding uplands. Each of the three blocks contained one site of each treatment type, which consisted of "Control", "Girdle", and "Ash-Cut", where "Girdle" and "Ash-Cut" treatments were intended to mimic short- and long-term changes in site conditions following EAB infestation, respectively. Within "Girdle" sites, all *F. nigra* stems ≥2.5 cm in diameter at breast height (DBH) (1.37 m) were hand-girdled with a drawknife in a 15–30 cm circumferential band to a depth sufficient to sever all phloem and cambium tissue. All *F. nigra* stems ≥2.5 cm DBH within "Ash-Cut" sites were felled by chainsaw and allowed to remain onsite. Both treatment types were applied in the winter of 2012/2013. The lower diameter limit for treatment of *F. nigra* was based on reports that EAB-induced mortality is typically confined to ash stems >2.5 cm DBH (McCullough et al. 2015). No additional treatment of epicormic sprouting that occurred following treatment was undertaken.

Vegetation data collection

Vegetation surveys were conducted annually from 2012 to 2015 in late July and early August. Surveys were timed to coincide with the peak of total herbaceous species cover. At each site, at least three 0.04 ha (11.3 m radius) permanent vegetation monitoring plots were established, centered on randomly generated coordinates (ArcGIS, ESRI, Redlands, California). Additional monitoring plots were added in accordance with each site's area, such that at least 15% of the total site area was surveyed. Each monitoring plot contained a set of three nested subplots, located at 120° intervals from an initial random bearing, at 5.5 m from plot center. Center points of plots and subplots were monumented to allow measurements to be taken at identical locations each year. Plots and subplots were used to quantify classes of vegetation as follows: *overstory* (woody stem DBH ≥ 10 cm, plot radius 11.3 m, plot area 400 m^2), *saplings* (woody stem DBH >2.5 and <10 cm, plot radius 4 m, three 50 m^2 subplots), *large woody stems* (stem DBH ≤2.5 and >50 cm in height, plot radius 1.5 m, three 7 m^2 subplots), and *small woody stems* (stems of potential overstory species ≤50 cm in height and stems of non-overstory species 15–50 cm in total height, plot radius 0.56 m, three 1 m^2 subplots).

Overstory stems and saplings were identified to species and DBH was measured to the nearest 0.5 mm using a diameter tape. Breast height was measured using a fixed-length rod prior to each diameter measurement to minimize potential error between observers. Large woody stems and small woody stems were identified and counted. Ocular estimates of the percent cover of herbaceous species and non-canopy woody species <15 cm in height were conducted within the small woody stem subplot (0.56 m radius). Estimates were assigned using the 10 cover classes established for the North Carolina Vegetation Survey as follows: trace, 0%–1%, 1%–2%, 2%–5%, 5%–10%, 10%–25%, 25%–50%, 50%–75%, 75%–95%, and >95%, where "trace" is defined as solitary individuals that comprise very little cover (Peet et al. 1998; Lee et al. 2008). Herbaceous vegetation was typically identified to species, with the exception of graminoids, as subplots often contained multiple morphological leaf forms that overlapped and interspersed such that estimation of cover beyond the genus level was prone to unacceptable potential levels of error. The percent cover values of the two *Dryopteris* species found in these sites, *Dryopteris carthusiana* (Vill.) H. P. Fuchs (spinulose woodfern) and *Dryopteris intermedia* (Willd.) A. Gray (intermediate woodfern), were combined for analyses, due to occasional damage (e.g., missing or broken pinnules) that masked diagnostic characters and the potential for hybridization (Reznicek et al. 2011). Ocular estimates were always performed by at least two observers, and at least one observer was present at all surveys across the 4 years of study.

Analytical methods

Measurements of DBH were used to calculate per-stem BA, which were then used to estimate BA ($m^2 \cdot ha^{-1}$) at the plot (overstory) or subplot (sapling) level. Counts of stems within plots and subplots were used to calculate stem density ($stems \cdot ha^{-1}$). Relative dominance for each species was calculated as the sum of BA from all plots for a species divided by the total BA of all species within a given site. Relative density for each species was calculated as the

Table 1. Pre-treatment (2012) overstory summary statistics by study site (mean ± standard error for diameter at breast height (DBH), basal area (BA), and density).

		F. nigra				All non-*F. nigra* species				
	Area (ha)	DBH (cm)	Maximum DBH (cm)	BA ($m^2\cdot ha^{-1}$)	Density ($stems\cdot ha^{-1}$)	DBH (cm)	Maximum DBH (cm)	BA ($m^2\cdot ha^{-1}$)	Density ($stems\cdot ha^{-1}$)	Species richness
"Control" 1	0.30	18.2±1.0	34.3	6.2±1.3	225±90	20.1±1.0	43.4	18.2±2.2	500±50	7
"Girdle" 1	0.29	20.7±0.9	37.1	16.1±3.6	442±131	20.4±1.0	39.1	12.3±1.7	325±52	8
"Ash-Cut" 1	0.61	14.7±0.5	30.9	13.9±2.5	758±121	18.1±0.9	47.7	17.8±2.5	567±94	9
"Control" 2	0.23	24.3±0.8	37.6	23.8±1.9	483±58	16.4±1.6	39.3	5.2±1.3	200±29	6
"Girdle" 2	0.33	21.9±1.3	43.2	20.5±3.6	458±51	19.8±2.1	33.8	4.5±2.1	125±38	5
"Ash-Cut" 2	0.35	20.9±0.7	49.5	28.0±2.0	742±22	17.4±1.2	30.8	4.8±1.4	183±30	4
"Control" 3	0.81	20.4±0.9	62.3	27.5±4.0	700±46	17.8±1.2	46.7	9.1±1.2	300±54	10
"Girdle" 3	0.61	19.0±1.0	51.0	20.5±3.8	608±88	19.1±1.2	41.8	8.4±1.9	258±109	7
"Ash-Cut" 3	1.19	17.4±0.6	55.0	16.1±2.6	590±42	15.1±0.9	45.1	5.3±1.1	275±58	4

sum of the stem counts from all plots for that species divided by the total number of stems of all species within a given site. Importance values (IV) were calculated following Iverson and Prasad (1998) as (100 × relative density) + (100 × relative dominance), although final IVs were divided by 2 so that values could be compared to Forest Inventory and Analysis (FIA) estimates presented in Fig. 1 (Prasad and Iverson 2003). Estimates of aboveground biomass of all stems ≥3 cm in DBH were calculated using the generalized biomass equations presented in Chojnacky et al. (2014), which require DBH and species only as inputs. Relative growth rates (RGR) were calculated as a single value over the course of the study as the change in calculated biomass at the plot (overstory) or subplot (sapling) level over three growing seasons, normalized by initial biomass. Stems that died or recruited from lower vegetation strata over the course of the study were excluded from RGR calculations.

Mixed-effects models were fit to the collected data with the R package lme4 (Bates et al. 2015) using year and treatment as fixed effects. Woody BA models incorporated plot (overstory) or subplot (sapling) nested within site as random effects. Large and small woody stem count data from subplot clusters were summed to yield a single value per plot, which was included in models as a nested random effect within site. Similarly, herbaceous cover data from subplots were averaged to yield a single cover value per plot, which was included as a random effect nested within site. Growth rate models included treatment and site only as the fixed and random effects, respectively. Basal area, growth rate, and percent cover data were square-root transformed before fitting linear models to resolve violations of non-normality and non-constant variance assumptions. Although the use of generalized linear models using Poisson or negative binomial distributions for count data has recently been suggested as a preferred technique (O'Hara and Kotze 2010), models fit using these methods performed poorly with the stem count data in this study. As such, linear models were fit to stem count data that were transformed as $\ln(x + 1)$. Visual examination of residual plots from fitted models did not reveal significant violations of the assumptions of normality or homogeneity of variance, although minor heteroskedasticity in the distribution of residuals of stem count and herbaceous cover data for individual species was observed, as would be expected given that these data were zero-inflated. Pairwise comparisons were made using the package lsmeans (Lenth 2016) utilizing the Tukey-HSD method to adjust p-values. A significance level of $p < 0.05$ was used for all comparisons. Standard errors for presentation in figures were calculated using a method of accounting for within-subjects designs presented in Morey (2008).

Results

Pre-treatment forest composition and response to treatment

Overstory summary statistics for all nine study sites are shown in Table 1. Within a block, overstory characteristics were similar, and stands appeared to be of comparable ages, with no evidence of recent logging or other large-scale disturbances within the wetland. However, differences in *F. nigra* BA and density between blocks were observed. Within Block 1, which is in the northeast portion of the ONF, BA and density of *F. nigra* were lowest, which is in agreement with the patterns in IV from FIA data (Fig. 1). Importance values for *F. nigra* overstory and saplings calculated for 20 km by 20 km cells range from 3 to 13 on the ONF and from 5 to 11 for the cells that include these study sites (Fig. 1) (Prasad and Iverson 2003). Within these wetlands, mean pre-treatment *F. nigra* IV for these strata was considerably higher than FIA IVs calculated across broader geographic scales in the region (Table 2).

