



Nitrogen cycling responses to simulated emerald ash borer infestation in *Fraxinus nigra*-dominated wetlands

Joshua C. Davis · Joseph P. Shannon · Matthew J. Van Grinsven ·
Nicholas W. Bolton · Joseph W. Wagenbrenner · Randall K. Kolka ·
Thomas G. Pypker

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Abstract Understanding short- and long-term responses of forest nutrient cycling to disturbance is vital to predicting future forest function. Mortality of ash trees (*Fraxinus* spp.) due to emerald ash borer [EAB, *Agrilus planipennis* (Coleoptera: Buprestidae)] invasion is likely to alter ecosystem processes within infested stands throughout North America. In particular, the loss of *Fraxinus nigra* (black ash) from *F. nigra*-dominated swamps may significantly impact the biogeochemical cycles within these ecologically

important wetlands. A multiyear manipulative study of nine *F. nigra*-dominated wetlands in Michigan, USA was undertaken to investigate the potential response of above- and belowground biogeochemical processes to EAB. Short- and long-term changes to site conditions following infestation were emulated by respectively girdling or felling *F. nigra* saplings and overstory trees. Following disturbance, a short-term reduction in demand for soil nitrogen (N) by dominant canopy species was hypothesized to result in increased soil N availability and a subsequent increase in N uptake by retained species. Though reduced total N return via litterfall indicated decreased demand, this resulted in minimal impacts to soil N availability following treatment. Additionally, increased N uptake by co-dominant *Acer rubrum* (red maple) and *Betula*

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J. C. Davis (✉)
Smithsonian-Mason School of Conservation, George
Mason University, 1500 Remount Rd., Front Royal,
VA 22630, USA
e-mail: jdavis61@gmu.edu

J. C. Davis · J. P. Shannon · M. J. Van Grinsven ·
N. W. Bolton
School of Forest Resources and Environmental Science,
Michigan Technological University, 1400 Townsend Dr.,
Houghton, MI 49931, USA

M. J. Van Grinsven
Department of Earth, Environmental, and Geographical
Sciences, Northern Michigan University, 1401 Presque
Isle Avenue, Marquette, MI 49855, USA

J. W. Wagenbrenner
USDA Forest Service, Pacific Southwest Research
Station, 1700 Bayview Drive, Arcata, CA 99521, USA

R. K. Kolka
Center for Research on Ecosystem Change, USDA Forest
Service, Northern Research Station, 1831 Hwy 169 East,
Grand Rapids, MN 55744, USA

T. G. Pypker
Department of Natural Resource Sciences, Thompson
Rivers University, 805 TRU Way, Kamloops,
BC V2C 0C8, Canada

allegghaniensis (yellow birch) was not observed; these combined responses may be attributable to increased immobilization of N by soil microbes. In the 3 years following treatment, the response of foliar characteristics of residual stems—including decreased N concentrations and increased leaf mass per area—appeared to be driven primarily by aboveground conditions and a change from shade- to sun-acclimated leaves. While increased microbial immobilization of N may reduce long-term changes in site fertility, these responses may also limit the potential for short-term positive growth responses of extant woody vegetation. In the longer term, replacing N-rich *F. nigra* leaf litter with that of *A. rubrum* and *B. alleghaniensis*, which have lower N content, is likely to have important feedback effects on soil processes.

Keywords Soil nitrogen · Black ash · Forested wetlands · Invasive species · Disturbance ecology

Introduction

The threats posed by invasive insects are both profound and multi-faceted (Lovett et al. 2006), and include significant alteration to forest structure and ecosystem processes (Gandhi and Herms 2010). The impacts from the invasive emerald ash borer in North America [EAB, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae)] have received considerable recent attention (Kolka et al. 2018) due to the damaging effects of EAB on forest composition and ecosystem function and the ubiquity of the genus *Fraxinus* (ash) across eastern North America (Cappaert et al. 2005; Herms and McCullough 2014). Members of the genus are common in a wide variety of forests, though most species generally comprise relatively minor proportions of the canopy (MacFarlane and Meyer 2005), particularly in upland forests (Kashian 2016). In contrast, *Fraxinus nigra* Marshall (black ash) is frequently a major component of forested wetlands (Wright and Rauscher 1990) and in portions of the range may occur in nearly pure stands (Erdmann et al. 1987). In the Upper Peninsula of Michigan, USA, *F. nigra* is frequently the dominant species in the *F. nigra*-*Ulmus americana* L. (American elm)-*Acer rubrum* L. (red maple) forest type, particularly in areas with poor drainage or organic soils

(Erdmann et al. 1987). In addition, *F. nigra* is among the preferred hosts of EAB (Pureswaran and Poland 2009; Tanis and McCullough 2012), and has low resistance to infestation (Whitehill et al. 2012; Rigsby et al. 2015). As such, the mortality of *F. nigra* from these forests is expected to lead to many impacts on ecosystem processes (Kashian and Witter 2011; Klooster et al. 2018), and while some of these effects may be temporary as forests recover, others may result in a persistent shift in state (Davis et al. 2017; Looney et al. 2017). Recent reports on the effects of *F. nigra* mortality on forest hydrology (Slesak et al. 2014; Van Grinsven et al. 2017; Shannon et al. 2018) and greenhouse gas emissions (Van Grinsven et al. 2018; Noh et al. 2018) begin to highlight the breadth of these impacts, while also illustrating the complicated nature of interactive processes in these ecosystems. Investigations into the potential effects of EAB and other disturbance agents across different timescales is paramount to understanding the longer-term nature of such impacts on ecosystem function, as well as the potential to mitigate negative consequences.

The loss of a large proportion of the woody vegetation has been shown to have significant direct and indirect effects on biogeochemical cycles within these ecosystems (Gandhi and Herms 2010), which may have lasting effects on future forest recovery. Following *F. nigra* mortality, both above- and belowground growing conditions may be altered. Belowground, soil nutrient dynamics may be affected via multiple mechanisms (Hunter 2001); among these, the direct effect of changing plant demand for nitrogen (N) and indirect effects of soil microclimate on decomposition and nutrient mineralization rates are of particular importance to biogeochemical cycling (Vitousek and Melillo 1979). In addition, aboveground changes in the light environment and microclimate, such as increased light availability and air temperature, are expected to stimulate morphological and biochemical acclimation of leaves to the new growing conditions (Naidu and DeLucia 1997, 1998; Jones and Thomas 2007).

Given their fundamentally interconnected nature, perturbation of above- or belowground ecosystem properties and processes are likely to induce changes throughout the system, potentially resulting in cascading effects throughout the forest community (Castello et al. 1995; Ellison et al. 2005). Damage due to phytophagous insects has frequently been

associated with increased soil N availability (Jenkins et al. 1999; Orwig et al. 2008; Keville et al. 2013), which is subsequently either redistributed within the system or subject to export (Lovett et al. 2002). As a result, this increase in belowground N may result in either improved aboveground nutrient status of residual vegetation (Griffin et al. 2011; Levy-Varon et al. 2014) or nutrient losses from the system (Swank et al. 1981; Eshleman et al. 1998), potentially with negative consequences for downstream ecosystems and long-term site productivity (Lovett et al. 2002). In turn, changes in aboveground plant properties may impact soil processes through the role of the canopy in regulating the soil physical environment and litter production, the characteristics of which exert strong influences on nutrient cycling (Prescott 2002). As such, it is critical to consider the implications of EAB-induced mortality on both above- and belowground processes (Bardgett et al. 1998). Additionally, potential changes within these systems are likely to occur at different temporal scales. Such changes may include short-term/fast cycle impacts such as direct effects on litter input quantity or plant demand, as well as long-term/slow cycle effects, including changes in litter quality, community composition, and nutrient cycling rates (Hunter 2001; Lovett et al. 2006). It is thereby necessary to consider effects across a range of conditions and time scales to fully understand how EAB infestation may affect forest processes (Stadler et al. 2005).

