



Foundation Species Loss Affects Leaf Breakdown and Aquatic Invertebrate Resource Use in Black Ash Wetlands

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Abstract

The invasion by emerald ash borer (*Agrilus planipennis*) of extensive black ash wetlands in the upper Great Lakes region of North America is expected to alter plant community structure and composition and, therefore, abiotic factors like temperature and hydrology. We conducted two experiments to examine how changes in leaf litter could alter ecosystem function via 1) changes in litter breakdown and 2) aquatic invertebrate feeding. For the first experiment, we placed litter bags containing black ash (*Fraxinus nigra*), swamp white oak (*Quercus bicolor*), and lake sedge (*Carex lacustris*), in either control or clear-cut black ash plots. We found that black ash litter broke down 2–3 times faster than other species and broke down faster in control plots than in clear-cuts. There was no effect of clear cutting on swamp white oak or lake sedge breakdown rates. For the second experiment, we fed shredding caddisfly larvae (*Limnephilus indivisus*) one of six species: black ash, swamp white oak, lake sedge, balsam poplar (*Populus balsamifera*), American elm (*Ulmus americana*), or speckled alder (*Alnus incana*) for 14 days. Caddisflies had the highest survival and greater resource use when given black ash or speckled alder, which are abundant in black ash wetlands. These results suggest that loss of black ash will alter ecosystem processes via changes in the physical environment, changes in leaf litter properties, and changes in shredder processing rates of leaf litter.

Keywords Ecosystem linkages · Foundation species · Litter breakdown · Limnephilid caddisfly · Forest wetland

Introduction

There is mounting evidence that global loss of biodiversity will alter global ecosystem function; for example, plant and

detritivore biodiversity loss could alter productivity and decomposition at rates comparable to other anthropogenic stressors (such as climate change, nutrient pollution, acidification; Hooper et al. 2012). In some instances, the loss

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of a single species can alter the structure and function of an ecosystem. Within some forested ecosystems, foundation tree species – i.e., those that modulate ecosystem structure and function – are threatened by introduced exotic insects and diseases (Ellison et al. 2005; Flower and Gonzalez-Meler 2015; Lovett et al. 2016). Extreme defoliation and/or mortality of foundation tree species can alter biogeochemical cycles, resource availability, and plant and animal communities (Gandhi and Herms 2010; Flower and Gonzalez-Meler 2015; Nisbet et al. 2015; Lovett et al. 2016).

One way foundation tree species loss affects terrestrial and aquatic ecosystems is through changes in organ matter inputs, primarily leaf litter (Williams 2005; Batzer et al. 2014). Temporary forested wetlands may be particularly susceptible to changes in leaf litter because litter is the basis of the detrital food webs and the nutrients made available during leaf litter decomposition may support algal food web pathways (Williams 2005; Williams et al. 2008; Stoler and Relyea 2011; Stephens et al. 2013; Batzer et al. 2014). Many studies have demonstrated that changes in litter species and associated litter quality (i.e., nutrient, lignin, and tannin concentration) can affect aquatic ecosystem processes – with consequences for the community composition and biomass production of aquatic fauna (Rubbo and Kiesécker 2004; Stoler and Relyea 2011; Earl et al. 2014; Nisbet et al. 2015; Stoler et al. 2016).

Black ash (*Fraxinus nigra*)-dominated wetland forests are prevalent across the eastern United States and western Great Lakes region of North America. Black ash grows on hydric soils and, as a foundation species, regulates the ecosystem function and community composition of these wetlands – primarily by influencing hydrologic dynamics (Slesak et al. 2014; Telander et al. 2015). Black ash wetlands are seasonally ponded and range from small depressional ponds to extensive flat swamps that cover hundreds of hectares; within the swamp wetlands, microtopography creates ponded areas with highly variable surface areas and hydroperiods. These wetlands can host an abundance of aquatic macroinvertebrates, whose community is characterized and dominated by molluscs (Sphaeriidae, Lymnaeidae, Physidae), annelids (Lumbriculidae, Hirudinea), caddisflies (Limnephilidae, Leptoceridae), and dipterans (Chironomidae, Culicidae; Batzer et al. 2005; Batzer and Palik 2007).

Currently, these forests are threatened by the exotic invasive emerald ash borer (EAB; *Agrilus planipennis*; Poland and McCullough 2006), which causes near complete mortality of ash (*Fraxinus* spp.; Klooster et al. 2014). Infestation will likely cause these forested wetlands to regress (at least in the short-term) to open-canopy wetlands dominated by graminoids and shrubs (Looney et al. 2017; Diamond et al. 2018), with far reaching ecological consequences (Nisbet et al. 2015; Youngquist et al. 2017). In the face of imminent EAB invasion into the western Great Lakes region, researchers are testing whether they can maintain structure and function of these

forests by transitioning them from ash to other canopy tree species that are not susceptible to EAB (Looney et al. 2015; D’Amato et al. 2018). One concern is that because black ash leaves have relatively low C/N ratios and provide a high-quality resource (Palik et al. 2006), replacement with species with lower nutrient quality might alter nutrient cycles, food web structure, and productivity (Palik et al. 2006; Stephens et al. 2013).

The aim of our study was to determine how changes in litter inputs, either from management-induced regression to graminoid/shrub-dominated wetlands (via clear-cutting as a pre-emptive silvicultural strategy to limit the spread of EAB) or assisted replacement with other canopy species might affect ecosystem function of black ash wetlands. We conducted two experiments that examined 1) in-situ leaf litter breakdown and 2) ex-situ leaf litter consumption by a shredding invertebrate and the effect of litter type on invertebrate growth and survival. In the first experiment, we tested how rates of leaf litter breakdown are affected by litter species and habitat. The rate at which leaf litter decomposes in wetlands is tied to environmental factors (e.g., temperature, ponding) and litter chemical composition (e.g., C/N ratios, lignin concentration) (Aerts 1997; Baker et al. 2001; Battle and Golladay 2001). Differences in decomposition among leaf litter species (black ash vs. graminoid/shrub/non-black ash trees) and habitats (open vs. closed canopy) will have implications for nutrient cycling as well as energy flow through aquatic food webs.

In the second experiment, we tested how changes in leaf litter species would affect resource use and survival of a limnephilid caddisfly. We chose a limnephilid caddisfly because they are ecologically important and abundant in northern ephemeral forested wetlands (Richardson and Mackay 1984; Colburn 2004; Batzer et al. 2005; Batzer and Palik 2007). In addition to directly consuming leaf litter and using it as a case building material, shredding limnephilid caddisflies play important roles in aquatic food webs because they increase rates of leaf litter breakdown and may bridge detrital and algal pathways by mobilizing nutrients (Wissinger et al. 1999; Graça and Canhoto 2006; Boyero et al. 2012; Klemmer et al. 2012). Our focal species, *Limnephilus indivisus*, is common, can contribute significant biomass to invertebrate assemblages in ephemeral forested wetlands in northern Minnesota (Batzer et al. 2004; Batzer and Palik 2007; Youngquist, personal observations), and feeds primarily on leaf material in black ash wetlands within the study area (Eggert, unpublished data). Thus, changes in litter palatability could alter breakdown rates and caddisfly populations, ultimately impacting wetland food webs.