Following treatment application, abundant epicormic branching was observed in both the "Girdle" and "Ash-Cut" treatments. Although some of these sprouts died from browsing or other unknown causes over the course of the study, many continued to grow vigorously, in some cases reaching heights of more than 6 m by the third year post-treatment (J.C. Davis, personal observation). In the "Girdle" treatment, foliage in the upper canopy was produced in the first year post-treatment but none was produced during subsequent growing seasons. No instances of phloem closure over the girdles were observed.

Overstory

Prior to treatment application, *F. nigra* on average comprised greater than 66% of the total overstory BA, while the remainder consisted of a mix of species, dominated by *Betula alleghaniensis* Britton (yellow birch) and *A. rubrum* (Table 2). Although BA of non-*F. nigra* overstory species increased in both the "Control" and "Girdle" sites over the 3 year study period (10.66 ± 0.19 to 11.29 ± 0.40 $m^2\cdot ha^{-1}$ and 8.36 ± 0.16 to 8.63 ± 0.20 $m^2\cdot ha^{-1}$, respectively) and decreased in the "Ash-Cut" sites (8.56 ± 0.41 to 8.47 ± 0.18 $m^2\cdot ha^{-1}$), these differences were not significant for any treatment type. Basal area of individual species also did not change significantly. Similarly, overstory RGR was not significantly affected by the mortality of *F. nigra* in these sites, for either all non-*F. nigra* stems combined ("Control": 0.024 ± 0.004 $g\cdot g^{-1}\cdot year^{-1}$, "Girdle": 0.036 ± 0.007 $g\cdot g^{-1}\cdot year^{-1}$, "Ash-Cut": 0.035 ± 0.004 $g\cdot g^{-1}\cdot year^{-1}$) or individual species. Growth rates by 10 cm increment DBH size class were also calculated and showed no difference in response both between treatments for a given size class and within a treatment between size classes (data not shown).

Table 2. Pre-treatment (2012) basal area (BA) and density calculations (mean ± standard error, calculated across all study sites ($n = 9$)) for the five species with highest BA or density within each stratum, sorted by overstory BA.

	Overstory				Saplings					Large woody stems		Small woody stems	
	BA (m²·ha⁻¹)	Relative dominance (%)*,†	Density (stems·ha⁻¹)	Relative density (%)†,‡	BA (m²·ha⁻¹)	Relative dominance (%)	Density (stems·ha⁻¹)	Relative density (%)	Importance value§	Density (stems·ha⁻¹)	Relative density (%)	Density (stems·ha⁻¹)	Relative density (%)
Fraxinus nigra	19.2±2.3	66.3±6.8	556±57	64.9±5.0	1.000±0.273	36.2±8.1	329±96	30.7±7.6	59.8±5.4	1898±1406	17.8±7.7	21105±13017	41.7±11.4
Betula alleghaniensis	3.2±0.6	11.5±2.3	90±18	10.6±2.2	0.325±0.102	11.7±2.6	127±40	10.6±1.7	11.3±2.0	231±172	1.9±0.9	1975±1358	3.5±2.5
Acer rubrum	2.7±0.8	9.9±3.0	94±23	11.0±2.9	0.224±0.077	14.4±5.0	98±39	14.9±5.6	10.6±3.0	1055±481	16.0±7.6	21944±12638	31.9±11.3
Thuja occidentalis L.	0.9±0.4	3.1±1.5	29±13	3.6±1.8	0.031±0.022	1.1±0.7	7±5	0.5±0.4	3.0±1.5	17±17	0.7±0.7	370±185	0.4±0.4
Tsuga canadensis	0.6±0.3	2.2±1.1	9±5	1.1±0.6	0.002±0.002	0.2±0.2	3±3	0.7±0.7	1.6±0.8	N/A	N/A	1111±786	2.3±1.9
Abies balsamea	0.6±0.3	1.7±0.8	35±17	3.3±1.4	0.522±0.131	24.3±5.0	257±64	27.9±5.6	6.3±1.7	514±192	10.4±4.2	1462±910	4.4±3.0
Ulmus americana	0.4±0.3	1.6±1.0	20±9	2.8±1.5	0.164±0.077	6.3±2.9	47±20	5.3±2.5	2.8±1.2	345±130	16.7±10.8	1259±469	6.6±3.9
Acer saccharum Marsh.	0.1±0.1	0.3±0.2	4±2	0.6±0.3	0.056±0.037	2.3±1.2	27±14	3.1±1.6	0.9±0.4	270±129	4.5±2.4	1327±845	2.4±1.3
Alnus incana					0.076±0.057	1.7±1.1	85±62	3.9±2.7	1.2±0.9	1350±1273	7.7±7.4	1111±1111	1.8±1.8

*Relative dominance was calculated as BA(species)/BA(all species) × 100 for all plots summed in a given site.

†Species list is not comprehensive; as a result, relative dominance and relative density in a column will not sum to 100.

‡Relative density was calculated as Density(species)/Density(all species) × 100 for all plots summed in a given site.

§Importance value was calculated using combined overstory and sapling data as (Relative dominance + Relative density)/2.

Saplings

The sapling layer was comprised primarily of *F. nigra*, but relative dominance was low compared to the overstory (Table 2). *Abies balsamea* (L.) Mill. (balsam fir) was more dominant in the sapling layer than in the overstory, whereas *B. alleghaniensis*, despite occupying a similar proportion of the BA as in the overstory, was exceeded by both *A. balsamea* and *A. rubrum* in relative sapling dominance.

No significant change in sapling BA was observed (Fig. 2*a*); however, total non-*F. nigra* sapling RGR was significantly higher ($p = 0.039$) in the "Girdle" sites compared to "Control", representing a nearly threefold greater RGR over three growing seasons (Fig. 2*b*). Sapling RGR was not significantly different in the "Ash-Cut" treatment compared to either the "Girdle" or "Control" treatments. The RGR of individual species followed similar patterns, although with no statistically significant differences.

Large and small woody stems

Large *F. nigra* stems had the highest relative density followed closely by *U. americana* and *A. rubrum* (Table 2), although mean absolute density of *U. americana* across all sites was relatively low. *Alnus incana* (L.) Moench (gray alder) stems were also abundant in this layer. In contrast with upper canopy layers, *B. alleghaniensis* abundance was very low. Small woody stems were strongly dominated by *F. nigra* and *A. rubrum*, which together comprised 73.6% of the small woody stems in these sites. Note that in some sites, these strata contained one or very few species of which abundance was relatively low, which led to apparent discrepancies between absolute and relative densities (Table 2), as was the case for *U. americana* (often high relative density due to a lack of regeneration of other species but low absolute density).

Compared to the first post-treatment growing season (2013), large *A. incana* stems increased in the "Ash-Cut" treatment by the third post-treatment growing season (2015) ($p = 0.010$), yet the 2015 tally was not greater than the pre-treatment value (Fig. 3*a*). No other significant differences within treatments were observed; however, the increase in *F. nigra* large woody stems within "Ash-Cut" sites from 2012 to 2015 approached significance ($p = 0.085$).