Our understanding of the potential impacts of forest pathogens and pests on plant response and ecosystem nutrient dynamics are primarily drawn from studies of abiotic or anthropogenic disturbances (Likens et al. 1970; Vitousek and Melillo 1979; Goulet and Bellefleur 1986). These investigations provide a useful framework by which to understand the effects of biotic disturbances on forest processes (Orwig et al. 2008). However, it is important to recognize that the effects of biotic disturbances on nutrient cycling may differ fundamentally from other disturbance types (Castello et al. 1995), and substantially different responses frequently exist even among various biotic disturbances (Hunter 2001). By contrast, anthropogenic disturbance has been used successfully to simulate the effects of biotic disturbances, with generally good agreement on the timing and extent of impacts (e.g. Yorks et al. 2003; Orwig et al. 2013; Trahan et al. 2015). Adding further complication to the prediction

of anticipated impacts, the majority of studies of forest disturbance effects on biogeochemical cycles have been conducted in upland systems, while the limited research within forested wetlands has focused on managed systems (Nakagawa et al. 2012). As such, the extent to which patterns suggested by results from upland forests and managed wetlands are applicable to the *F. nigra*-dominated forested wetlands of the upper Great Lakes region is unknown.

A multiyear manipulative study was initiated on the Ottawa National Forest, Michigan, USA to assess the potential impacts of EAB on ecosystem processes in *F. nigra*-dominated wetlands. Across a series of stands, the mortality of *F. nigra* was experimentally induced via girdling and ash-felling to emulate the range of potential short- and long-term changes in site conditions following EAB infestation and their effects on above- and belowground nitrogen cycling as well as canopy morphological and biochemical acclimation. The objective of this investigation was to evaluate the potential effects of *F. nigra* mortality on nutrient cycling components expected to exhibit short-term effects of disturbance, including soil nitrogen availability, nitrogen uptake, and foliar characteristics. The nature of these components and how they are affected by disturbance can then be used to assess how long-term site fertility and future vegetation recovery may be affected by the loss of the dominant canopy species. Additionally, the inclusion of two levels of experimental disturbance may provide further insight into the drivers of change in these ecosystem processes, as sudden mortality or changes in growing conditions (e.g. via *Fraxinus* basal area reduction or salvage logging) may induce a different ecological response from death or other losses over a longer duration (e.g. unmanaged EAB infestation; Orwig et al. 2013). We hypothesize that the loss of the dominant species in these forests will drive changes in the functional role of co-dominant tree species in nitrogen and energy cycling, resulting in fundamental shifts in patterns of forest resource acquisition. Specifically, we hypothesized that (i) *F. nigra* mortality will lead to a short-term reduction in total demand for nitrogen and thus increased inorganic soil nitrogen availability, subsequently resulting in (ii) increased nitrogen return via litterfall of co-dominant species, indicating greater nitrogen availability to and uptake by these stems. In addition, (iii) changes in the foliage of co-dominant

species that reflect a shift from shade- to sun-grown foliar characteristics are expected.

Methods

Study site description

Study sites were located on the Ottawa National Forest in the western Upper Peninsula of Michigan, USA (Fig. 1). Average monthly temperatures range from a minimum of $-11.3\text{ }^{\circ}\text{C}$ in January to a maximum of $18.2\text{ }^{\circ}\text{C}$ in July (1981–2010 normals data from the Bergland Dam, MI station, UTM Zone 16 N 304840 5162412; Arguez et al. 2010). Thirty year mean annual precipitation was 1010 mm year^{-1} , with the majority occurring from June through November (Arguez et al. 2010). Surface water in these wetlands is generally present from the onset of snowmelt until mid-summer and typically remained near the soil surface throughout the growing season during this study (Van Grinsven et al. 2017). In these sites, surface soils were comprised of woody peat Histosols ranging in depth from 5 cm to greater than 690 cm with a mean depth of 140 cm, which were underlain by clay or clay loam glaciolacustrine deposits (Van Grinsven et al. 2017).

Nine wetlands were selected based upon similarity in overstory composition, size, and landscape position. No site exhibited any evidence of EAB infestation prior to or during the course of the study. Overstory basal area and density of *F. nigra* (mean \pm standard error) across the nine sites was $19.2 \pm 2.3\text{ m}^2\text{ ha}^{-1}$

and $556 \pm 57\text{ stems ha}^{-1}$, respectively, which correspond to a relative dominance of $66.3 \pm 6.8\%$ and relative density of $64.9 \pm 5.0\%$ (Davis et al. 2017). Wetland area ranged from 0.23 to 1.19 ha, and all study sites were located in isolated depressions within first-order watersheds. The blockTools package (Moore 2011) for the R statistical environment (version 3.2.0, R Core Team 2015) was used to create groups ($n = 3$) of study sites by geographical location, such that in-group spatial variation was minimized. Each group contained one site of each treatment, which consisted of ‘Control,’ ‘Girdle,’ and ‘Ash-Cut’. The ‘Girdle’ and ‘Ash-Cut’ treatments were intended to mimic potential short- and long-term changes in site conditions following EAB infestations, respectively. Scaled and weighted values for initial estimates of percent *F. nigra* basal area, total site area, and average depth of organic soil were calculated and used to assign treatments within each group such that among-treatment variation in these values was minimized. Treatments in the ‘Girdle’ and ‘Ash-Cut’ sites were applied in the winter of 2012/2013. In ‘Girdle’ sites, all *F. nigra* stems $\geq 2.5\text{ cm}$ in diameter at 1.37 m were hand-girdled with a drawknife in a 15–30 cm band to a depth sufficient to sever all phloem and cambium tissue. All *F. nigra* stems $\geq 2.5\text{ cm}$ at 1.37 m within ‘Ash-Cut’ sites were felled by chainsaw and left onsite. Within the ‘Girdle’ treatment sites, canopy leaf-out of all sampled trees occurred for a single year post-treatment; canopy mortality was complete by the second growing season following treatment application. In each of the ‘Girdle’ and ‘Ash-Cut’ sites, epicormic branches originating from

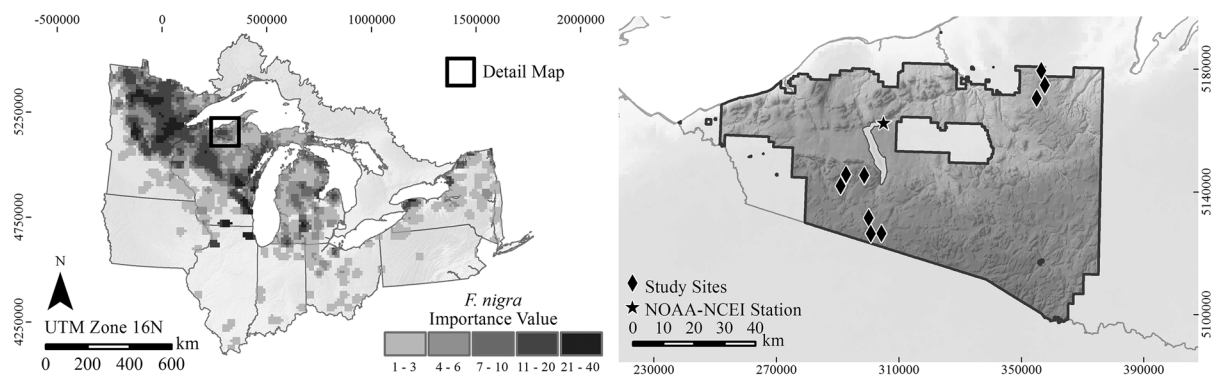


Fig. 1 Regional map (left) with Forest Inventory and Analysis importance value (Prasad and Iverson 2003) and detail map of the Ottawa National Forest in western Upper Michigan (right)

with study site locations (diamonds). Each block of sites contained one replicate of each treatment (Davis et al. 2017)

the main stem just below the girdle or cut sprouted in the first growing season following treatment. Though some of these sprouts died over the course of the study, many continued to grow throughout the study, with some reaching heights in excess of 6 m. (Davis et al. 2017). No additional treatment of epicormic sprouting was undertaken, and no instances of phloem closure across girdles was observed.

Within each study site, three instrument clusters were established at spatially distributed random locations throughout the wetland, where cluster centers were located such that all instrumentation was > 5 m from the wetland edge and > 10 m from another cluster. Instrumentation was accessed via raised boardwalks.

Sample collection

Ion exchange resin (IER) bags (Binkley and Matson 1983) were used to evaluate inorganic soil nitrogen availability, using a modification of the protocol described in Giblin et al. (1994). Bags were constructed of undyed nylon/Lycra® fabric, each containing 5 g of mixed bed IER (Dowex Marathon MR-3, Sigma-Aldrich Corp., St. Louis, MO, USA), and closed with a nylon cable tie. Bags were soaked for 1 h in a 1.2 M HCl solution, rinsed in deionized water, and frozen in polyethylene bags until deployment. At each study site, a group of three IER bags was buried at each of ten locations randomly generated in ArcGIS (Esri, Redlands, CA, USA) such that groups were located a minimum of 5 m from either the study site edge or another resin bag group, and at least 1 m from any other infrastructure. To minimize disruption of upper soil layers, three angled incisions into the soil were made approximately 30 cm away from and toward the center flag marking each location. One bag was placed in each incision so that the lowermost point was at a depth of 10 cm below the soil surface, after which the soil was replaced. The remaining two IER bags were placed in this manner at 120° intervals around the center point.