Methods

Study Area

Our study area was located in black ash wetlands within the Chippewa National Forest, in north central Minnesota; the site

used for our project is part of an on-going field experiment to assess effects of adaptive silvicultural management on black ash wetlands (Slesak et al. 2014; Looney et al. 2015; Looney et al. 2017). This black ash stand is an expansive flat wetland in which small pools fill and dry throughout the year. Within this expansive wetland, we utilized two treatments (four replicates each), clear-cut black ash and control, that were implemented on 1.62 ha circular plots in the winter of 2011–2012, over snow when the ground was frozen. In the clear-cut treatment, all standing trees >6 cm in diameter at breast height were removed and most small stems were knocked over by equipment trafficking. The control treatment consisted of uncut, mature forest. In fall 2011 and spring 2012, 12 species of trees were planted in each plot (including controls) to investigate their potential to replace black ash and mitigate EAB impacts. These included, yellow birch (*Betula alleghaniensis*), balsam poplar (*Populus balsamifera*), eastern cottonwood (*P. deltoides*), quaking aspen (*P. tremuloides*), tamarack (*Larix laricina*), northern white cedar (*Thuja occidentalis*), American basswood (*Tilia americana*), red maple (*Acer rubrum*), American elm (*Ulmus americana*), hackberry (*Celtis occidentalis*), swamp white oak (*Quercus bicolor*), and Manchurian ash (*F. mandshurica*). Leaf litter used in Experiment 1 and Experiment 2 was collected from this experimental area and species selections were based on those most likely to replace ash, either naturally or assisted (Looney et al. 2015; Looney et al. 2017). The exception was swamp white oak litter for Experiment 1, which was collected from the St. John's University campus in central Minnesota (see Methods below).

The climate of the study area is continental, with 1981–2010 mean temperatures averaging -13.7 °C in January and 16.5 °C in July (PRISM Climate Group, 2018). Mean precipitation was 742 mm yr^{-1} , which falls primarily during the growing season (May through September; PRISM Climate Group 2018). Our sites are classified as WFn55 (northern wet *Fraxinus* swamp) and WFn64 (northern very wet *Fraxinus* swamp) based on the native plant community classification system developed for northern Minnesota (MNDNR 2003). Black ash was the dominant overstory tree (91% basal area); American elm, American basswood, balsam fir (*Abies balsamea*), balsam poplar, quaking aspen, bur oak (*Q. macrocarpa*), and speckled alder (*Alnus incana*) were minor components (Looney et al. 2015; Looney et al. 2017). Graminoids (*Carex lacustris* and *Calamagrostis canadensis*) were the dominant vegetation in clear-cut sites (Looney et al. 2017; Diamond et al. 2018).

Experiment 1: Leaf Litter Breakdown

Experimental Design and Implementation We tested for the effects of clear-cutting black ash forest on leaf litter breakdown of three different species: black ash, lake sedge (*C. lacustris*), and swamp white oak. Lake sedge was chosen because it can be a dominant early successional species in the clear-cut sites and may represent a natural plant community

after EAB invasion and ash mortality in many wetlands; we chose swamp white oak because it had one of the best survival rates of the tested species that could be planted to replace black ash (Looney et al. 2015) and is now being promoted as a replacement species in the region. We collected senesced black ash and lake sedge leaves from the study area in the Chippewa National Forest. Seedling swamp white oak were planted within the study area; however, they had not yet produced enough leaf material for use in the decomposition study. Therefore, we obtained swamp white oak leaves from trees growing on St John's University campus, located 200 km southeast of the study area. Leaf litter was dried at 55 °C until a stable weight was obtained (e.g., Reinhart and VandeVoort 2006). We added 5 g of dried leaf litter to mesh bags ($\sim 19 \times 30$ cm) with 4 mm mesh openings, which are large enough to allow invertebrates access to the litter.

Litter bags were placed in four clear-cut or control plots on November 6, 2015 (day 0), as described below. We prepared an additional group of 10 bags for each species to measure leaf breakage and loss due to handling (i.e., moving bags during transport, placing and recovering bags from field locations); we corrected initial sample weights for this handling loss. We calculated initial ash-free dry weight (AFDW) by combusting subsamples of each species in a muffle furnace at 525 °C for 2 h. We used a blocked nested design such that within each plot we had three replicate sub-plots and at each sub-plot we placed five litter bags of each species (60 litter bags per species per treatment; Fig. S1). Control and clear-cut treatments were paired in four spatial blocks. In each plot we selected sub-plots in relation to a well at the center of the 1.62 ha plot, which was used to monitor water-table levels as part of a larger study (Slesak et al. 2014). Sub-plots were 10 m from the well at 0, 120, and 240 degrees (Fig. S1).

At each sub-plot we also placed ibutton™ data loggers (model DS1921G, Maxim Integrated Products, Inc., Sunnyvale, CA), housed in PVC pipe, to monitor year-round water/ground temperatures. Temperature loggers were checked April, August, and October 2016. Some temperature loggers stopped working periodically; each treatment replicate (plot) had temperature data from 1 to 3 loggers (sub-plot) at any given point in time.

We recollected 12 litter bags per species per treatment on experimental days 166, 194, 222, 286, and 348 (April, May, June, August, and October 2016). Leaf litter was rinsed over a 1 mm sieve to remove invertebrates and debris, dried at 55 °C until weight was stable, and weighed. Subsamples were taken to determine percent carbon and nitrogen content. Carbon and nitrogen were analyzed via combustion on a Leco 628 CHN Total Carbon / Nitrogen combustion analyzer. Nitrogen mass in each litterbag was calculated by multiplying %N by leaf litter weight. Invertebrates greater than 1 mm in length were sorted into family or higher taxonomic groups and preserved in 7% formalin.