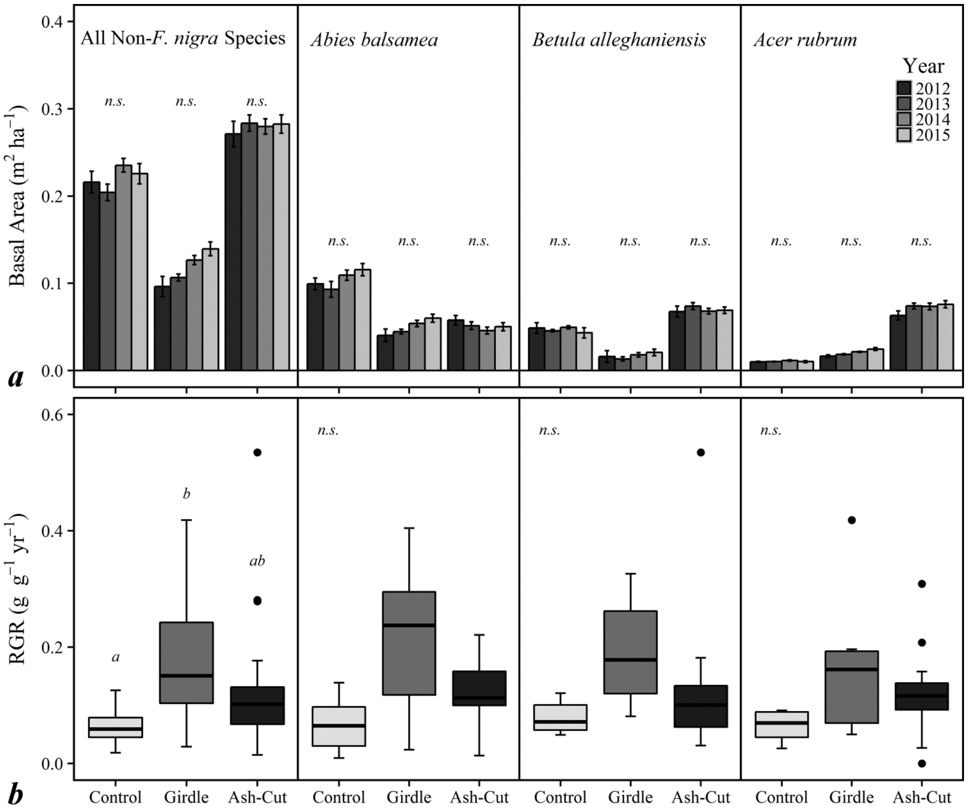
Total small woody stem densities varied significantly between study years, although no apparent effect of treatment was observed, as demographics of all species combined were similar across treatments (Fig. 3*b*). Compared to pre-treatment, small *F. nigra* stems increased significantly within the "Control" sites in the third post-treatment growing season (2015) ($p < 0.001$), although no change was observed in either the "Girdle" or the "Ash-Cut" treatments. *Acer rubrum* stems in the "Ash-Cut" treatment increased by the second year post-treatment (2012–2014) ($p = 0.009$), while small *B. alleghaniensis* stems increased in the "Girdle" sites over the same period ($p = 0.003$). Although *B. alleghaniensis* small woody stems also increased in the "Ash-Cut" sites, they declined to pre-treatment levels by 2015, and a similar increase followed by decline was observed in the "Control" sites over the same timeframe.

Herbaceous species

The most common herbaceous vascular plant species present in these wetlands were members of the genus *Carex*, which occurred in 67% of study plots in the pre-treatment study period and were the taxa with the greatest mean percent cover (Table 3). Fern species, including *Osmunda cinnamomea* L. (cinnamon fern), *Onoclea sensibilis*, L. (sensitive fern), *Athyrium filix-femina* (L.) Roth (common ladyfern), *D. carthusiana*, and *D. intermedia* were common and tended to comprise a large proportion of the herbaceous cover. Facultative wetland (FACW) species (Reed 1988) dominated the herbaceous cover in pre-treatment surveys (Fig. 4*a*).

Following treatment, cover of all herbaceous vascular (VASC) (Fig. 4*a*) plants, which frequently exceeded 50 cm in height, increased by 101% and 75% in both "Girdle" and "Ash-Cut" sites, respectively (2012–2015) ($p < 0.001$), while no significant change

Fig. 2. Sapling (stems 2.5 cm < DBH < 10 cm) (*a*) basal area by year and (*b*) relative growth rate (RGR) across three growing seasons for all non-*Fraxinus* species combined and the non-*Fraxinus* sapling species with the greatest basal area. Basal area data are mean ± standard error. Relative growth rate boxplots represent the 25th (lower edge) and 75th percentiles (upper edge) and medians (middle line). Fences extend to 1.5 times the interquartile range, with outliers beyond these values indicated by discrete points. Labels in RGR panels that do not share a letter indicate a statistically significant difference ($p < 0.05$) between treatments.



was observed in the "Control" sites. When species were examined by wetland indicator status, non-graminoid obligate wetland (OBL) species (Fig. 4*a*) increased in both "Girdle" and "Ash-Cut" treatments (2012–2015) ($p = 0.004$ and $p < 0.001$) and by 2015 occupied a similar proportion of the herbaceous cover as the FACW species, despite much greater cover of FACW species in the pretreatment surveys. Neither the FACW nor the combined facultative and facultative upland (FAC + FACU) groups responded significantly to treatment.

Among individual taxa, *Carex* species exhibited the strongest treatment response, reaching percent cover values of 321% and 413% of the pre-treatment cover in the "Girdle" and "Ash-Cut" treatments, respectively (Fig. 4*b*, 2012 to 2015) ($p < 0.001$). A number of additional species exhibited positive responses to treatment, including *Scutellaria lateriflora* L. (blue skullcap), *Lycopus uniflorus* Michx. (northern bugleweed), and *Caltha palustris* L. (yellow marsh marigold), although the effect varied in magnitude and by treatment type. While representing a substantial proportion of the pre-treatment cover, none of the fern species present in these sites responded to treatment.

Discussion

Overstory

Jones and Thomas (2004) put forth a set of three hypotheses that suggest potential responses to the residual forest canopy following gap creation: immediate, positive effects on growth rates, "thinning" or "gap shock" resulting from increased stress, manifested in decreased growth rates, or a combination of these two, resulting in offsetting impacts that result in a delayed growth response. A delayed response resulting from increased stress, despite a change in resource availability, may provide an explanation for the lack of observable positive effects on retained canopy trees during this study.

The "Ash-Cut" treatment represents a much more rapid change in the overstory than is likely to be experienced in the near-term following an actual EAB infestation. This treatment may then be more appropriately considered in light of other disturbances that create "sudden" gaps, such as windthrow or commercial thinning, rather than the "gradual" gaps that result from mortality due to insects or disease (Krasny and Whitmore 1992). Increased mortality that may follow sudden gap formation has been attributed to a change in local environmental conditions that increases stress on remaining trees, including increased wind damage (Chen et al. 1992; Garber et al. 2011), snow and ice loading (Sprugel and Bormann 1981), or photodamage (Harrington and Reukema 1983; Lovelock et al. 1994; Jones and Thomas 2004). Mortality of overstory stems reduced total non-*F. nigra* BA in the "Ash-Cut" sites of this study, although these reductions were small and not statistically significant. Observable aboveground damage to retained trees resulting from treatment application in the "Ash-Cut" sites was rare and can only be directly implicated in the deaths of a small number of individuals, and thus, this observed mortality may result from the effects of the "Ash-Cut" treatment on growing conditions.

By omitting mortality and recruitment from the analysis, the RGRs of stems present throughout the course of the study were compared. These comparisons, however, did not show any significant response to treatment. These results stand in contrast with those reported by Flower et al. (2013), which showed a positive growth effect in co-occurring species during EAB infestation in

Fig. 3. Woody stem density (mean ± standard error) for all species combined and the most abundant (*a*) large (stems ≤2.5 cm DBH and >50 cm in height) and (*b*) small (stems ≤50 cm in height) woody species. Labels that do not share a letter indicate a statistically significant difference ($p < 0.05$) between years within a given treatment.