Three seasonal deployments and retrievals of IER bags occurred each year for 2 years, with each deployment keyed to phenological events. Initial deployments occurred after leaf-fall and prior to treatment in mid-November 2012. These bags were removed and new bags inserted in the same location after the leaves of all deciduous tree species were fully

expanded in the spring (late June/early July 2013, “Spring”). The second set of bags was removed and replaced at the onset of senescence (late August/early September 2013, “Summer”). The third set of IER bags remained in place until leaf fall in mid-November 2013 (“Autumn”). Deployments were repeated on the same schedule in 2013/2014 with this second cycle of bags offset from the initial bag locations by 60°. After removing the IER bags from the soil, they were thoroughly rinsed with deionized water and placed in polyethylene bags. Bags were immediately stored in a cooler with ice in the field and subsequently at – 20 °C upon return to the laboratory and until extraction.

Twenty 0.5 m² litter traps constructed of polyvinyl chloride pipe frames and fiberglass window screen material were installed at each site. A pair of litter traps was located opposite each other at 3 m from the center point of each instrument cluster, while the remaining 14 were placed at randomly generated points adjacent to boardwalks, with a minimum of 3 m between traps. Traps were elevated to prevent contamination from surface water or soil. Leaf litter was collected monthly at each site within all treatments between mid-June and mid-October from 2012 to 2014. Collected litter was returned to the laboratory where it was dried at 65 °C until no further weight change was observed, after which it was stored at room temperature. All litter samples were subsequently sorted into *F. nigra* and non-*F. nigra* components and weighed, while litter from five traps at each site was further sorted to separate *Betula alleghaniensis* Britton (yellow birch) and *A. rubrum* litter. Litter from all months for a given trap and species were pooled for nutrient analyses (see “Sample processing and analysis”). Litter trap locations and the subset of traps that received supplemental sorting remained fixed between study years. However, if a sample in a given month was unusable (e.g. a tipped or damaged trap), a substitute sample from another trap from the site was used, so that each composite annual sample for nutrient analysis contained litter from each month of the growing season.

Live foliage samples were obtained by shotgun at each site in late August from 2012 to 2015, prior to the onset of senescence. For each of the three major overstory species (*F. nigra*, *A. rubrum*, and *B. alleghaniensis*), five dominant or co-dominant overstory stems nearest the randomly generated locations

used for vegetation measurements in a related study (Davis et al. 2017) were sampled. Samples were taken from at least three different east- or west-facing branches (Law et al. 2008) of the upper third of the crown, yielding a composite sample of at least 25 leaves for each tree. Within the ‘Girdle’ sites, foliage samples were obtained using the same criteria from epicormic branching that occurred following treatment. Foliage samples were immediately placed in a zip-top polyethylene bag and stored in a cooler with ice while onsite, and subsequently stored at 4 °C until further processing.

Sample processing and analysis

Prior to extraction, IER bags were thawed at 4 °C overnight, after which they were again rinsed with deionized water to remove any remaining soil particles. Any bags that exhibited evidence of damage were discarded. Within a given sample period, each group of bags was extracted together in 50 ml of 2 M KCl solution (Kjønaas 1999) per bag for 1 h at 150 strokes per minute on an orbital shaker table (New Brunswick Innova 2100, Eppendorf, Hamburg Germany). The resulting eluent was passed through a 1.6 µm glass fiber filter (Grade A, Sterlitech Corp., Kent, WA, USA) and frozen at –20 °C in a polypropylene centrifuge tube until analysis. Colorimetric analysis of the inorganic nitrogen content of each sample was performed on a microplate reader (SpectraMax M2, Molecular Devices LLC, Sunnyvale, CA, USA) using the techniques described for NH_4^+ and NO_3^- in Sinsabaugh et al. (2000) and Doane and Horwath (2003), respectively. Each polystyrene well plate contained triplicate aliquots of each sample along with a set of standards prepared in 2 M KCl. The concentration of each sample was calculated from the measured absorbance values of the standards on each plate and the mean absorption of each set of triplicates.

Live foliage samples obtained in 2012 and 2013 were dried at 65 °C until a stable weight was reached. In 2014 and 2015, the area of 25 fresh leaves from each sample tree was measured with a leaf area meter set to a resolution of 1 mm² (LI-3100, LI-COR Inc., Lincoln, NB, USA), after which the leaves were dried as above. Foliage samples obtained in 2015 received additional processing to determine chlorophyll content (Warren 2008; see Online Resource 1 for additional details on processing) prior to drying. Dried

litter and live foliage samples were ground to a fine powder (8000 M Mixer/Mill, Spex SamplePrep LLC, Metuchen, NJ, USA), from which the mass-based carbon and nitrogen (N_{MASS} , Reich et al. 1992) concentration was determined via elemental combustion analysis (ECS 4010 CHNSO Analyzer, Costech Analytical Technologies Inc., Valencia, CA, USA).

Analytical methods

The mass of NH_4^+ and NO_3^- eluted from the IER was determined from the measured concentration and volume of eluent, from which the mass of the nitrogen component of each molecule was then calculated. These values were standardized by resin mass and time in soil, yielding soil N availability as the mass of N per mass of resin per day ($\mu\text{g g}^{-1} \text{day}^{-1}$). A large early snowfall event in November 2014 prevented access to six of the nine sites for collection of the final set of IER bags until the following spring. As a result, data from all final collections were excluded from statistical analyses. Mixed effects models fit to these data used season and treatment as fixed effects, and group nested within site as random effects. Soil N data were square root transformed to correct non-normality and heteroscedasticity of the residuals of the statistical models.

Leaf mass per area (LMA) for live foliage was calculated as oven-dry mass divided by leaf area (g m^{-2}). Measured live foliage N_{MASS} and LMA were then used to determine leaf nitrogen on an area basis (N_{AREA} , g m^{-2} , Reich et al. 1992). Mixed models fit to live foliage N and LMA data used treatment and year as fixed effects, and sample tree nested within site as random effects. Data were log transformed prior to fitting models with the exception of LMA, for which a square root transformation was superior at correcting non-normality and heteroscedasticity in the model residuals.

Litter sample N_{MASS} was multiplied by the mass of litterfall for a given species to calculate N return via litterfall for each year ($\text{kg ha}^{-1} \text{year}^{-1}$). Mean values for litter mass and litter N return by species, study site, and year were calculated and models were fit using year and treatment as fixed effects, with study site as the sole random effect. Data were log transformed prior to fitting models to meet assumptions of normality and homoscedasticity of model residuals.

All analyses were performed in R (R Core Team 2015). Comparisons of pre-treatment litter and fresh foliage N_{MASS} site means were made using the Kruskal–Wallis rank sum test (R Core Team 2015) followed by pairwise comparisons using Nemenyi tests in the PMCMR package (Pohlert 2014). Mixed effects models were fit using the lme4 package (Bates et al. 2015). Visual examination of residual plots from models fit to data transformed as previously described did not reveal significant deviations from the assumptions of normality or homoscedasticity. Post-hoc pairwise comparisons and comparisons of trends were made using the lsmeans package (Lenth 2016) using the Tukey–HSD method to adjust p values. A significance level of $\alpha \leq 0.05$ was used for all comparisons. Standard errors were calculated using a method of accounting for within-subjects designs (Morey 2008).