Experiment 2: Caddisfly Resource Use

Leaf Collection and Conditioning

We tested effects of six species of leaf litter on caddisfly survival and growth. The species we tested were black ash, American elm, balsam poplar, lake sedge, speckled alder, and swamp white oak. All leaves, including swamp white oak leaves, were collected from the control sites on Chippewa National Forest. The planted swamp white oak produced enough leaves for this bio-assay; thus, we used leaves from plants at the Chippewa sites and not from St. John's University trees, as in the litter breakdown experiment. To collect tree leaves as they senesced, we placed 1 mm mesh bags over the branches on September 18, 2015. We collected the leaf bags between October 26, 2015 and November 6, 2015. During the same time, we collected senesced lake sedge leaves by cutting leaves directly from the plants. We stored the leaves indoors until May 5, 2016. Prior to the start of the experiment, we conditioned leaves by submerging them for 2 weeks in a ponded area adjacent to one of the experimental plots. After conditioning, we transported the leaves to aerated aquaria in a lab maintained at 13 °C.

Caddisfly Collection

On May 17, 2016, we collected caddisflies (*Limnephilus indivisus*) from a wetland in the Suomi Hills Recreation Area in the Chippewa National Forest, which was ~47 km SE of the study area (47.42721 N, 93.60611 W). We chose to collect individuals from this site because they had a higher density than the wetlands where leaves were collected and conditioned. Because the caddisflies captured here were of the same species and within the same forest type as where we collected the leaves, we assumed they would have similar responses. The case length of individuals collected ranged from 9 to 25 mm in size. We used a subset of caddisflies ($n = 76$), spanning this entire range of case length sizes, to establish a size curve relating case length, larval length, and larval dry weight (see Statistical Analysis, below). Dry weight was determined by removing larvae from their cases and drying them at 50 °C for a minimum of 24 h. For the experiment, we used a subset of individuals with a case length of 10–18.5 mm.

Experimental Design and Implementation

Using a randomized design, we tested the effect of litter type on caddisfly growth and survival. We assigned individual caddisflies to one of the six different leaf-species treatments; each treatment was replicated 22 times ($n = 132$). We measured the case length of each individual prior to the start of the experiment. The experiment began on May 20, 2016 (Day

0) and ended on June 3, 2016 (Day 14). We placed each caddisfly in its own microcosm, consisting of a 200 mL clear, plastic container, holding approximately 150 mL of water and a 23 cm strip of flagging tape (Presco Texas brand) to provide habitat structure. We collected water for the microcosms from the same location as the leaves; water was filtered through a 45 µm sieve to remove fine particulate organic matter, aerated, and maintained at 13 °C. We changed the water in each microcosm every 2–3 days. The caddisflies were maintained on a 10:14 light: dark cycle at 13 °C.

Using a 9 mm diameter cork borer, we cut circular discs from leaves, taking care to avoid major veins, stems and holes in the leaves. Lake sedge leaves were cut into squares resulting in the same area as the leaf discs (64 mm²). All whole leaves and pre-cut disks were kept in aerated microcosms. We calculated average leaf disk weight by drying 18–23 pre-cut leaf discs from each species on days 0, 10 and 14 at 50 °C for at least 48 h; we sampled from different days to account for any changes in weight over the study period. Each individual caddisfly was given five discs of their assigned leaf species on day 0. We monitored leaf disc use daily and replaced any that were completely consumed to ensure that resource availability would not be a limiting factor for feeding or case construction purposes. We recorded the number of disks replaced each day as an indirect measurement of rate of resource use (material used for feeding and case building). On day 7, we refreshed the food of all remaining caddisflies by removing uneaten leaf discs and adding five new disks. Remaining disks were dried and weighed to calculate amount used. Because of a clerical error, only data from 7 to 8 individuals per treatment were useable. The experiment was terminated on Day 14 because of low survival in non-black ash treatments.

We checked survival daily; deceased individuals were removed and measured for their case and larval lengths. The larvae were placed in a drying oven at 50 °C for a minimum of 48 h before being weighed for larval dry mass. On Day 14, we measured final case and larval length. The uneaten food discs were also removed at this time and both the larvae and leaf discs were placed in a drying oven at 50 °C for at least of 48 h. We determined larval dry mass and dry mass of uneaten leaf disks to estimate the amount used from day 7–14. Carbon and nitrogen concentration of conditioned leaves were analyzed via combustion on a Leco 628 CHN Total Carbon / Nitrogen combustion analyzer.

Statistical Analysis

Experiment 1: Leaf Litter Breakdown For all leaf litter analyses we used linear mixed effects models with sub-plot nested in plot and spatial block as random intercepts. Fixed effects were leaf litter species and/or black ash treatment; for nutrient analyses, we also included time as a fixed effect (see below). We used the Kenward-Roger method of approximating

denominator degrees of freedom to evaluate fixed effects (Kenward and Roger 1997) and Tukey multiple comparison test to assess pairwise differences in species and treatments.

For leaf litter breakdown we tested for differences among leaf litter species and black ash treatment. We estimated the decay coefficient (k) for each species at each plot by regressing natural log of percent AFDW remaining against time (experimental-days), where k is equal to the negative slope. We also calculated k using degree-days. Degree-days enabled us to account for differences in temperature within and among plots. We calculated degree days by summing average daily temperatures above 0 °C. If sub-plots were missing some temperature data, we used the average temperature for the plot for the missing values.

For nutrient analyses, we tested for effects of species, time, and treatment on C/N ratios and on the mass of nitrogen at time t relative to the original concentration (time = 0; hereafter, relative nitrogen mass). We log-transformed C/N ratios and relative nitrogen mass to improve model fit.

To test for temperature differences among treatments, we calculated four daily temperature metrics: average, maximum, minimum and range. We then used daily values to calculate seven-day averages for each metric (weekly average, maximum, minimum, and temperature range). We log-transformed temperature range to improve model fit. We also tested for differences in degree-days among treatments.

For invertebrate abundances, we used generalized linear models with a negative binomial distribution to test for interactive effects of leaf litter species, black ash treatment, and time; we used block as a covariate. We did not use mixed models because the models would not converge and/or had singular fit. We analyzed abundance data for the most common (> 15% litter bags) detritivorous taxa to ensure adequate model fit (e.g., Batzer et al. 2004; Reinhart and VandeVoort 2006): Ceratopogonidae (larvae), Chironomidae (larvae), Collembola (adult), Coleoptera (adult), Gastropoda, Oligochaeta, and Tipulidae (larvae). We did not analyze Trichoptera data because they were only observed in 19 litter bags (total 20 individuals).

Experiment 2: Caddisfly Resource Use We analyzed effects of leaf litter species on five metrics: survival, change in larval length, change in larval weight (instantaneous growth rate), change in case length, and resource use. To test for effects of leaf litter on survival, we used a Cox proportional hazards regression (Cox 1972); black ash was used as the baseline for calculating relative mortality hazards.