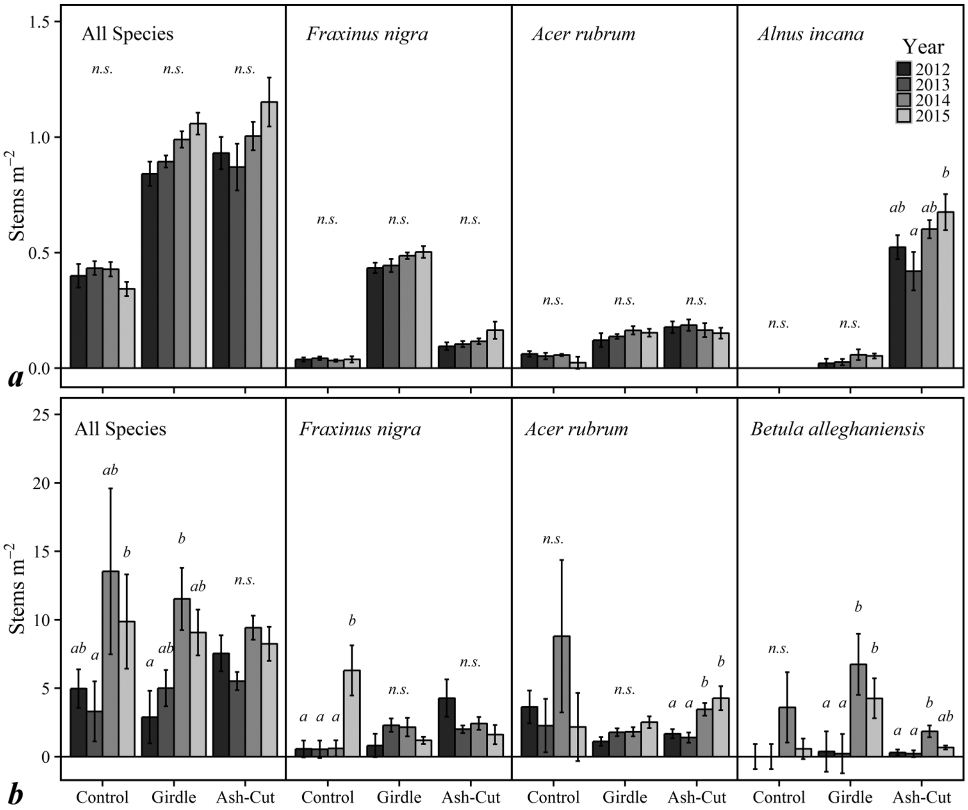


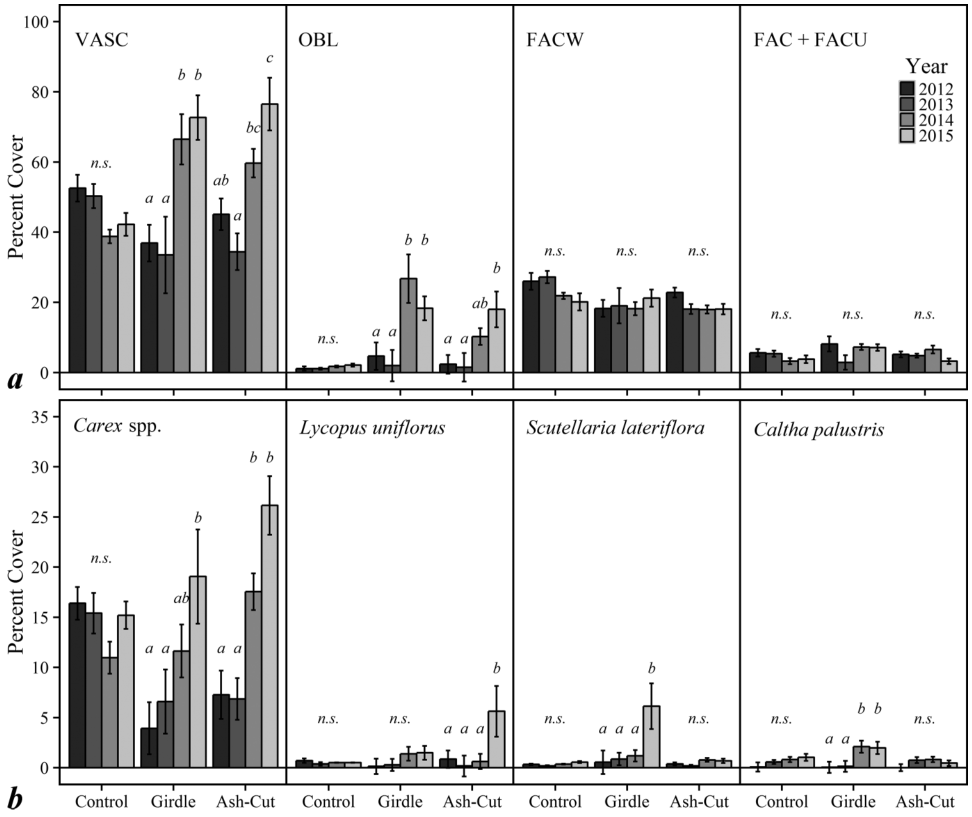
Table 3. Pre-treatment (2012) percent cover (mean ± standard error, calculated across all study sites (n = 9)) of all non-woody vascular plant species that occur in ≥10% of herbaceous study plots (n = 90).

	Frequency (n)	Percent cover
Carex spp. L.	60	8.6±2.5
Dryopteris spp. Adans.	40	4.1±1.3
Onoclea sensibilis	35	3.9±1.5
Rubus pubescens Raf.	33	2.1±1.1
Scutellaria lateriflora	32	0.4±0.1
Galium spp. L.	30	0.2±0.1
Poaceae (Barnhart)	28	2.4±1.5
Impatiens capensis Meerb.	22	1.7±1.0
Osmunda cinnamomea	21	8.5±3.0
Coptis trifolia (L.) Salisb.	17	0.1±<0.1
Maianthemum canadense Desf.	16	0.1±0.1
Mitella nuda L.	16	0.2±0.1
Trientalis borealis Raf.	15	0.1±0.1
Oxalis acetosella Raf.	12	0.1±<0.1
Equisetum pratense Ehrh.	11	0.2±0.1
Lycopus uniflorus	10	0.6±0.4
Athyrium filix-femina	9	2.3±1.3
Bidens spp. L.	9	0.4±0.3
Equisetum sylvaticum L.	9	0.3±0.1

riparian forests of northern Ohio, although this study was conducted over 6 years. A positive effect of competitive release on growth rates is a commonly reported response to both selection harvests (Latham and Tappeiner 2002; Pedersen and Howard 2004) and in the gradual gaps created by invasive insects and pathogens, such as beech bark disease (Twery and Patterson 1984; DiGregorio et al. 1999), hemlock woolly adelgid (*Adelges tsugae* Annand) (Small et al. 2005; Ford et al. 2012), or gypsy moth (*Lymantria dispar* L.) (Muzika and Liebhold 1999; Jedlicka et al. 2004). However, nearly all of these studies examined growth rates over longer time frames (Twery and Patterson 1984; Latham and Tappeiner 2002; Pedersen and Howard 2004; Small et al. 2005) or used more sensitive measurement techniques than those used in this study, such as increment cores (Muzika and Liebhold 1999) or dendrometers (Ford et al. 2012). The lack of radial growth rate response could also result from a change in resource allocation to foliage or root production; however, no change in nitrogen uptake or litter production from retained stems was observed following treatment (Davis 2016).

Stress-related symptoms of gap or thinning shock may be exhibited in a number of ways, including reduced growth, chlorotic foliage, and mortality (Sharma et al. 2006). All of these indicators, including chlorotic foliage (Davis 2016), were observed in the overstory of the treated sites, suggesting an increase in stress of residual trees that may have reduced the potential for a positive growth response. In addition to potential changes in wind damage, snow loading, and photodamage, a change in site hydrology may also induce a stress response. Mean growing season water table height was reported to be unaffected by either treatment, although a reduction in the rate of drawdown was observed, leading to significant differences in water table height late in the growing season and prolonged inundation of the root zone (Van Grinsven 2015), which may increase stress on residual trees (Erdmann et al. 1987; Kozlowski 1997). The response to some of these stressors may, however, be moderated in an actual infestation, where canopy mortality will occur more gradually, allowing residual stems more time to acclimate. The rate of mortality in the "Girdle" sites (complete overstory mortality at the stand level within 2 years) is more rapid

Fig. 4. Areal cover (mean ± standard error) of vascular plants by (*a*) functional group and (*b*) select common taxa. Functional groups in Fig. 4*a* represent all herbaceous vascular (VASC) species, non-graminoid obligate wetland (OBL), facultative wetland (FACW), and facultative plus facultative upland (FAC + FACU) species. Labels that do not share a letter indicate a statistically significant difference ($p < 0.05$) between years within a given treatment.



than the maximal rates that have been previously reported (5–6 years) (Knight et al. 2013; Smith et al. 2015).

Saplings

Release from suppression of understory trees through gap creation is a common response across nearly all closed-canopy forests and has played a significant role in the development of successional dynamics theories (Runkle 1982; Bormann and Likens 1994). The response of the sapling layer is important to the near-term future of these sites, as expansion of existing canopy crowns is unlikely to fill gaps of the size created in this study. The observed increased sapling growth rate (Fig. 2*b*) suggests a positive effect of release resulting from mortality of the *F. nigra* overstory. This increased growth rate did not result in a significant increase in non-*Fraxinus* sapling BA, although an increasing trend appears to be emerging in the "Girdle" treatment (Fig. 2*a*). Overall patterns of growth rate evident in the combined sapling data appear to repeat across other commonly co-occurring species; as such, the lack of statistical significance can perhaps be attributed to relatively small samples sizes for each individual species (Fig. 2*b*). That no significant response in sapling growth rate within "Ash-Cut" sites was observed is notable, as these stems would theoretically be expected to receive the greatest increase in available resources. However, they are also likely subject to the greatest change in environmental conditions, and thus the lack of response may be attributable to the balance between resource availability and abiotic stressors.

Large and small woody stems

As with saplings, the creation of gaps is often predicted to result in increased seedling establishment, an effect that has been reported in both experimentally created gaps (Gray and Spies 1996; Coates 2002) and those resulting from other invasive insects, such as the hemlock woolly adelgid (Orwig and Foster 1998; Ford et al. 2012). Although no increase resulting from treatment in total small woody stems was observed in this study, individual species densities did change, with increased *A. rubrum* and *B. alleghaniensis* density by the second post-treatment growing season, while *F. nigra* stem density remained unchanged (Fig. 3*b*). The demographics of *F. nigra* stems in the treated sites is the expected result of the removal of seed sources (Klooster et al. 2014), as evidenced by the relatively constant density of stems in the "Girdle" and "Ash-Cut" sites in 2015, while in the same year, *F. nigra* small woody stems increased significantly in the "Control" sites. Similar results have been reported in studies of EAB infestation elsewhere in the region. Kashian and Witter (2011) reported abundant capacity for potential *Fraxinus* regeneration within infested sites in the Lower Peninsula of Michigan, but a decline in newly germinated seedlings over time. In a separate study, *Fraxinus pennsylvanica* Marshall (green ash) below the size infested by EAB was common throughout southern Michigan, but new regeneration declined with time since EAB invasion (Burr and McCullough 2014). Klooster et al. (2014) described comparable results across Michigan and Ohio, labeling established *Fraxinus* seedlings an "orphaned cohort" resulting from mortality of all larger stems, the subsequent lack of seed source, and absence of a persistent seedbank for any *Fraxinus* species in the region. Although seed-bearing epicormic sprouts and recruited understory stems have recently been reported from *F. pennsylvanica* dominated wetlands (Kashian 2016), it is unknown if young stems or epicormic branching in *F. nigra* dominated stands will survive to reach reproductive maturity.