Results

Soil nitrogen availability

Significant seasonal effects in soil NH_4^+ were observed within treatments, indicating that NH_4^+ availability was typically greater in Summer and Autumn across all treatments as compared to Spring (Online Resource 1, Table A1), though no seasonal pattern in NO_3^- availability was evident. No significant differences in square-root transformed ion exchange resin capture of NH_4^+ and NO_3^- for a given season were observed among treatments over the 2 years post-treatment (Fig. 2). However, the positive slope of the model fit to NO_3^- capture within the ‘Girdle’ treatment was significantly different from

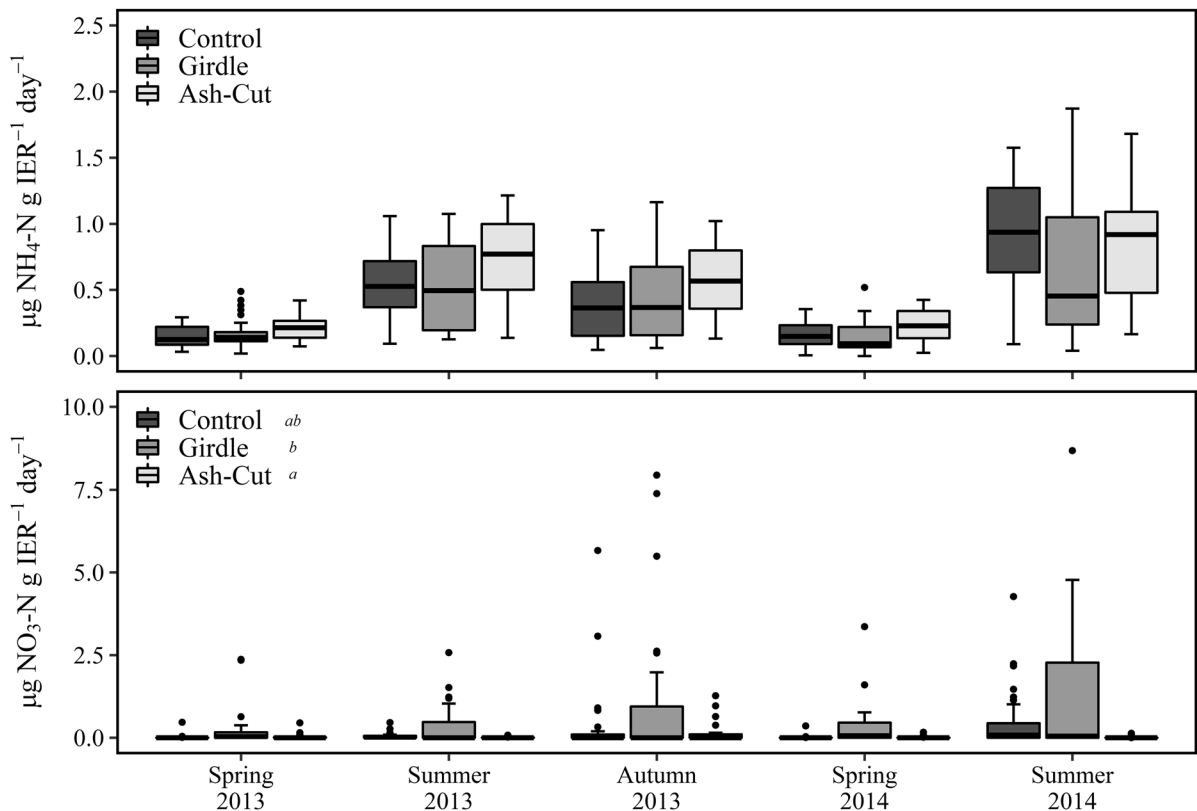


Fig. 2 Soil NH_4^+ (upper) and NO_3^- (lower) capture on ion exchange resins by season. Boxes represent the 25th and 75th percentiles and medians (middle line); fences extend to 1.5 times the interquartile range. Points are observations outside 1.5 times the interquartile range. Note that the scale in the both panels have been reduced for ease of interpretability, resulting in the omission of 4 observations ($17.25 \mu\text{g NO}_3\text{-N g}^{-1} \text{day}^{-1}$ in

Autumn 2013, 12.71, 23.85, 44.28 $\mu\text{g NO}_3\text{-N g}^{-1} \text{day}^{-1}$ in Summer 2014 from ‘Girdle’ sites; $3.84 \mu\text{g NH}_4\text{-N g}^{-1} \text{day}^{-1}$ from a ‘Control’ site in Summer 2014). Labels placed next to the legend that do not share a letter indicate a statistically significant difference in slope of models fit to square-root transformed values across seasons

the ‘Ash-Cut’ treatment ($p = 0.002$), though this trend was not significantly different from the ‘Control.’

Foliar nitrogen, LMA, and chlorophyll

Prior to treatment, mean (\pm standard error) foliar N_{MASS} ranged from $18.14 \pm 0.53 \text{ mg g}^{-1}$ in *A. rubrum* to $23.31 \pm 0.67 \text{ mg g}^{-1}$ in *B. alleghaniensis*. Foliar N_{MASS} was significantly greater in *F. nigra* and *B. alleghaniensis* compared to *A. rubrum* ($p = 0.006$ and $p < 0.001$, respectively; Fig. 3). Foliar N_{MASS} responses to disturbance varied by species and treatment (Fig. 4). No significant change in *A. rubrum* N_{MASS} was observed in any year within the ‘Girdle’ treatment, however *A. rubrum* N_{MASS} declined in ‘Ash-Cut’ sites in 2013 and 2014 compared to pre-treatment ($p = 0.002$ and $p = 0.036$, respectively), but returned to pre-treatment levels by 2015 (Fig. 4). *Betula alleghaniensis* N_{MASS} responded consistently to treatment, with significant declines in N_{MASS} compared to pre-treatment across all years in both the ‘Girdle’ and ‘Ash-Cut’ ($p < 0.001$ for all years and treatments, Fig. 4). Canopy foliage sampled from treated *F. nigra* trees in ‘Girdle’ sites during the first year post-treatment was significantly elevated in N concentration compared to pre-treatment ($p < 0.001$, Fig. 4). Within the ‘Girdle’ treatment, the N_{MASS} of foliage samples taken from *F. nigra* epicormic branching was greater than both the pre-treatment canopy foliage ($p < 0.001$ for all years) and the single

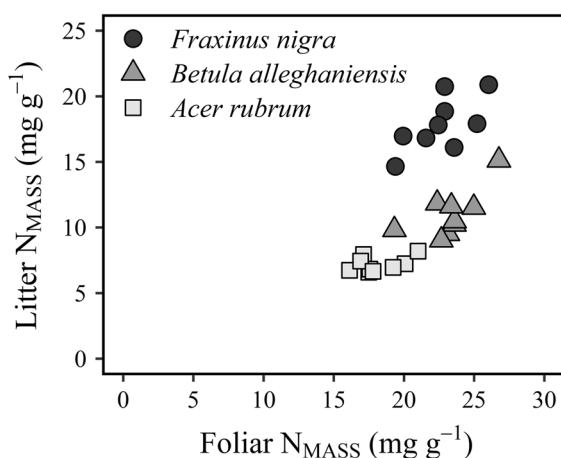


Fig. 3 Pre-treatment nitrogen concentrations by mass (N_{MASS}) for fresh foliage and litter across all sites

year of canopy foliage that occurred post-treatment ($p < 0.001$). No significant differences in transformed N_{AREA} among treatments were observed in either 2014 or 2015 (Fig. 5).

Acer rubrum LMA (Fig. 6) in the ‘Ash-Cut’ sites was significantly higher compared to ‘Control’ ($p = 0.036$) in 2014, but declined slightly in 2015 such that the difference was no longer significant ($p = 0.112$). LMA values in *B. alleghaniensis* foliage from both ‘Girdle’ and ‘Ash-Cut’ sites in 2014 were significantly greater than ‘Control’ sites ($p = 0.010$ and $p = 0.006$, respectively), but were not significantly different in 2015 ($p = 0.167$ and $p = 0.111$) due to increased LMA in the ‘Control’ sites ($p < 0.001$). In contrast to the similar or greater LMA observed in the treated sites compared to controls for other species in 2014, *F. nigra* epicormic foliage LMA from ‘Girdle’ sites was lower compared to ‘Control’ canopy foliage ($p = 0.004$), but was no longer significantly different in 2015 ($p = 0.152$).

Mass-based chlorophyll content (Chl_{MASS} ; Online Resource 1, Fig. A1 upper panel) of *A. rubrum* foliage was significantly lower in the ‘Ash-Cut’ compared to ‘Control’ ($p = 0.044$). The Chl_{MASS} of epicormic *F. nigra* foliage in the ‘Girdle’ sites was significantly greater than in canopy foliage from ‘Control’ sites ($p < 0.001$). No significant differences in *B. alleghaniensis* Chl_{MASS} were observed, though concentrations were lower in both ‘Girdle’ and ‘Ash-Cut,’ and the difference approached significance in the ‘Ash-Cut’ treatment ($p = 0.097$). While patterns of area-based chlorophyll content (Chl_{AREA} ; Online Resource 1, Fig. A1 lower panel) were similar to Chl_{MASS} across treatments and species, no significant differences were observed for any species.