To assess growth we used number of days alive during the study to calculate daily change in larval length ($[\text{final length} - \text{initial length}] / \text{days alive}$) and instantaneous growth rate ($\ln[\text{final weight}/\text{initial weight}] / \text{days alive}$). We estimated initial larval length and dry weight using pre-experiment measurements from the 76 caddisflies; we used linear regression

to formulate equations based on case length: $\ln(\text{Larval-length})$ (mm) = $2.99 + 0.74 * \text{Case-length}$ (mm) ($r^2_{\text{larval length}} = 0.67$; $p < 0.0001$) and Larval-dry-weight (g) = $-0.01 + 0.0016 * \text{Case-length}$ (mm) ($r^2_{\text{dry weight}} = 0.54$; $p < 0.0001$). We also calculated the daily change in case length ($[\text{final length} - \text{initial length}] / \text{days alive}$), to determine if materials were being used for case building.

We tested whether the rate of resource use differed among leaf species by calculating the average daily amount replenished for all individuals throughout the 14 day study ($[\# \text{ disks replaced} * \text{average disk weight}] / \text{days alive}$) and daily amount used ($[\# \text{ disks added} * \text{average disk weight}] - \text{amount left} / \text{days alive}$) for two time periods (days 0–7 and days 7–14). We focused our analyses on daily amount replenished because it was highly correlated with daily amount used (Pearson's $r = 0.969$, $p < 0.0001$) and because we were missing data on amount used for the first week.

With the exception of instantaneous growth rate, we used analysis of covariance (ANCOVA) to test for differences in growth and resource use among leaf litter species; initial case length was a covariate to account for initial size differences affecting feeding rate and change in larval and case length. For instantaneous growth rate, we used ANOVA because initial size is incorporated in the calculation. All data were rank transformed to fit model assumptions. Dunnett's test of multiple comparisons was used to compare black ash to non-black ash treatments. Finally, we tested for differences in C/N among species using ANOVA and Tukey's multiple comparison test to assess pairwise differences in species and treatments.

All statistics and graphics, for both experiments, were conducted in the R statistical environment (R Core Team 2016). We used the following packages: *car* (Fox and Weisberg 2011), *lme4* (Bates et al. 2015), *lmerTest* (Kuznetsova et al. 2017), and *multcomp* (Hothorn et al. 2008), and *survival* (Therneau 2015), *multcomp* (Hothorn et al. 2008); data were visualized with *ggplot2* (Wickham 2009).

Results

Experiment 1: Leaf Litter Breakdown

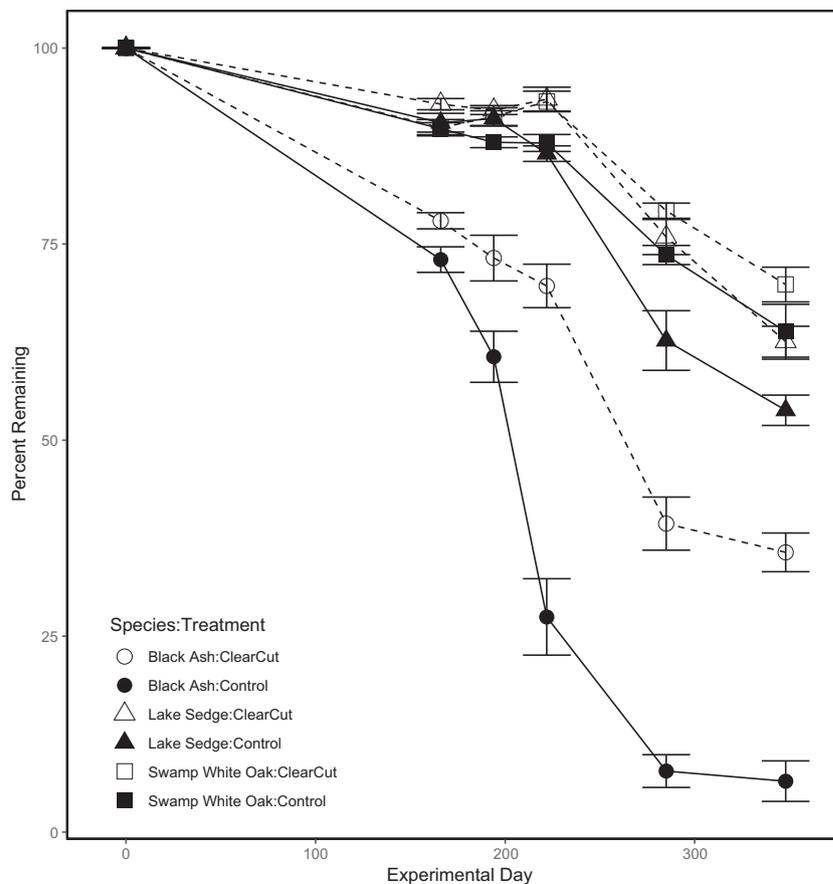
There was an interactive effect of species and treatment on the decay coefficient (k) and results were the same for calculations using either experimental-days or degree-days ($F_{2,44} > 71$, $p < 0.0001$; Table S1). Black ash broke down the fastest and leaves placed in control plots broke down faster than those in clear-cut plots (Table 1; Fig. 1). There was no difference in k rates between swamp white oak and lake sedge leaves in either control or clear-cut. There was an interactive effect of species, treatment, and time on C/N ($F_{10,345} = 2.3$, $p = 0.012$; Table S1)

Table 1 Average decay coefficients (d^{-1}) and standard error (SE) for leaf litter in clear-cut and control treatments calculated as degree days (DD) and experimental days (ED). Superscript letters denote differences among species and treatments based on Tukey's post-hoc test for both response variables

Species	Treatment	$k - DD$ (SE)	$k - ED$ (SE)
Black Ash	Clear-cut ^a	0.00038 (0.00003)	0.0033 (0.0001)
	Control ^b	0.00119 (0.00009)	0.0098 (0.0008)
Lake Sedge	Clear-cut ^c	0.00016 (0.00001)	0.0013 (0.0001)
	Control ^{a,c}	0.00025 (0.00004)	0.0018 (0.0001)
Swamp White Oak	Clear-cut ^c	0.00011 (0.00001)	0.0010 (0.0001)
	Control ^c	0.00014 (0.00002)	0.0013 (0.0002)

and relative nitrogen mass remaining ($F_{10,343} = 5$, $p < 0.0001$; Table S1). Black ash leaves had significantly lower C/N than lake sedge or swamp white oak and C/N decreased in all species over time (Fig. 2); there were no overall patterns with regard to differences among treatments within species. However, in terms of nitrogen mass, black ash lost nitrogen over time (final: $54 \pm 4\%$ of original) while lake sedge and swamp white oak gained nitrogen by the end of the study (final: $115 \pm 5\%$ and $125 \pm 4\%$ of original, respectively). Differences among treatments within species changed over time (Fig. 2).