In *F. nigra* dominated wetlands of northern Minnesota exhibiting natural dieback, regeneration has been shown to be dominated by shrub species such as *A. incana*, prompting observers to suggest that this forest type may eventually be succeeded by scrub-shrub wetlands (Palik et al. 2012). Although the number of *A. incana* large woody stems in the "Ash-Cut" sites increased over the course of the post-treatment period (Fig. 3*a*), this appears to result from increased recruitment from the small woody stem class, as no increase in *A. incana* seedlings was observed. Large woody stems of potential overstory species outnumbered *A. incana* across all sites, despite these increases. Additionally, while *A. incana* stems are frequently abundant in terms of absolute density, this did not appear to inhibit regeneration of other species, as mean relative density was relatively low (Table 2). This suggests that there is currently ample prospect for regeneration of potential overstory species, in contrast with observations from *F. nigra* stands in northern Minnesota (Palik et al. 2012).

Prior to treatment, *B. alleghaniensis* comprised a small proportion of the large and small woody stems (Table 2), which may be ascribed to a lack of suitable substrate, primarily exposed mineral soil or down coarse woody debris, that is important to the regeneration of this species (Godman and Krefting 1960; Shields et al. 2007). Additionally, coniferous coarse woody debris tends to promote *B. alleghaniensis* establishment (Marx and Walters 2008; Bolton and D'Amato 2011) but is not abundant in these hardwood-dominated wetlands. Although increased *B. alleghaniensis* small woody stems were observed in both the "Girdle" and "Ash-Cut" sites in 2014, a similar pattern was observed in the "Control" sites (Fig. 3*b*) and thus may be attributable to a mast year for this species across the region rather than an effect of treatment. The gradual gaps resulting from EAB mortality are unlikely to create favorable substrate conditions, such as exposed mineral soil, for *B. alleghaniensis* seedling establishment in the near-term. As a result, it appears unlikely that the canopy openings resulting from EAB alone are sufficient to promote future *B. alleghaniensis* overstory dominance equivalent to that currently present in these sites.

In addition to the response of individual species to EAB-induced mortality, the pre-disturbance understory density and composition will likely play a major role in future vegetation dynamics. The density and diversity of large and small woody stems varied considerably by site prior to treatment, as can be seen in the greater density of all large woody stems in the "Girdle" and "Ash-Cut" sites and the larger proportion comprised by *F. nigra* in the "Girdle" sites and *A. incana* in the "Ash-Cut" treatment (Fig. 3*a*). Pre-treatment differences can also be observed in sapling BA (Fig. 2*a*). As all comparisons were made relative to pre-treatment data, these differences did not affect the relative responses reported here. However, these differences may prove important to the long-term vegetation response to EAB infestation. Stands with greater densities of saplings and large woody stems may recover more rapidly following disturbance, and the species composition of these layers will likely have lasting effects on overstory composition, although species-specific responses may moderate the influence of pre-disturbance characteristics.

Herbaceous species

The greatly increased cover of herbaceous species represents the most dramatic impact of simulated EAB-induced mortality in the present study. Although the response of the herbaceous layer lagged the treatment application by two to three growing seasons, strong effects were observed across both treatments (Fig. 4*a*). The differential response of OBL versus FACW species, suggests a response to reported changes in hydrology (Van Grinsven 2015), as the FACW species did not respond to treatment, despite being the dominant wetland indicator class in the pre-treatment surveys. In addition to the significant increases in cover of species present in the pre-treatment surveys (Fig. 5*b*), a number of OBL species, including *Alisma triviale* Pursh (northern water-plantain) and *Cicuta bulbifera* L. (water hemlock), were not observed in any of the sites prior to treatment but appeared in the latter years of the study. The single invasive species identified in these wetlands, *Solanum dulcamara* L. (climbing nightshade), did not increase in cover. A number of invasive plants, however, are potential threats to forested wetlands of the region (Weber et al 2007; Marlor et al. 2014), and the potential for increased invasibility following EAB mortality in these forests should be considered likely (Davis et al. 2005; Hausman et al. 2010).

The interaction between the herbaceous layer and the large and small woody stems may prove important in determining the future fate of woody species in these communities. Erdmann et al. (1987) described the conversion of *F. nigra* dominated wetlands to herbaceous or scrub-shrub wetlands following clearcutting and warned that removal of significant portions of the overstory may result in a total loss of tree species, including established regeneration. Herbaceous species are known to compete strongly with woody vegetation in some forest types (Royo and Carson 2006; Gilliam 2007) and may increase in cover following disturbance (Roberts 2004; Elliott et al. 2015). Given the height obtained by many of the herbaceous species in these forests, increased herbaceous cover following disturbance may enhance competition with both newly established seedlings and larger stems. As was observed in the "Girdle" sites in these wetlands, even the types of gradual gaps associated with relatively slow tree mortality and the retention of standing dead trees can result in greatly increased herbaceous cover (Fig. 5). Similar effects have been seen in studies that examined the response of herbaceous species to *Tsuga canadensis* (L.) Carrière (eastern hemlock) decline resulting from hemlock woolly adelgid infestation (Yorks et al. 2003; Eschtruth et al. 2006; Ford et al. 2012).

Herbaceous cover has been implicated in the inhibition of woody regeneration in a number of ecosystem types. The effect of dense fern cover has received particular attention and has been linked to reduced establishment, density, and growth of tree seedlings (Maguire and Forman 1983; George and Bazzaz 1999*a*, 1999*b*), which may influence the development rate and composition of a forest canopy following disturbance (Royo and Carson 2006; Gilliam 2007). Graminoid species, such as *Calamgrostis canadensis* (Michx.) P. Beauv. (bluejoint), have also been shown to influence future canopy development in boreal forests (Lieffers et al. 1993). Although fern species are among the most common herbaceous plants in these wetlands, they did not respond significantly to either treatment. Additionally, increased *Carex* cover, as well as other species, did not impact seedling survival by the third year post-treatment. As such, it is perhaps cause for cautious optimism that the recent increase in herbaceous cover has yet to reduce the potential for future woody vegetation recovery in these forests.

Erdmann et al. (1987) linked the increase in herbaceous cover and poor regeneration of woody species to observations of a higher water table following overstory removal, a change in hydrology also reported from a study in Minnesota similar to the present one (Slesak et al. 2014). Although the changes in hydrology following treatment in these sites were relatively minor, the reported increases in late-season water table height (Van Grinsven 2015) may explain the strong response of OBL species over other functional groups (Fig. 4*a*) and, as discussed, may have contributed to stress in woody species that reduced the potential response to competitive release (Erdmann et al. 1987; Kozlowski 1997). Given the available data, the possibility for increases in water table height following disturbance in similar wetland types across the region persists, and the effects of such changes on vegetation should remain a concern.

Predicting the future fate of this forest type in the presence of EAB is, at best, an uncertain task. Based upon the results of this and other studies, the continued presence of *Fraxinus* species in forests throughout infested regions seems unlikely, due to high mortality rates and the lack of seed sources or a persistent seed-

Fig. 5. Serial photographs of a single subplot within a "Girdle" treatment. Photographs were taken yearly at the time of survey (late July). Green hues were enhanced during the conversion to a black and white image to improve contrast.

bank. Surviving small stems are unlikely to reach reproductive maturity (Kurmis and Kim 1989; Klooster et al. 2014) before succumbing to infestation, although recent reports from *F. pennsylvanica* dominated stands suggests that persistence of the genus is possible, although at much lower levels (Kashian 2016). Within *F. nigra* dominated wetlands, overstory stems of co-occurring species appear likely to survive, and the increased growth rate of saplings may rapidly fill gaps resulting from *F. nigra* mortality. Should woody species remain abundant in these forests, it appears that the canopy will eventually be dominated by *A. rubrum* as occurs elsewhere in the region (Erdmann et al. 1987), although *F. nigra* mortality may improve otherwise poor regeneration and recruitment of *B. alleghaniensis* in the present forest. While increased herbaceous cover has not inhibited seedling response in this study, the potential for intensified competition from herbaceous species to reduce future woody regeneration remains a concern. Continued work within this forest type, as well as investigations into potential means of maintaining forest cover in similar habitats of the region (Looney et al. 2015), are critical to determining how these forests may respond in the future and identifying means of mitigating the negative impacts of EAB.