Litter mass and nitrogen content

Prior to treatment, litter N_{MASS} varied by species: N concentrations in *F. nigra* litter were significantly greater than *B. alleghaniensis* ($p = 0.050$), which in turn were significantly greater than those in *A. rubrum* ($p = 0.040$, Fig. 3). Compared to pre-treatment N_{MASS} , litter N_{MASS} of *F. nigra* was significantly higher in both 2013 and 2014 in ‘Girdle’ sites ($p = 0.008$ and 0.003 , Fig. 7), and in 2014 in ‘Ash-Cut’ sites ($p = 0.002$) while measured values in the 2013 ‘Ash-Cut’ treatments approached significance ($p = 0.057$) compared to 2012. No significant change

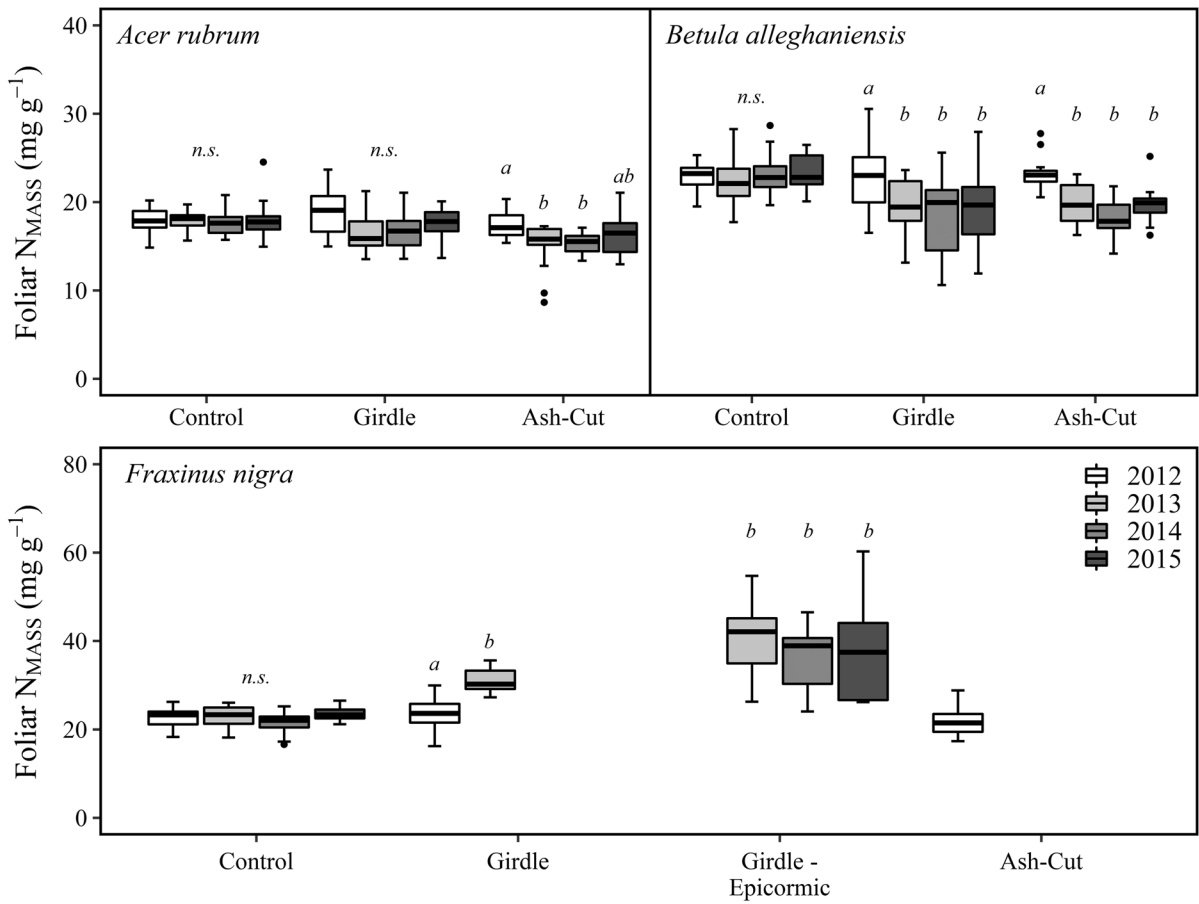


Fig. 4 Mass-based foliar concentration (N_{MASS}). Boxplots represent the 25th and 75th percentiles and medians (middle line). Fences extend to 1.5 times the interquartile range, with observations beyond these values indicated by discrete points. Labels that do not share a letter indicate a statistically significant difference within a treatment across years. Significance values

in litter N_{MASS} of *A. rubrum* or *B. alleghaniensis* was observed (Fig. 7). Significant declines in *F. nigra* litterfall were observed in both treatment types in the first year following treatment (‘Girdle’ $p = 0.003$, ‘Ash-Cut’ $p < 0.001$, Fig. 8 upper panel), and remained highly significant in 2014 ($p < 0.001$ for both treatments). Nitrogen return via *F. nigra* litter (Fig. 8, lower panel) followed a similar pattern, though decreases in the ‘Girdle’ treatment were not significant until the second year post-treatment ($p = 0.004$), while they were significant immediately following treatment in the ‘Ash-Cut’ sites ($p = 0.003$ in both 2013 and 2014). Total *A. rubrum* litter deposition (Fig. 8, upper panel) increased significantly in the ‘Girdle’ treatment in 2013 ($p = 0.043$),

in the ‘Girdle—Epicormic’ foliage are compared to the pre-treatment (2012) canopy foliage within the ‘Girdle’ treatment. An asterisk (*) indicates significant differences between canopy and epicormic foliage within a given year. Note that upper and lower panels differ in scale

but returned to approximately pre-treatment levels by 2014. No significant changes in litterfall or litter-N return from *B. alleghaniensis* were observed (Fig. 8).

Discussion

Based on the results of previous studies into the effects of disturbance on forest N cycling, decreased demand for soil N following *F. nigra* mortality was hypothesized to result in increased soil N availability, in turn leading to improved aboveground nutrient status of residual overstory stems. Such a pattern did not emerge in this investigation. Rather, these results, in concert with the results of previously published

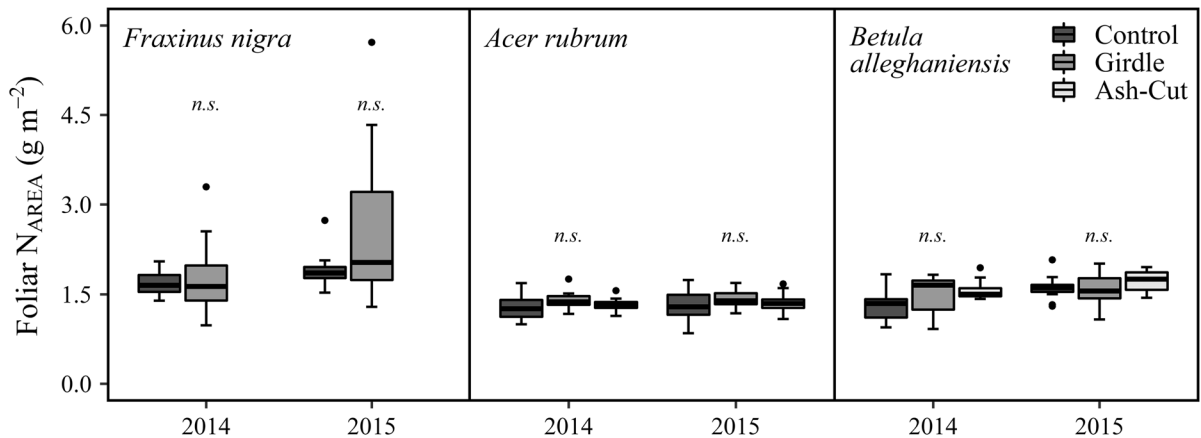


Fig. 5 Area-based foliar concentration (N_{AREA}) by species. Boxplots represent the 25th and 75th percentiles and medians (middle line). Fences extend to 1.5 times the interquartile range,

with observations beyond these values indicated by points. Note that *F. nigra* samples in the ‘Girdle’ treatment were taken from epicormic branching

investigations at these sites, suggest that in the short term, belowground growing conditions were controlled primarily by microbial activity, while aboveground effects were dominated largely by responses to changing light conditions, as discussed in the sections that follow.