Fig. 1 Percent ash-free dry weight (AFDW) remaining after bag placement in control or clear-cut treatments. Mass loss differences among species and treatments are reported in Table 1



Temperatures between treatments were similar in winter months and then began to diverge in March 2016 (~week 20). There was a time-by-treatment interactive effect on all temperature metrics ($F_{49,982} \geq 12$, $p \leq 0.0001$; Table S1). Overall, ground temperatures in clear-cuts were cooler than controls in the spring and fall and warmer than controls in the summer (Fig. 3). Clear-cuts experienced more extreme temperatures, recording higher highs and lower lows than in controls; the weekly average minimum temperature was always cooler in clear-cuts. There was also a time-by-treatment interactive effect on degree days ($F_{5,398} = 4.5$, $p \leq 0.0001$; Table S1, Fig. S2). Differences between treatments were observed on experimental days 194, 222, and 348.

For the abundance of invertebrates found in the leaf litter, there was an interactive effect of species, treatment, and time on Chironomidae and Oligochaeta ($\text{ChiSqr} = 15.6$, $\text{df} = 8$, $p = 0.048$; Table S2). There was a treatment-by-time interaction for Gastropoda ($\text{ChiSqr} = 23.2$, $\text{df} = 4$, $p = 0.0001$; Table S2) and a species-by-time interaction for Tipulidae ($\text{ChiSqr} = 16.1$, $\text{df} = 8$, $p = 0.041$; Table S2). Abundances of Ceratopogonidae, Coleoptera, and Collembola differed among treatments ($\text{ChiSqr} > 7.3$, $\text{df} = 1$, $p < 0.007$; Table S2) and over time ($\text{ChiSqr} > 15.4$, $\text{df} = 4$, $p < 0.004$; Table S2). Total Oligochaeta abundance was highest in control plots; total abundances of all other groups were higher in clear-

Fig. 2 Top—Differences in C/N between species over time. Values are averaged over all treatments. Bottom—Percent mass of nitrogen remaining relative to initial mass; closed circles are control and open circles are clear-cut treatments. Day 0 was November 6, 2015. Error bars are standard error. Letters indicate differences among species (top) and among species and treatments (bottom). * Indicate differences among treatments, within a given species

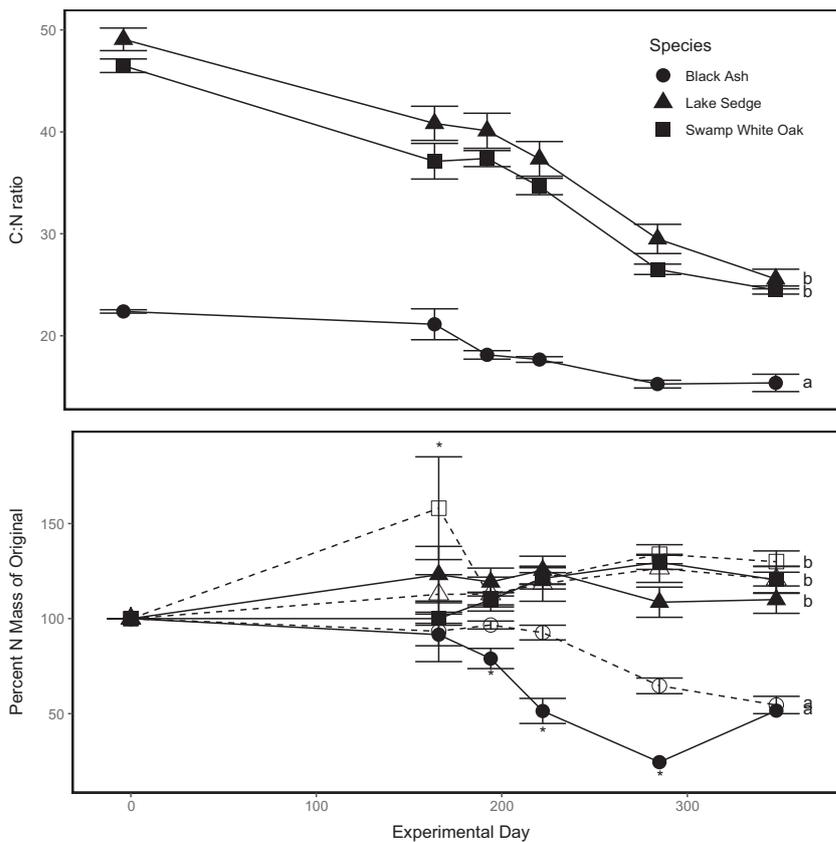
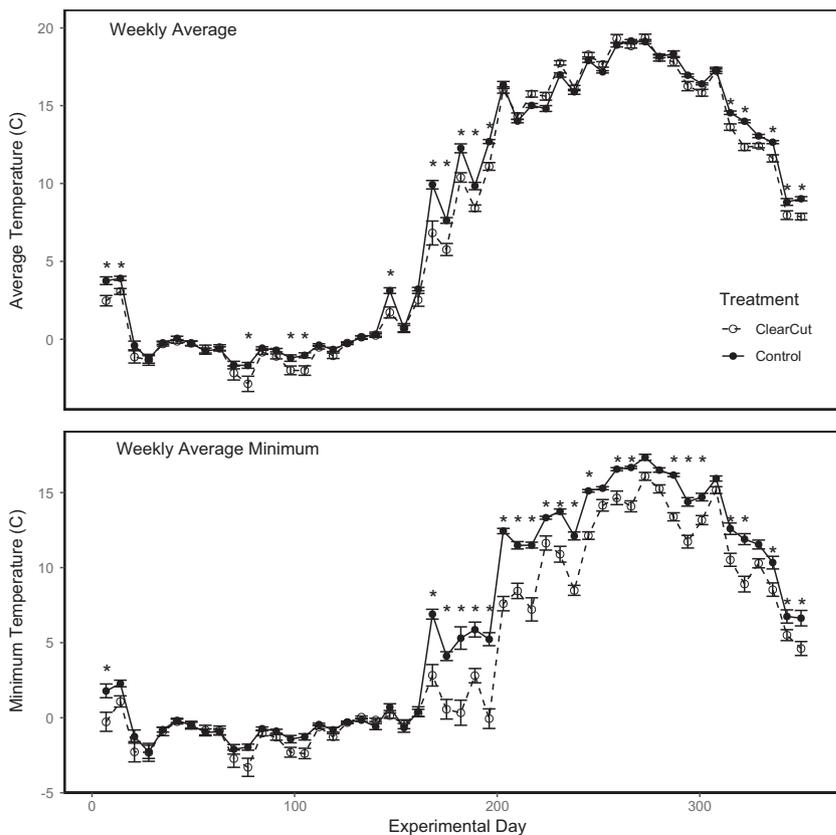


Fig. 3 Average and minimum temperatures in control and clear-cut sites. * indicate differences between treatments at a given week



cuts (Table 2, Fig. S3). When leaf litter species was a factor, abundance of Chironomidae, Oligochaeta, and Tipulidae were generally lower on black ash leaves; Chironomidae and Oligochaeta were highest on black ash leaves in the control plots in April (day 166) and decreased over time (Fig. S3).