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References

Arguez, A., Durre, I., Applequist, S., Squires, M., Vose, R., Yin, X., and Bilotta, R. 2010. NOAA's U.S. Climate normals (1981–2010). Annual and seasonal precipitation and temperature. NOAA National Centers for Environmental Information. [accessed 4 February 2016]. doi:10.7289/V5PN93JP.

Aukema, J.E., Leung, B., Kovacs, K., Chivers, C., Britton, K.O., Englin, J., Frankel, S.J., Haight, R.G., Holmes, T.P., Liebhold, A.M., McCullough, D.G., and Von Holle, B. 2011. Economic impacts of non-native forest insects in the continental United States. PLoS ONE, **6**(9): e24587. doi:10.1371/journal.pone.0024587. PMID:21931766.

Baker, M.E., and Wiley, M.J. 2004. Characterization of woody species distribution in riparian forests of Lower Michigan, U.S.A. using map-based models. Wetlands, **24**(3): 550–561. doi:10.1672/0277-5212(2004)024[0550:COWSDI]2.0.CO;2.

Bates, D., Maechler, M., Bolker, B, and Walker, S. 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. **67**(1): 1–48. doi:10.18637/jss.v067.i01.

Beasley, R.S., and Granillo, A.B. 1988. Sediment and water yields from managed forests on flat coastal plain sites. Water Resour. Bull. **24**(2): 361–366. doi:10.1111/j.1752-1688.1988.tb02994.x.

Beckage, B., Clark, J.S., Clinton, B.D., and Haines, B.L. 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. Can. J. For. Res. **30**(10): 1617–1631. doi:10.1139/x00-075.

Bolton, N.W., and D'Amato, A.W. 2011. Regeneration responses to gap size and coarse woody debris within natural disturbance-based silvicultural systems in northeastern Minnesota, USA. For. Ecol. Manage. **262**(7): 1215–1222. doi:10.1016/j.foreco.2011.06.019.

Bormann, F.H., and Likens, G. 1994. Pattern and process in a forested ecosystem. 1st ed. Springer-Verlag, New York.

Bosch, J.M., and Hewlett, J.D. 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. J. Hydrol. **55**(1–4): 3–23. doi:10.1016/0022-1694(82)90117-2.

Burr, S.J., and McCullough, D.G. 2014. Condition of green ash (*Fraxinus pennsylvanica*) overstory and regeneration at three stages of the emerald ash borer invasion wave. Can. J. For. Res. **44**(7): 768–776. doi:10.1139/cjfr-2013-0415.

Cappaert, D., McCullough, D.G., Poland, T.M., and Siegert, N.W. 2005. Emerald ash borer in North America: a research and regulatory challenge. Am. Entomol. **51**(3): 152–165. doi:10.1093/ae/51.3.152.

Chen, J., Franklin, J.F., and Spies, T.A. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. Ecol. Appl. **2**(4): 387–396. doi:10.2307/1941873. PMID:27759269.

Chen, Y., and Poland, T.M. 2010. Nutritional and defensive chemistry of three North American ash species: possible roles in host performance and preference by emerald ash borer adults. Great Lakes Entomol. **43**(1–4): 20–33.

Chojnacky, D.C., Heath, L.S., and Jenkins, J.C. 2014. Updated generalized biomass equations for North American tree species. Forestry, **87**(1): 129–151. doi:10.1093/forestry/cpt053.

Coates, K.D. 2002. Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. For. Ecol. Manage. **155**(1): 387–398. doi:10.1016/S0378-1127(01)00574-6.

Davis, J.C. 2016. Vegetation dynamics and nitrogen cycling responses to simulated emerald ash borer infestation in *Fraxinus nigra*-dominated wetlands of Upper Michigan, USA. Ph.D. dissertation, School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, Mich.

Davis, M.A., Thompson, K., and Grime, J.P. 2005. Invasibility: the local mechanism driving community assembly and species diversity. Ecography, **28**(5): 696–704. doi:10.1111/j.2005.0906-7590.04205.x.

DiGregorio, L.M., Krasny, M.E., and Fahey, T.J. 1999. Radial growth trends of sugar maple (*Acer saccharum*) in an Allegheny northern hardwood forest affected by beech bark disease. J. Torr. Bot. Soc. **126**(3): 245–254. doi:10.2307/2997279.

Elliott, K.J., Vose, J.M., Knoepp, J.D., Clinton, B.D., and Kloeppel, B.D. 2015. Functional role of the herbaceous layer in Eastern deciduous forest ecosystems. Ecosystems, **18**(2): 221–236. doi:10.1007/s10021-014-9825-x.

Emerald Ash Borer Information Network. 2016. Initial county EAB detections in North America. Available from http://www.emeraldashborer.info/documents/MultiState_EABpos.pdf [accessed 4 February 2016].

Erdmann, G.G., Crow, T.R., Peterson, R.M., Jr., and Wilson, C.D. 1987. Managing black ash in the Lake States. USDA For. Serv., North Central Forest Experiment Station, St. Paul, MN. Gen. Tech. Rep. NC-115. Available from http://www.nrs.fs.fed.us/pubs/gtr/gtr_nc115.pdf [accessed 4 February 2016].

Eschtruth, A.K., Cleavitt, N.L., Battles, J.J., Evans, R.A., and Fahey, T.J. 2006. Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. Can. J. For. Res. **36**(6): 1435–1450. doi:10.1139/x06-050.

Flower, C.E., Knight, K.S., and Gonzalez-Meler, M.A. 2013. Impacts of the emerald ash borer (*Agrilus planipennis* Fairmaire) induced ash (*Fraxinus* spp.) mortality on forest carbon cycling and successional dynamics in the eastern United States. Biol. Invasions, **15**(4): 931–944. doi:10.1007/s10530-012-0341-7.

Ford, C.R., Elliott, K.J., Clinton, B.D., Kloeppel, B.D., and Vose, J.M. 2012. Forest dynamics following eastern hemlock mortality in the southern Appalachians. Oikos, **121**(4): 523–536. doi:10.1111/j.1600-0706.2011.19622.x.

Gandhi, K.J.K., and Herms, D.A. 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biol. Invasions, **12**(2): 389–405. doi:10.1007/s10530-009-9627-9.

Garber, S., Lam, T.Y., and Maguire, D.A. 2011. Growth and mortality of residual Douglas-fir after regeneration harvests under group selection and two-story silvicultural systems. West. J. Appl. For. **26**(2): 64–70.

George, L.O., and Bazzaz, F. 1999*a*. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. Ecology, **80**(3): 833–845. doi:10.1890/0012-9658(1999)080[0833:TFUAAE]2.0.CO;2.

George, L.O., and Bazzaz, F. 1999*b*. The fern understory as an ecological filter: growth and survival of canopy-tree seedlings. Ecology, **80**(3): 846–856. doi:10.1890/0012-9658(1999)080[0846:TFUAAE]2.0.CO;2.

Gilliam, F.S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience, **57**(10): 845–858. doi:10.1641/B571007.

Godman, R.M., and Krefting, L.W. 1960. Factors important to yellow birch establishment in Upper Michigan. Ecology, **41**(1): 18–28. doi:10.2307/1931935.

Gray, A.N., and Spies, T.A. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. J. Ecol. **84**(5): 635–645. doi:10.2307/2261327.

Haack, R.A., Jendek, E., Liu, H., Marchant, K.R., Petrice, T.R., Poland, T.M., and Ye, H. 2002. The emerald ash borer: a new exotic pest in North America. Newsl. Mich. Entomol. Soc. **47**(3–4): 1–5.

Harrington, C.A., and Reukema, D.L. 1983. Initial shock and long-term stand development following thinning in a Douglas-fir plantation. For. Sci. **29**(1): 33–46.

Hausman, C.E., Jaeger, J.F., and Rocha, O.J. 2010. Impacts of the emerald ash borer (EAB) eradication and tree mortality: potential for a secondary spread of invasive plant species. Biol. Invasions, **12**(7): 2013–2023. doi:10.1007/s10530-009-9604-3.

Herms, D.A., and McCullough, D.G. 2014. Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annu. Rev. Entomol. **59**: 13–30. doi:10.1146/annurev-ento-011613-162051. PMID:24112110.

Iverson, L.R., and Prasad, A.M. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecol. Monogr. **68**(4): 465–485. doi:10.1890/0012-9615(1998)068[0465:PAOTSF]2.0.CO;2.