Soil nitrogen availability

A change in soil N availability is perhaps the most commonly reported biogeochemical change following biotic disturbance of forest ecosystems (Lovett et al. 2006). In North American forests, increased NH_4^+ availability has been observed in forests affected by the invasive hemlock wooly adelgid [HWA, *Adelges tsugae* Annand; (Jenkins et al. 1999; Orwig et al. 2008)] and the native mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins, Clow et al. 2011; Griffin et al. 2011; Keville et al. 2013). However, no change in NH_4^+ availability was observed following treatment in this study (Fig. 2). In contrast, girdling has been used to successfully simulate the biogeochemical effects of HWA and MPB infestation, yielding positive soil N availability responses similar to actual infestation (Yorks et al. 2003; Orwig et al. 2013; Trahan et al. 2015). Post-girdling mortality in these studies occurred over a similar time frame as *F. nigra* mortality in the ‘Girdle’ treatment, and effects on NH_4^+ availability were observable 1 to 2 years post-treatment. Large increases in NH_4^+ have also been reported following salvage

logging of *Tsuga canadensis* (L.) Carriere (eastern hemlock, Kizlinski et al. 2002; Orwig et al. 2013). As girdling and other forms of disturbance have proven effective at simulating impacts of phytophagous insects, yielding effects on soil NH_4^+ similar to true infestations, the lack of response in this study is likely attributable to the influence of other contributors to the ecosystem N cycle.

Much of the research on biogeochemical responses to disturbance has been conducted in upland systems. However, increased soil water N content has been observed in forested wetlands following harvest (Trettin et al. 1997), harvest followed by site preparation (McLaughlin et al. 2000), and fire (Belova et al. 2014). Similarly, increased export of N in streams draining disturbed forested wetlands has also been observed (Bayley et al. 1992; Nieminen 2004). Though exceptions to this pattern of increased N availability have also been observed (e.g. Westbrook and Devito 2004; Nakagawa et al. 2012), given the results of similar studies across both upland and wetland forests, the lack of soil NH_4^+ increase in either treatment type was contrary to study hypotheses.

This lack of soil N response may be attributable, in part, to changes in the microbial community, a major competitor for soil N (Kuzyakov and Xu 2013). Decomposition rates in northern peatlands are predominantly controlled by the elevated water table, resulting in accumulation of the partially decomposed organic matter characteristic of surface soils in these

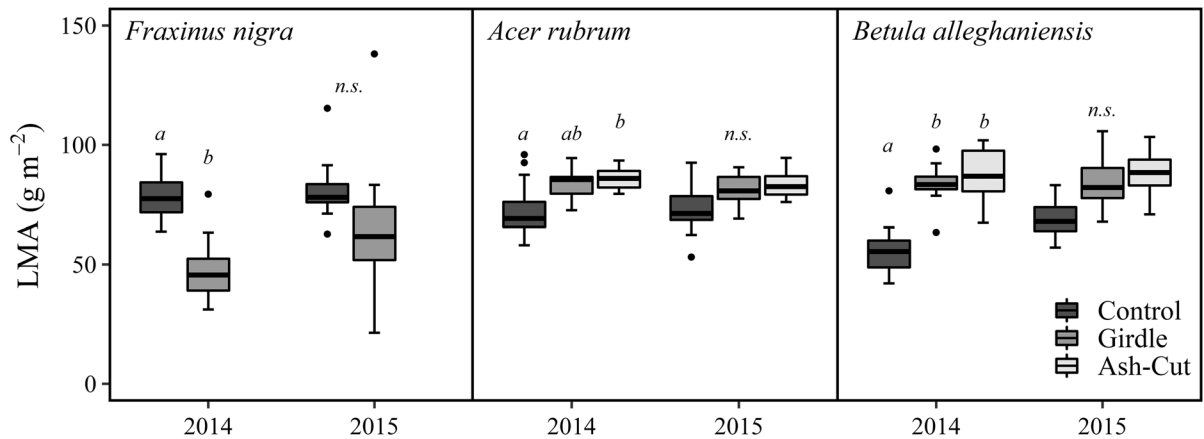


Fig. 6 Leaf mass per area (LMA) by species. Boxes represent the 25th and 75th percentiles and medians (middle line). Fences extend to 1.5 times the interquartile range, with outliers beyond these values indicated by points. Labels that do not share a letter

indicate a statistically significant difference across treatments within a year. Note that *F. nigra* samples in the ‘Girdle’ treatment were taken from epicormic branching

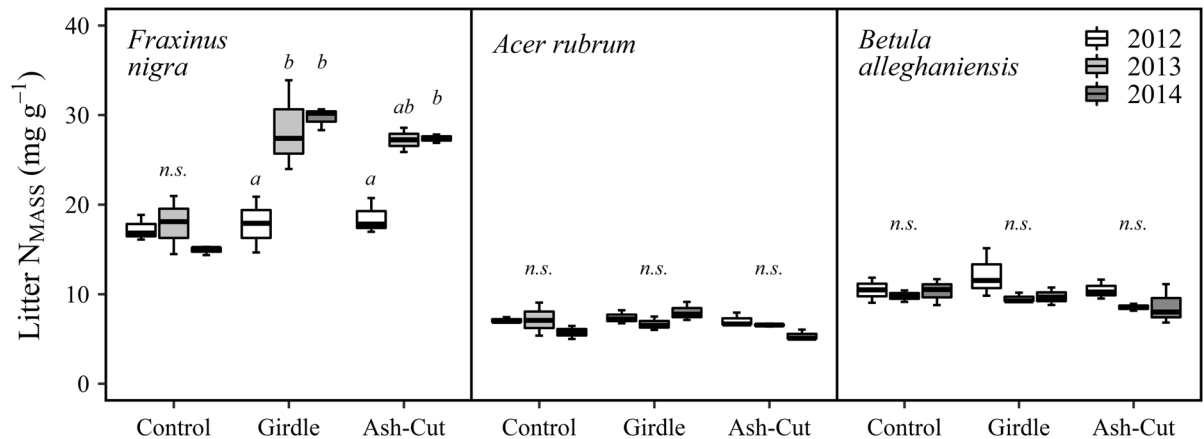


Fig. 7 Litter nitrogen concentrations by mass (N_{MASS}) and species. Boxplots represent the 25th and 75th percentiles and medians (middle line). Fences extend to 1.5 times the

interquartile range. Labels that do not share a letter indicate a statistically significant difference within a treatment across years

ecosystems (Gorham 1991). This pool of organic matter is assumed to be relatively labile in the presence of oxygen, as evidenced by increased decomposition rates with increasing oxygen availability (Kasimir-Klemedtsson et al. 1997; Laiho 2006). If microbial activity in these saturated soils is secondarily limited by N availability (Hart and Stark 1997; Kaye and Hart 1997), then the reduction in competition for N by plant roots such as that imposed by our experimental treatment (Kuzyakov and Xu 2013) may allow for increased uptake and immobilization by microbial communities. Soil heterotrophs are known to respond rapidly to changes in N availability (Zak

et al. 1990; Brooks et al. 1998; Zogg et al. 2000; Micks et al. 2004), which may subsequently be immobilized in soil organic matter (Koopmans et al. 1996; Nadelhoffer et al. 1999a, b; Magill et al. 2000). As such, increased microbial uptake of NH_4^+ in concert with decreased uptake by plants (Norton and Firestone 1996), may be responsible for the lack of response in NH_4^+ availability observed in this study. In addition to the large, relatively labile pool of C present in the accumulated peat, microbial activity associated with fine root mortality following *F. nigra* decline and continued inputs of leaf litter may serve as an additional N sink. Both types of plant residues