We report here preliminary data on water-table levels for the growing season of 2016 (Slesak unpublished data). Between May 1, 2016 and October 31, 2016, almost all plots experienced 2–3 dry periods lasting for a total of 6–16 days during June and July. The exceptions were Block 2 Clear-Cut and Block 5 Control, which did not dry at the well center, and Block 2 Control, which was dry for the entire period except for a few days in August and September. Average water depth at the well was 9 cm in control plots and 15 cm in clear-cut plots. This pattern was largely driven by a single block: the average water-table was higher in three of the control plots than their paired clear-cut plot, whereas in Block 2 the clear-cut was ponded the entire time and its paired control was dry.

Experiment 2: Caddisfly Resource Use

Carbon-nitrogen ratios were significantly different among litter species ($F_{5,12} = 72$, $p < 0.0001$; Table 3) and ranged from 18.0 for speckled alder to 53.3 for balsam poplar. There was a significant effect of litter type on caddisfly survival (Table 4). The risk of death increased by a factor of 3.3 when caddisflies were given American elm ($p = 0.025$), a factor of 3.9 when given balsam poplar ($p = 0.009$), and a factor of 3.0 when given lake sedge leaves ($p = 0.04$), compared to when they were given black ash leaves (Fig. 4). There was no difference in survival probability between caddisflies given black ash and speckled alder or swamp white oak.

Table 3 C/N by weight of conditioned leaves used in caddisfly bioassay. Superscript letters denote differences among species based on Tukey's post-hoc test

Species	C/N (SE)
Speckled Alder ^a	18.0 (0.5)
Black Ash ^b	23.4 (1.3)
American Elm ^b	25.2 (0.9)
Swamp White Oak ^c	40.6 (2.0)
Lake Sedge ^{c d}	48.8 (3.7)
Balsam Poplar ^d	53.3 (2.9)

Litter type had a significant effect on all metrics of caddisfly growth and resource use (Table 4). For change in case length, individuals given black ash leaves increased their case length by 0.12 ± 0.6 mm each day (average \pm SE). On average, individuals fed alder reduced case length by 0.03 ± 0.05 mm each day, but there was no significant difference in daily change in case length between individuals fed black ash and speckled alder. Individuals given American elm, balsam poplar, lake sedge, or swamp white oak had cases that decreased in length significantly ($p < 0.02$), compared to those fed black ash. For these species, cases decreased in length between 0.09 ± 0.05 mm and 0.36 ± 0.07 mm each day (American elm and lake sedge, respectively). There were differences among litter types on estimated instantaneous growth rate (Fig. 5) and larval length (Fig. 5). Caddisflies given black ash had a positive growth rate while those given balsam poplar or lake sedge lost weight ($p < 0.001$); there was no significant differences in growth rate among individuals fed black ash, speckled alder, American elm, or swamp white oak. Caddisflies given swamp white oak, lake sedge, or balsam poplar had negative change in larval length compared to those given black ash ($p < 0.02$); there was no differences in change in larval length

Table 2 Total invertebrate abundances from leaf litter bags throughout Experiment 1, by collection month. 36 litter bags were collected at each time period for each treatment

Taxonomic Group	Treatment	April	May	June	August	October	Total
Ceratopogonidae	Control	12	45	11	10	13	91
	Clear-cut	55	66	39	18	66	244
Chironomidae	Control	55	90	11	7	25	188
	Clear-cut	53	38	94	25	152	362
Collembola	Control	4	12	4	6	8	34
	Clear-cut	4	9	11	17	65	106
Coleoptera	Control	19	28	25	15	2	89
	Clear-cut	103	50	64	31	14	262
Gastropoda	Control	75	64	41	94	116	390
	Clear-cut	126	49	231	153	374	933
Oligochaeta	Control	43	33	115	66	16	273
	Clear-cut	18	6	6	10	7	47
Tipulidae	Control	14	8	24	14	13	73
	Clear-cut	20	10	37	19	98	184
Trichoptera	Control	1	6	1	0	0	8
	Clear-cut	3	3	3	3	0	12

Table 4 Statistical results for Experiment 2: Caddisfly Resource Use. The predictor, Species, is leaf litter species. The test statistic for Survival was Wald Statistics; for all other tests, the statistic was F

Response	Predictor	DF num	DF den	Test Statistic	P
Survival	Species	5	NA	11.8	0.024
Change in Case Length	Species	5	121	12.0	<0.0001
Instantaneous Growth Rate	Species	5	121	6.1	<0.0001
Change in Larval Length	Species	5	121	5.4	0.0001
Resource Use	Species	5	121	70.5	<0.0001

among individuals given black ash, speckled alder, or American elm. Resource use was different among leaf litter species given to caddisflies, (Fig. 5), in which caddisflies used significantly more black ash each day than all other species ($p < 0.04$).

Discussion

Shifts in tree species composition affect forest ecosystem function through multiple mechanisms, one of which is changes in leaf litter quality and quantity. In our study we demonstrated that changes to the dominant vegetation in black ash wetlands, either by invasion by EAB or forest management in response to this threat, could alter nutrient and carbon cycles and resource use by an aquatic macroinvertebrate detritivore. Specifically, we found that black ash leaves breakdown faster than swamp white oak or lake sedge leaves, that changes in environment associated with clear-cutting slows down leaf litter breakdown for black ash, and that larval

caddies had lower survival and growth when fed non-black ash leaves.

Leaf Litter Breakdown

Our results, showing more rapid ash leaf litter breakdown compared to other hard-wood species, mirror those of others. For instance, Palik et al. (2006), found black ash broke down faster in seasonal wetlands than two upland species, quaking aspen and sugar maple (*Acer saccharum*); and across North America and Europe, *Fraxinus* species have some of the fastest breakdown rates among hardwood species (Peterson and Cummins 1974; Melillo et al. 1982; Alonso et al. 2010; Stephens et al. 2013). Our findings and those of others indicate that most canopy trees that could replace ash in forests affected by EAB, either naturally or through assisted planting, could have leaf litter that decomposes more slowly than native ash species.