Jedlicka, J., Vandermeer, J., Aviles-Vazquez, K., Barros, O., and Perfecto, I. 2004. Gypsy moth defoliation of oak trees and a positive response of red maple and black cherry: an example of indirect interaction. Am. Midl. Nat. **152**(2): 231–236. doi:10.1674/0003-0031(2004)152[0231:GMDOOT]2.0.CO;2.

Jones, T.A., and Thomas, S.C. 2004. The time course of diameter increment responses to selection harvests in *Acer saccharum*. Can. J. For. Res. **34**(7): 1525–1533. doi:10.1139/x04-034.

Kashian, D.M. 2016. Sprouting and seed production may promote persistence of green ash in the presence of the emerald ash borer. Ecosphere, **7**(4): e01332. doi:10.1002/ecs2.1332.

Kashian, D.M., and Witter, J.A. 2011. Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on southeastern Michigan landscapes. For. Ecol. Manage. **261**(3): 480–488. doi:10.1016/j.foreco.2010.10.033.

Klooster, W.S., Herms, D.A., Knight, K.S., Herms, C.P., McCullough, D.G., Smith, A., Gandhi, K.J., and Cardina, J. 2014. Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). Biol. Invasions, **16**(4): 859–873. doi:10.1007/s10530-013-0543-7.

Kneeshaw, D.D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology, **79**(3): 783–794. doi:10.1890/0012-9658(1998)079[0783:CGCATR]2.0.CO;2.

Knight, K.S., Brown, J.P., and Long, R.P. 2013. Factors affecting the survival of ash (*Fraxinus* spp.) trees infested by emerald ash borer (*Agrilus planipennis*). Biol. Invasions, **15**(2): 371–383. doi:10.1007/s10530-012-0292-z.

Kovacs, K.F., Haight, R.G., McCullough, D.G., Mercader, R.J., Siegert, N.W., and Liebhold, A.M. 2010. Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. Ecol. Econ. **69**(3): 569–578. doi:10.1016/j.ecolecon.2009.09.004.

Kozlowski, T.T. 1997. Responses of woody plants to flooding and salinity. Tree Physiol. Monogr. **17**(7): 490. doi:10.1093/treephys/17.7.490.

Krasny, M.E., and DiGregorio, L.M. 2001. Gap dynamics in Allegheny northern hardwood forests in the presence of beech bark disease and gypsy moth disturbances. For. Ecol. Manage. **144**(1): 265–274. doi:10.1016/S0378-1127(00)00391-1.

Krasny, M.E., and Whitmore, M.C. 1992. Gradual and sudden forest canopy gaps in Allegheny northern hardwood forests. Can. J. For. Res. **22**(2): 139–143. doi:10.1139/x92-019.

Kurmis, V., and Kim, J.H. 1989. Black ash stand composition and structure in Carlton County, Minnesota. University of Minnesota Staff Paper Series Number 69. Available from https://www.forestry.umn.edu/sites/forestry.umn.edu/files/Staffpaper69.pdf [accessed 4 February 2016].

Latham, P., and Tappeiner, J. 2002. Response of old-growth conifers to reduction in stand density in western Oregon forests. Tree Physiol. **22**(2–3): 137–146. doi:10.1093/treephys/22.2-3.137. PMID:11830410.

Lee, M.T., Peet, R.K., Roberts, S.D., and Wentworth, T.R. 2008. CVS-EEP protocol for recording vegetation. Available from http://cvs.bio.unc.edu/protocol/cvs-eep-protocol-v4.2-lev1-5.pdf [accessed 2 August 2016].

Lenth, R.V. 2016. Least-squares means: the R package lsmeans. J. Sta. Softw. **69**(1): 1–33. doi:10.18637/jss.v069.i01.

Lieffers, V.J., Macdonald, S.E., and Hogg, E.H. 1993. Ecology of and control strategies for *Calamagrostis canadensis* in boreal forest sites. Can. J. For. Res. **23**(10): 2070–2077. doi:10.1139/x93-258.

Looney, C.E., D'Amato, A.W., Palik, B.J., and Slesak, R.A. 2015. Overstory treatment and planting season affect survival of replacement tree species in emerald ash borer threatened *Fraxinus nigra* forests in Minnesota, USA. Can. J. For. Res. **45**(12): 1728–1738. doi:10.1139/cjfr-2015-0129.

Lorimer, C.G., and Frelich, L.E. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Can. J. For. Res. **19**(5): 651–663. doi:10.1139/x89-102.

Lovelock, C., Osmond, C., and Jebb, M. 1994. Photoinhibition and recovery in tropical plant species: response to disturbance. Oecologia, **97**(3): 297–307. doi:10.1007/BF00317318.

Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., and Fitzhugh, R.D. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. Bioscience, **56**(5): 395–405. doi:10.1641/0006-3568(2006)056[0395:FERTEP]2.0.CO;2.

MacFarlane, D.W., and Meyer, S.P. 2005. Characteristics and distribution of potential ash tree hosts for emerald ash borer. For. Ecol. Manage. **213**(1): 15–24. d10.1016/j.foreco.2005.03.013.

Maguire, D.A., and Forman, R.T. 1983. Herb cover effects on tree seedling patterns in a mature hemlock–hardwood forest. Ecology, **64**(6): 1367–1380. doi:10.2307/1937491.

Marlor, K.M., Webster, C.R., and Chimner, R.C. 2014. Disturbance and wetland type alter reed canarygrass cover in northern Michigan. Invasive Plant Sci. Manage. **7**(1): 121–131. doi:10.1614/IPSM-D-13-00039.1.

Marx, L., and Walters, M.B. 2008. Survival of tree seedlings on different species of decaying wood maintains tree distribution in Michigan hemlock–hardwood forests. J. Ecol. **96**(3): 505–513. doi:10.1111/j.1365-2745.2008.01360.x.

McCullough, D.G., Schneeberger, N.F., Katovich, S.A., and Siegert, N.W. 2015. Pest alert: emerald ash borer. USDA For. Serv., Northeastern Area, State & Private Forestry, Newtown Square, Pa. NA-PR-02-04. Available from http://www.na.fs.fed.us/spfo/pubs/pest_al/eab/eab.pdf [accessed 20 June 2016].

Mercader, R.J., Siegert, N.W., Liebhold, A.M., and McCullough, D.G. 2011. Influence of foraging behavior and host spatial distribution on the localized spread of the emerald ash borer, *Agrilus planipennis*. Popul. Ecol. **53**(2): 271–285. doi:10.1007/s10144-010-0233-6.

Moore, R.T. 2011. blockTools: Block, assign, and diagnose potential interference in randomized experiments. R package version 0.5-3.

Morey, R.D. 2008. Confidence intervals from normalized data: a correction to Cousineau (2005). Tutorials Quantitative Methods Psychol. **4**(2): 61–64. doi:10.20982/tqmp.04.2.p061.

Muzika, R.M., and Liebhold, A.M. 1999. Changes in radial increment of host and nonhost tree species with gypsy moth defoliation. Can. J. For. Res. **29**(9): 1365–1373. doi:10.1139/x99-098.

Nowacki, G.J., and Abrams, M.D. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. Ecol. Monogr. **67**(2): 225–249. doi:10.1890/0012-9615(1997)067[0225:rgacfr]2.0.co;2.

Nuckolls, A.E., Wurzburger, N., Ford, C.R., Hendrick, R.L., Vose, J.M., and Kloeppel, B.D. 2009. Hemlock declines rapidly with hemlock woolly adelgid infestation: impacts on the carbon cycle of southern Appalachian forests. Ecosystems, **12**(2): 179–190. doi:10.1007/s10021-008-9215-3.

O'hara, R.B., and Kotze, D.J. 2010. Do not log-transform count data. Methods Ecol. Evol. **1**(2): 118–122. doi:10.1111/j.2041-210X.2010.00021.x.

Orlova-Bienkowskaja, M.J., and Bieńkowski, A.O. 2016. The life cycle of the emerald ash borer *Agrilus planipennis* in European Russia and comparisons with its life cycles in Asia and North America. Agric. For. Entomol. **18**(2): 182–188. doi:10.1111/afe.12140.

Orwig, D.A., and Foster, D.R. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. J. Torr. Bot. Soc. **125**(1): 60–73. doi:10.2307/2997232.

Palik, B.J., Ostry, M.E., Venette, R.C., and Abdela, E. 2012. Tree regeneration in black ash (*Fraxinus nigra*) stands exhibiting crown dieback in Minnesota. For. Ecol. Manage. **269**: 26–30. doi:10.1016/j.foreco.2011.12.020.

Pedersen, B.S., and Howard, J.L. 2004. The influence of canopy gaps on overstory tree and forest growth rates in a mature mixed-age, mixed-species forest. For. Ecol. Manage. **196**(2): 351–366. doi:10.1016/j.foreco.2004.03.031.

Peet, R.K., Wentworth, T.R., and White, P.S. 1998. A flexible, multipurpose method for recording vegetation composition and structure. Castanea, **63**(3): 262–274.