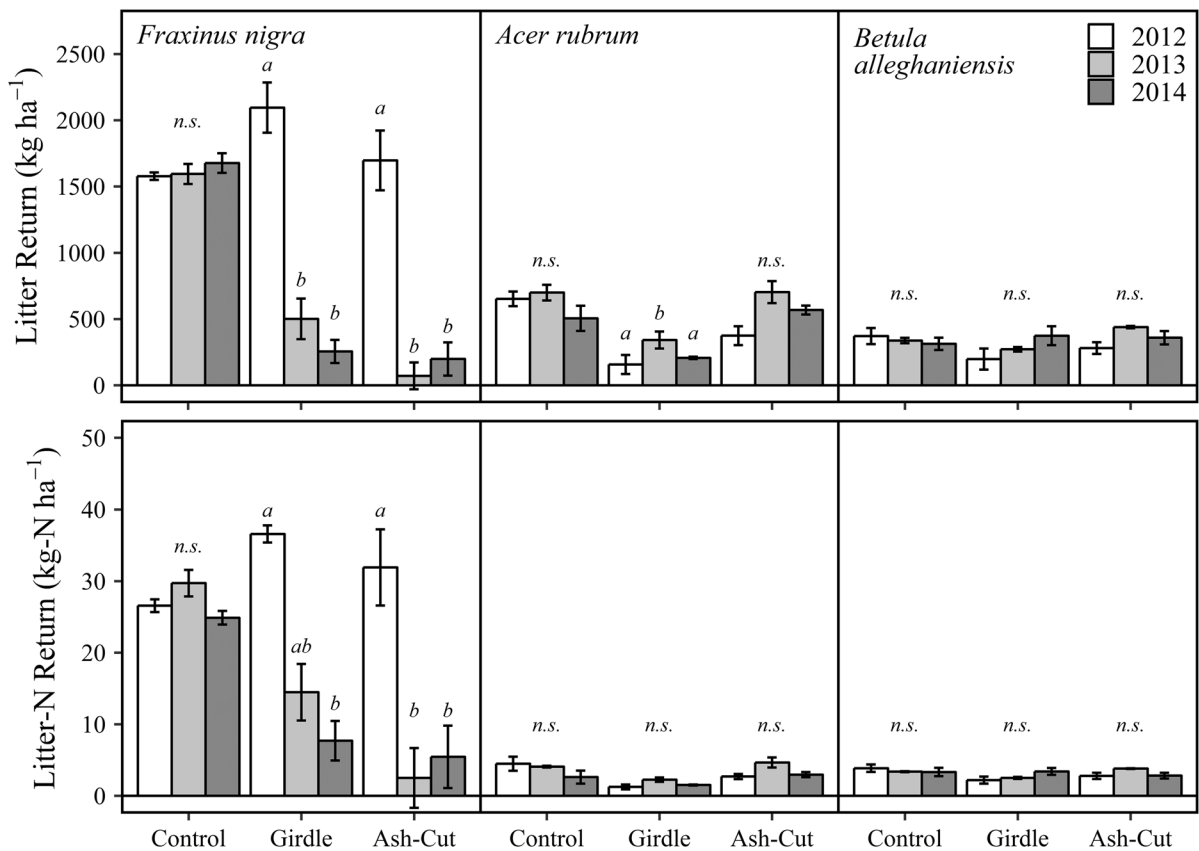


Fig. 8 Mean litterfall mass (upper panel) and litterfall N return (lower panel) of dominant overstory species. Error bars represent \pm one standard error. Labels that do not share a letter

indicate a statistically significant difference within a treatment across years

typically result in net N immobilization during the initial stages of decomposition (Aber and Melillo 1980; McLaugherty et al. 1984; Attiwill and Adams 1993). Finally, reported N mineralization rates in other *F. nigra*-dominated wetlands of the region are lower than surrounding upland forests, as would be expected given the frequently anoxic conditions (Zak and Grigal 1991). In forested wetland systems where gross mineralization rates are low, competition for N is strong and thus gross immobilization rates have been shown to be similar following disturbance, resulting in little change in net mineralization or N availability (Westbrook and Devito 2004; Nakagawa et al. 2012).

The increasing trend in available soil NO_3^- in the ‘Girdle’ treatment when compared to ‘Ash-Cut’ suggests that disturbance mechanism may have also played a role in the effects of *F. nigra* mortality on soil N. In addition to inputs of leaf litter and fine roots,

coarse woody debris has been shown to serve as a sink for available N. Among the potential mechanisms proposed by Vitousek and Melillo (1979) for retention of N within an ecosystem following disturbance was the uptake of NH_4^+ by decomposers, particularly in situations where disturbance results in large quantities of woody debris onsite. Since that time, the importance of N-poor woody debris as a sink for N (Laiho and Prescott 2004), reducing soil N availability (Zimmerman et al. 1995) and mitigating potential N losses (Carlyle et al. 1998; Brais et al. 2006) has been well-demonstrated. Within the ‘Ash-Cut’ sites, *F. nigra* stems were allowed to remain onsite after felling, and so represent a potentially large sink for NH_4^+ , as has been observed following harvest when woody debris remains on site (Vitousek and Matson 1984, 1985). As a result, the availability of NH_4^+ to nitrifiers, which tend to compete poorly in the

presence of high demand from heterotrophic microorganisms (Hart et al. 1994), may be reduced. Thus the role of woody debris as a sink for NH_4^+ provides a possible explanation for the lack of NO_3^- production in the ‘Ash-Cut’ sites compared to the ‘Girdle’ treatment (Fig. 2). Analogous effects have been predicted to result in the latter stages of MPB infestation when snags begin to fall to the forest floor (Edburg et al. 2012).

As NO_3^- is highly mobile in the soil, excess production frequently results in export via hydrologic pathways, as observed following mechanical disturbance of vegetation (Likens et al. 1970; Martin et al. 1986). Numerous studies have reported increased NO_3^- availability in soil following HWA (Jenkins et al. 1999; Orwig et al. 2008; Cessna and Nielsen 2012) and MPB (Clow et al. 2011) infestation. Additionally, export losses of NO_3^- in streamwater have also been observed following infestation by the invasive *Lymantria dispar* L. (gypsy moth, Webb et al. 1995; Eshleman et al. 1998) as well as native insect outbreaks [e.g. *Alosophila pomataria* Harris (fall cankerworm, Swank et al. 1981)]; *Ennomos subsignarius* Hübner [elm spanworm, (Lewis and Likens 2007)]. However, denitrification often plays an important role in the wetland N cycle (Saunders and Kalff 2001), and small depressional wetlands may be capable of retaining much of the increased NO_3^- available following harvest (Spoelstra et al. 2010). Thus, while soil NO_3^- availability was increasing within the ‘Girdle’ sites (Fig. 2) during time periods in which water was leaving the wetlands via ephemeral streams (Van Grinsven et al. 2017), further research will be required to determine if the increase in available NO_3^- leads to N losses from the ecosystem. Additionally, water tables in ‘Girdle’ and ‘Ash-Cut’ sites were significantly higher when compared to ‘Control’ during the growing season (Van Grinsven et al. 2017). It is likely that these changes in the water table affect the relative importance of denitrification on nitrate availability or export, though quantifying these effects will require additional investigation.

Van Grinsven et al. (2018) reported increased fluxes of CO_2 in both ‘Girdle’ and ‘Ash-Cut’ treatments in these study sites, providing additional evidence for increased demand for NH_4^+ by soil heterotrophs in these sites. Soil CO_2 efflux following disturbance is commonly observed to decline, following both high-severity disturbances (e.g. forest

harvest, Mattson and Swank 1989; Striegl and Wickland 1998; Kurth et al. 2014) and low-severity disturbances (e.g. tree girdling, Nave et al. 2011; Levy-Varon et al. 2014). The results of girdling studies have been shown to mimic patterns of declining soil respiration following insect infestation (Nuckolls et al. 2009; Moore et al. 2013), which are attributed to decreased root activity. Efflux of CO_2 from the soil surface has also been observed to remain constant or increase following disturbance; such positive effects are frequently ascribed to increased microbial activity (Hendrickson et al. 1989; Toland and Zak 1994; Lytle and Cronan 1998).

Foliar nitrogen, LMA, and chlorophyll

The link between belowground conditions and canopy characteristics in modified landscapes is well-established, with increased soil N availability associated with increased foliar N_{MASS} as a result of experimental additions of N (Aber et al. 1998; Gundersen et al. 1998; Magill et al. 2004), across stands of varying disturbance histories (Ollinger et al. 2002), following disturbance- or succession-simulating girdling (Nave et al. 2011; Levy-Varon et al. 2014), and after insect infestation (Griffin et al. 2011). However, disturbances that affect the aboveground growing environment, such as increased light availability in canopy gaps, may complicate predictions, as the covariation of these conditions may obscure the physiological response of remaining vegetation (Fownes and Harrington 2004; Kranabetter et al. 2010).