One reason for the rapid breakdown of ash leaf litter could be because of differences in C/N ratios among the three species tested. The quality of leaf litter – measured as nutrient concentration, lignin and cellulose concentration, and secondary compounds – affects both microbial decomposition and breakdown by detritivores and is predictive of breakdown rates (Melillo et al. 1982; Aerts 1997; Ostrofsky 1997; LeRoy and Marks 2006; Stoler et al. 2016). Our leaf litter breakdown results conform to this generalization: black ash, which had the lowest C/N, broke down faster than lake sedge and swamp white oak. We also observed a reduction in C/N over time, which likely results from leaves being colonized by bacteria, fungi, and periphyton that increase N concentration (Lousier and Parkinson 1978; Cross et al. 2005). While we did not directly measure nitrogen mineralization and immobilization, the relative changes in total nitrogen mass over time suggest that during the 12 months of this study black ash leaves likely had net mineralization of nitrogen while lake sedge and swamp white oak had net immobilization (Lousier and Parkinson 1978).

Loss of nitrogen mass over the course of the experiment in black ash leaves is likely a consequence of their rapid and nearly complete breakdown. These results suggest that nutrient processing and energy flow might be reduced with the loss of black ash. Drying leaves at the start of our experiment may

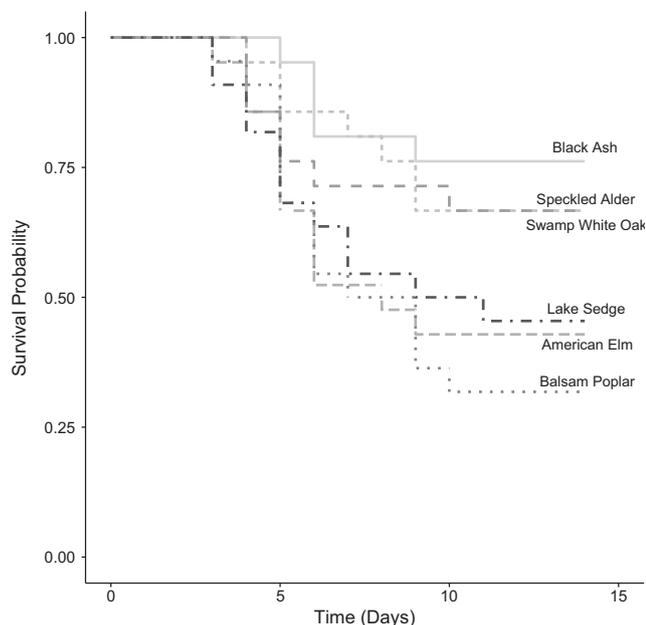
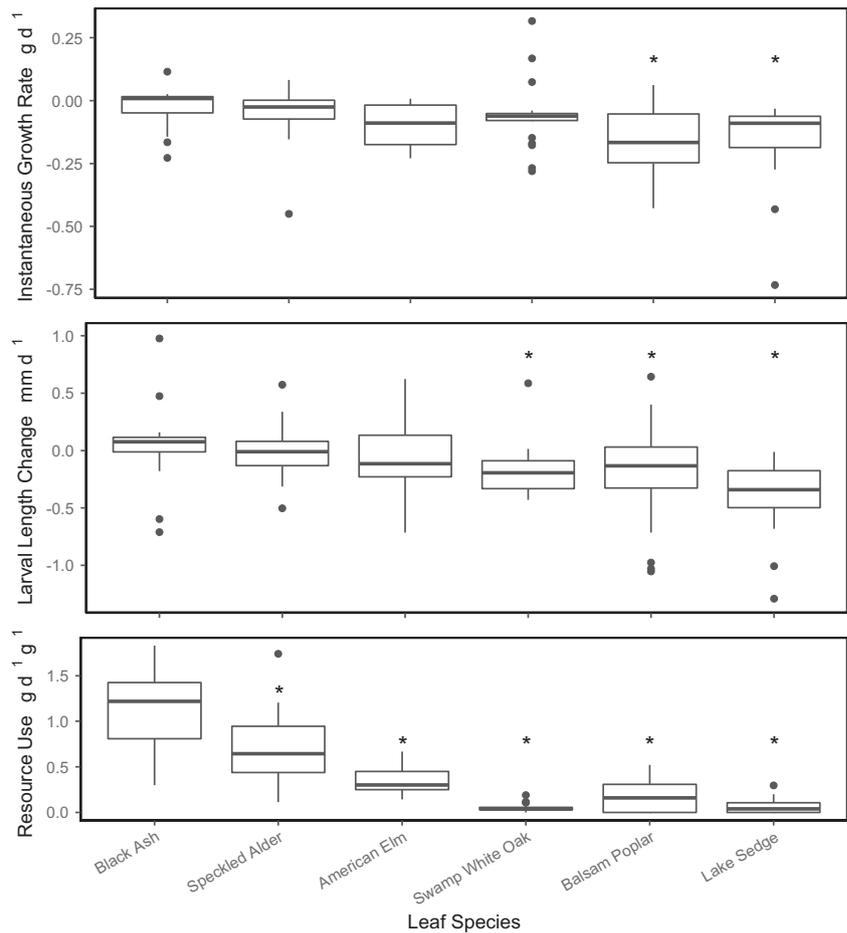


Fig. 4 Survival probability of caddisflies fed different species of leaf litter based on the Cox proportional hazards regression. Compared to black ash, survival was lower when individuals were fed American elm, balsam poplar, or lake sedge

Fig. 5 Instantaneous growth rate (top), daily change in larval length (middle), and average daily dry weight of leaves, per g of initial caddisfly dry weight, given to each individual caddisfly throughout the 2-weeks experiment (bottom). Amount given is a close approximation of resource use. * Denotes a significant difference in response from those fed black ash leaves, based on Dunnett's post-hoc tests



have changed the structural and chemical composition of the leaves, which may have altered initial colonization by fungi and bacteria as well as leaching of soluble substance (Boulton and Boone 1991). These changes could have altered the rate of breakdown compared to undried leaves (Boulton and Boone 1991). However, because all leaves were treated the same and our rates of breakdown mirror those of other studies where leaves were not dried (e.g. Palik et al. 2006), the overall patterns and conclusions from this study are robust.

We also found that black ash litter breakdown was significantly slower in clear-cut plots. Environmental factors, like temperature and hydrology, are known to play an important role in litter breakdown rates (Aerts 1997; Baker et al. 2001; Battle and Golladay 2001; Prescott 2010). We expected that temperature would be a determining factor for rates of breakdown. However, calculating k using experimental-days and degree-days showed the same results. While using degree-days should account for overall temperature effects, it may not account for patterns in temperature differences. Our data show that clear-cut plots were cooler in the spring and fall than control plots. In the clear-cut plots, high density coverage of graminoids may have shaded the ground from solar radiation and higher water-tables across all clear-cuts could slow the spring thaw and delay

breakdown (Slesak et al. 2014); in contrast, lower water-tables and soil moisture levels in the control plots would allow the ground to thaw faster. Furthermore, differences in number of degree-days between treatments disappeared between June and August. More dramatic temperature ranges (higher maximum and lower minimum) in the clear-cut during the summer may have obscured overall average temperature effect accounted for by degree-days.