Pimentel, D., Zuniga, R., and Morrison, D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol. Econ. **52**(3): 273–288. doi:10.1016/j.ecolecon.2004.10.002.

Poage, N.J., and Peart, D.R. 1993. The radial growth response of American beech (*Fagus grandifolia*) to small canopy gaps in a northern hardwood forest. Bull. Torr. Bot. Club, **120**(1): 45–48. doi:10.2307/2996662.

Poland, T.M., and McCullough, D.G. 2006. Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. J. For. **104**(3): 118–124.

Prasad, A.M., and Iverson, L.R. 2003. Little's range and FIA importance value database for 135 eastern US tree species. Northeastern Research Station, USDA Forest Service, Delaware, Ohio. Available from http://www.fs.fed.us/ne/delaware/4153/global/littlefia/index.html [accessed 4 February 2016].

Pugh, S.A., Liebhold, A.M., and Morin, R.S. 2011. Changes in ash tree demography associated with emerald ash borer invasion, indicated by regional forest inventory data from the Great Lakes States. Can. J. For. Res. **41**(11): 2165–2175. doi:10.1139/x11-138.

Pureswaran, D.S., and Poland, T.M. 2009. Host selection and feeding preference of *Agrilus planipennis* (Coleoptera: Buprestidae) on ash (*Fraxinus* spp.). Environ. Entomol. **38**(3) 757–765. doi:10.1603/022.038.0328.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rebek, E.J., Herms, D.A., and Smitley, D.R. 2008. Interspecific variation in resistance to emerald ash borer (Coleoptera: Buprestidae) among North American and Asian ash (*Fraxinus* spp.). Environ. Entomol. **37**(1): 242–246. doi:10.1603/0046-225X(2008)37[242:IVIRTE]2.0.CO;2. PMID:18348816.

Reed, P.B., Jr. 1988. National list of plant species that occur in wetlands: North Central (Region 3). U.S. Department of the Interior, Fish and Wildlife Service. Biological Report 88(26.3).

Reznicek, A.A., Voss, E.G., and Walters, B.S. 2011. Michigan flora. [online.] Available from http://michiganflora.net/genus.aspx?id=Dryopteris [accessed 4 February 2016].

Riekerk, H. 1983. Impacts of silviculture on flatwoods runoff, water-quality, and nutrient budgets. Water Resour. Bull. **19**(1): 73–79. doi:10.1111/j.1752-1688.1983.tb04559.x.

Rigsby, C.M., Muilenburg, V., Tarpey, T., Herms, D.A., and Cipollini, D. 2014. Oviposition preferences of *Agrilus planipennis* (Coleoptera: Buprestidae) for different ash species support the mother knows best hypothesis. Ann. Entomol. Soc. Am. **107**(4): 773–781. doi:10.1603/AN13185.

Rigsby, C.M., Showalter, D.N., Herms, D.A., Koch, J.L., Bonello, P., and Cipollini, D. 2015. Physiological responses of emerald ash borer larvae to feeding on different ash species reveal putative resistance mechanisms and insect counter-adaptations. J. Insect Physiol. **78**: 47–54. doi:10.1016/j.jinsphys.2015.05.001. PMID:25956198.

Roberts, M.R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. Can. J. Bot. **82**(9): 1273–1283. doi:10.1139/b04-091.

Royo, A.A., and Carson, W.P. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can. J. For. Res. **36**(6): 1345–1362. doi:10.1139/x06-025.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology, **63**(5): 1533–1546. doi:10.2307/1938878.

Schlesinger, G.G. 1990. *Fraxinus americana* L.; white ash. *In* Silvics of North America. Vol. 2. Hardwoods. *Edited by* R.M. Burns and B.H. Honkala. USDA Forest Service, Washington, D.C., Agriculture Handbook 654. pp. 333–348. Available from http://www.srs.fs.usda.gov/pubs/misc/ag_654_vol2.pdf [accessed 3 June 2016].

Sharma, M., Smith, M., Burkhart, H.E., and Amateis, R.L. 2006. Modeling the impact of thinning on height development of dominant and codominant loblolly pine trees. Ann. For. Sci. **63**(4): 349–354. doi:10.1051/forest:2006015.

Shields, J.M., Webster, C.R., and Nagel, L.M. 2007. Factors influencing tree species diversity and *Betula alleghaniensis* establishment in silvicultural openings. Forestry, **80**(3): 293–307. doi:10.1093/forestry/cpm013.

Siegert, N.W., McCullough, D.G., Williams, D.W., Fraser, I., Poland, T.M., and Pierce, S.J. 2010. Dispersal of *Agrilus planipennis* (Coleoptera: Buprestidae) from discrete epicenters in two outlier sites. Environ. Entomol. **39**(2): 253–265. doi:10.1603/EN09029. PMID:20388252.

Siegert, N.W., McCullough, D.G., Liebhold, A.M., and Telewski, F.W. 2014. Dendrochronological reconstruction of the epicentre and early spread of emerald ash borer in North America. Diversity Distrib. **20**(7): 847–858. doi:10.1111/ddi.12212.

Slesak, R.A., Lenhart, C.F., Brooks, K.N., D'Amato, A.W., and Palik, B.J. 2014. Water table response to harvesting and simulated emerald ash borer mortality in black ash wetlands in Minnesota, USA. Can. J. For. Res. **44**(8): 961–968. doi:10.1139/cjfr-2014-0111.

Small, M.J., Small, C.J., and Dreyer, G.D. 2005. Changes in a hemlock-dominated forest following woolly adelgid infestation in southern New England. J. Torr. Bot. Soc. **132**(3): 458–470. doi:10.3159/1095-5674(2005)132[458:CIAHFF]2.0.CO;2.

Smith, A., Herms, D.A., Long, R.P., and Gandhi, K.J.K. 2015. Community composition and structure had no effect on forest susceptibility to invasion by the emerald ash borer (Coleoptera: Buprestidae). Can. Entomol. **147**(3): 318–328. doi:10.4039/tce.2015.8.

Sprugel, D.G., and Bormann, F.H. 1981. Natural disturbance and the steady state in high-altitude balsam fir forests. Science, **211**(4480): 390–393. doi:10.1126/science.211.4480.390. PMID:17748274.

Tanis, S.R., and McCullough, D.G. 2015. Host resistance of five *Fraxinus* species to *Agrilus planipennis* (Coleoptera: Buprestidae) and effects of paclobutrazol and fertilization. Environ. Entomol. **44**(2): 287–299. doi:10.1093/ee/nvu005. PMID:26313182.

Twery, M.J., and Patterson, W.A., III. 1984. Variations in beech bark disease and its effects on species composition and structure of northern hardwood stands in central New England. Can. J. For. Res. **14**(4): 565–574. doi:10.1139/x84-104.

Van Grinsven, M.J. 2015. Implications of emerald ash borer disturbance on black ash wetland watershed hydrology, soil carbon efflux, and dissolved organic matter composition. Ph.D. dissertation, School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, Mich.

Weber, C.R., Cohen, J.G., and Kost, M.A. 2007. Natural community abstract for Northern Hardwood Swamp. Michigan Natural Features Inventory, Lansing, Mich. Available from http://mnfi.anr.msu.edu/abstracts/ecology/Northern_hardwood_swamp.pdf [accessed 4 February 2016].

Wei, X., Wu, Y., Reardon, R., Sun, T.-H., Lu, M., and Sun, J.-H. 2007. Biology and damage traits of emerald ash borer (*Agrilus planipennis* Fairmaire) in China. Insect Sci. **14**(5): 367–373. doi:10.1111/j.1744-7917.2007.00163.x.

Whitehill, J.G.A., Opiyo, S.O., Koch, J.L., Herms, D.A., Cipollini, D.F., and Bonello, P. 2012. Interspecific comparison of constitutive ash phloem phenolic chemistry reveals compounds unique to Manchurian ash, a species resistant to emerald ash borer. J. Chem. Ecol. **38**(5): 499–511. doi:10.1007/s10886-012-0125-7. PMID:22588569.

Wright, J.W., and Rauscher, H.M. 1990. *Fraxinus nigra* Marsh.; black ash. *In* Silvics of North America. Vol. 2. Hardwoods. *Edited by* R.M. Burns and B.H. Honkala. USDA Forest Service, Washington, D.C., Agriculture Handbook 654. pp. 344–347. Available from http://www.srs.fs.usda.gov/pubs/misc/ag_654_vol2.pdf [accessed 4 February 2016].

Yorks, T.E., Leopold, D.J., and Raynal, D.J. 2003. Effects of *Tsuga canadensis* mortality on soil water chemistry and understory vegetation: possible consequences of an invasive insect herbivore. Can. J. For. Res. **33**(8): 1525–1537. doi:10.1139/x03-073.