Foliar morphological and biochemical characteristics of retained overstory species in both ‘Girdle’ and ‘Ash-Cut’ sites generally reflected expected changes resulting from the exchange of shade- for sun-acclimated leaves in higher light conditions (Walters 2005), including decreased N_{MASS} and increased LMA (Figs. 4, 6). However, N_{AREA} (Fig. 5) remained unchanged, and Chl_{MASS} (Online Resource 1, Fig. A1 upper panel) showed little response, contrary to prediction. Few studies have considered the effect of light conditions on both the suite of leaf characteristics and species considered here. A positive relationship between LMA and light has been reported for both *A. rubrum* (Jurik 1986; Abrams and Kubiske 1990; Kloeppe et al. 1993; Gottschalk 1994; Lei and Lechowicz 1998) and *B. alleghaniensis* (Abrams and Kubiske 1990; Beaudet and Messier 1998). Decreased

N_{MASS} and Chl_{MASS} and increased N_{AREA} with increasing light have also been shown in *A. rubrum* saplings (Lei and Lechowicz 1998), and similar patterns between N_{AREA} and light for *B. alleghaniensis* have also been observed (Delagrangé et al. 2004). Thus the absence of an increase in foliar N_{MASS} in retained stems may be due in part to the masking effects of changes in physical leaf characteristics such as LMA in response to light conditions.

Increased competition between vegetation and soil microorganisms may also play a role in the response of foliar N_{MASS} . Both foliar N_{AREA} (DeJong et al. 1989) and N_{MASS} (Fownes and Harrington 2004) may increase with increasing N availability in the soil, potentially offsetting the negative correlation between N_{MASS} and light availability (Fownes and Harrington 2004). Given the decreased demand from *F. nigra* for soil N expected in the treated sites, a positive effect of increased soil N on foliar N of retained species was hypothesized. However, no increase in N availability was observed despite a reduction in overall N demand from the dominant woody species (see “Litter mass and nitrogen content”, below), and thus the foliar response may have been dominated by the plants’ response to changing light conditions. Finally, among the described stress responses of plants to a sudden change in light environment is chlorotic foliage (Sharma et al. 2006). Reduced Chl_{MASS} was observed in *A. rubrum* in the ‘Ash-cut’ sites and the reduction was nearly significant in the ‘Girdle’ sites. Though not significant, a similar pattern was observed in *B. alleghaniensis* (Online Resource 1, Fig. A1 upper panel). While decreased Chl_{MASS} may be expected in high-light environments (Walters 2005), these responses may also be an indicator of stress in retained overstory stems (Sharma et al. 2006). In a related study, no change in growth rate of residual overstory stems in the first 3 years following treatment was observed, which was suggested to be due in part to stress resulting from the abrupt change in growing conditions (Davis et al. 2017).

Litter mass and nitrogen content

The return of nutrients via litterfall is frequently used as a proxy for plant demand for soil nutrients (Attiwill and Adams 1993; Aerts and Chapin III 1999). As such, the decrease in N return via *F. nigra* litterfall (Fig. 8, lower panel) represents a significant reduction in

demand for soil N by this species. However, due to contrasting patterns in litterfall (Fig. 8, upper panel) and litter N_{MASS} (Fig. 7), N return via litterfall by *A. rubrum* and *B. alleghaniensis* remained essentially unchanged (Fig. 8, lower panel). These patterns indicate an overall reduction in total N demand for soil N by the dominant species, which together comprise approximately 88% of the overstory basal area (Davis et al. 2017). That litter N_{MASS} of *A. rubrum* and *B. alleghaniensis* was not significantly affected by treatment, despite an increase in fresh foliage N_{MASS} , is potentially due to inputs of lower canopy and sapling litter, from which fresh foliage was not sampled. The observed pattern, however, is similar to declines in N_{MASS} of fresh foliage (Fig. 4).

Prior to treatment, both *A. rubrum* and *B. alleghaniensis* had significantly lower mass-based N content than *F. nigra* (Fig. 3). Should regenerative capacity of these species overcome increased herbaceous competition (Davis et al. 2017) to become the dominant overstory species in a future forested wetland, the change in litter quality would likely affect the rate and quantity of nutrient cycling in these stands (Prescott 2002). A number of controls on litter decomposition rates have been investigated, with initial lignin and N content of freshly shed litter frequently cited as being among the most important controls (Melillo et al. 1982). In a mixed species forest, the presence of nutrient-rich litter may also positively influence combined litter decomposition rates of all species (Rothe and Binkley 2001). In general, there appears to be a positive effect of N content on initial rates of decomposition. As decomposition proceeds, however, the resulting increase in N concentration reduces the rate of decomposition (Berg et al. 1996).

This dual role of initial N concentrations has two major consequences for N cycling in forests. First, canopy and litter N concentrations tend to be positively correlated with soil N availability (Vitousek 1982; Reich et al. 1997; Ollinger et al. 2002), suggesting a positive feedback mechanism between above- and belowground processes that may enhance site fertility. In a review of management implications for *F. nigra*-dominated forests, D’Amato et al. (2018) summarized the recommendations for potential *F. nigra* replacement species, based on the results of experimental plantings. Though limited information is available in the literature, of the deciduous species

noted as “Recommended” in this review, only *Acer saccharinum* L. (silver maple) and *Tilia americana* L. (American basswood) have reported litter N concentrations [14 mg g^{-1} (Mungai and Motavalli 2006) and 15 mg g^{-1} (Holdsworth et al. 2008), respectively] that approached those of *F. nigra* in this study. Consideration of the biogeochemical role of *F. nigra* litter could prove valuable in selecting potential replacement species in these forests. Absent natural or management-mediated transition to such species, the loss of N-rich *F. nigra* litter may reduce N availability and thereby growth rates of the future forest, although species-specific rates of nutrient use efficiency may mitigate the magnitude of these effects (Aerts and Chapin III 1999). Secondarily, as compared to N-poor litter, N-rich litter is expected to have more residual mass remaining in the latter stages of decomposition when decomposition rates approach zero (Berg et al. 1996). Consequently, increased soil organic matter accumulation may occur in sites where composition shifts towards species with higher initial concentrations of litter N (Berg and Meentemeyer 2002), and is similar in effect to that which has been reported following experimental N addition (Nave et al. 2009). In *F. nigra*-dominated wetlands, the opposite effect may be the case, as the loss of N-rich litter following EAB infestation could result in the slowing of organic matter accumulation (Berg 2000). However, given the importance of the water table in controlling decomposition in peatlands, additional research is required to determine how significant a role litter species N content might play in peat formation in these forests. Thus, the combined effects of litter quality on site fertility and decomposition has the potential to reduce carbon accumulation rates in living biomass, while also potentially reducing soil carbon storage.

Conclusions

In *F. nigra*-dominated wetlands, the biogeochemical responses following EAB infestation are likely to fundamentally differ from those observed in other forests with *Fraxinus* components, due to the abundance of *F. nigra*, the characteristics of their co-dominant woody species, and the unique nature of ecological processes in these forests. In the short-term, these responses may have both positive and negative effects on ecosystem function. Following application

of experimental treatments, soil N availability exhibited minimal changes. The abundant organic matter that has accumulated on the forest floor and in the soil due to the extended periods of inundation during the growing season, as well as woody debris in the ‘Ash-Cut’ treatment, appears to be serving as a sink for soil N, mitigating potential changes in availability resulting from reduced plant demand. This response may have a positive effect on ecosystem function, as it reduces the potential for short-term N losses via hydrologic export. However, the increased competition for N may also have negative effects by limiting the potential for positive growth responses of remaining vegetation following disturbance, as neither *A. rubrum* nor *B. alleghaniensis* increased N uptake immediately following the treatments. Rather, the aboveground effects on foliar and litter characteristics of these species have been driven primarily by responses to light conditions. Though further study is required to determine the longer-term impacts of *F. nigra* mortality, these short-term responses and the characteristics of co-occurring species suggest some possible future effects. The lack of increased N availability to and uptake by remaining woody species immediately following disturbance has the potential to slow eventual vegetation recovery and the restoration of ecosystem services. Additionally, absent management intervention, *A. rubrum* or *B. alleghaniensis* are the species likely to replace *F. nigra* in these and similar systems. Both species have litter that is lower in N concentration, which will likely result in a reduction of the positive feedback relationships between litter quality, decomposition, and site fertility, which may ultimately have important implications for long-term carbon storage.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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