Differences in breakdown rates of black ash between control and clear-cut plots may also result from differences in soil moisture and hydrological regimes. Patterns of drying and ponding are known to influence leaf litter breakdown (e.g., Battle and Golladay 2001). Between 5/1/2016 and 10/31/2016, the average water-table was higher in three of the control plots relative to their paired clear-cut plots (Slesak, unpublished data). Higher soil moisture levels in these plots, especially within the microhabitats where litter bags were placed, may have contributed to faster rates of breakdown. Furthermore, with the exception of two plots that were continuously ponded at the well-center (one control and one clear-cut), all plots experienced varying patterns of ponding and drying, which could have affected litter breakdown rates of black ash among treatments.

A final consideration is the role of invertebrate detritivores and microbial activity. Invertebrate abundance in litter bags, with the exception of Oligochaeta, was higher in clear-cut plots than control plots. This may be related to additional food resources (e.g., algae, fine particulate organic matter) available for feeding groups other than shredders (i.e., scrapers, collector-gatherers) and/or the leaf litter in litter bags serving as resource islands for shredders like Tipulidae (e.g., Webster and Waide 1982; Benfield et al. 1991; Eggert and Wallace 2003). High abundance of aquatic Oligochaeta likely did not contribute to the rapid breakdown of leaf litter in the control plots because they are collector-gathers that feed on bacteria and fine particulate organic matter (e.g., Rodriguez et al. 2001). The low abundances of shredder caddisflies (e.g., Limnephilidae) in litter bags is likely related to the drying and rewetting patterns across all treatments; species without the respiratory adaptations to survive drying and low dissolved oxygen conditions (Wiggins 1996) would perish. Microbial decomposers likely played an important role in litter breakdown in this study. In temporary wetlands, microbial activity has been hypothesized to play a larger role than invertebrate shredders, especially when drying conditions may exclude shredders (e.g., Batzer et al. 2005; Battle and Golladay 2007; Wissinger et al. 2018). However, more studies are needed to resolve the relative importance of shredder and microbial communities for leaf litter breakdown within shallow wetland habitats, such as those in this study.

Over the course of our study we did not detect any environmental effects on the breakdown of lake sedge or swamp white oak litter. The results from these two species match another study that found no difference in decomposition between forested and emergent wetlands that are dominated by graminoids (Britson et al. 2016). It could be that the chemical composition of these species inhibit decomposition to an extent that other factors do not have a strong effect (e.g., Prescott 2010). Furthermore, single species studies do not reflect the mixed species litter that is naturally found. Results of mixed leaf litter often differ from single species studies, and we acknowledge that breakdown rates of swamp white oak and lake sedge may differ when placed in a more complex leaf litter environment (e.g., Kominoski et al. 2007). Our results suggest that short-term litter breakdown rates for recalcitrant species will not be impacted by changes in habitat structure (in wetlands with near total black ash mortality); however, breakdown of highly labile species could be affected by changes in habitat.

Caddisfly Resource Use

Our second experiment examined how changes in leaf litter would affect resource use by shredder caddisfly larvae. The results of our assay parallel the results of our litter breakdown study. Overall, *L. indivicus* individuals that were given litter

species with lower C/N ratios, notably black ash and speckled alder, had higher survival and resource use rates. While we did not measure leaf matter used for consumption versus case building material, our results suggest faster growth in individuals when given black ash and speckled alder. Caddisflies in these treatments increased their case length and our estimates of changes in larval length and mass show growth. While the relationships between case length and larval length or mass were relatively weak ($r^2 = 0.67$ and 0.54 , respectively), they were significant and similar to other methods of estimating initial size (Martins et al. 2014). Results of changes in caddisfly mass and larval length should be interpreted with caution, however, the patterns of survival, resource use, and three metrics of growth all showed similar results.

Individuals given lake sedge, swamp white oak, and balsam poplar avoided using these species; many individuals in these treatments seemed to consume their cases. In some scenarios, oak (*Quercus*) may be a poor resource for shredders (Mehring and Maret 2011; Santonja et al. 2018). Mehring and Maret (2011) found *L. indivicus* had low survivorship, growth, and leaf processing rates when fed white oak (*Q. alba*) and red oak (*Q. rubra*) compared to red maple. However, Hutchens et al. (1997) found oak leaves, when optimally conditioned (3 months vs 2 months), can be a high quality resource for caddisflies. Caddisflies in our study also did not use American elm. This result was unexpected because American elm had similar C/N to black ash and other studies have shown that elm is readily fed on by stream invertebrates (Bird and Kaushik 1985; Hooker and Marzolf 1987). The elm litter used were planted and were hybrids with another cultivar to increase tolerance to Dutch elm disease (Looney et al. 2015). It is unclear how this may have affected leaf palatability for the caddisflies from black ash wetlands in northern Minnesota.

A caveat to our experiment is that we conditioned our leaves in the field for only 14 days (sensu Graça et al. 2001; González and Graça 2003); much longer periods (> 60 days) of conditioning might make the higher C/N species more palatable (e.g., Herbst 1982; Golladay et al. 1983; Hutchens et al. 1997). This is evidenced by caddisflies eating their own cases in some of the treatments. However, given the ephemeral nature of the ponded areas in these wetlands and the necessity of rapid growth for caddisflies to reach metamorphosis prior to pond dry-down (*L. indivicus* free-swimming larval stage may only last a few months in the spring [Wiggins 1973]), the low nutritional quality of some litter species may still render them unsuitable resources. Data from the first experiment indicate that it could take over 1 year of conditioning for lake sedge and swamp white oak leaves to reach similar C/N as black ash.

During years with high levels of precipitation, leaf litter that breaks down slowly might become an important resource after being optimally conditioned (e.g., Hutchens et al. 1997) and when highly labile species are gone. However, during drier years, when the pressure to reach metamorphosis quickly

is the greatest, an abundance of high quality litter might be especially important. Our results suggest that shredding caddisflies in black ash wetlands may be accustomed to feeding on highly palatable leaf litter and therefore might not persist in these wetlands after EAB invasion and loss of black ash. Recent surveys support this inference by revealing higher trichopteran abundance in control black ash sites than clear-cut sites (MB Youngquist, unpublished data). The exception would be if alder, which is common in the understory in some black ash wetlands (MNDNR 2003; Palik et al. 2012), becomes a dominant species after EAB invasion; if so, caddisflies and other shredders may persist in that environment. Finally, less labile leaf litter that persists for multiple years could provide a substrate for nutrient rich biofilms, which could then be a high-quality resource; these less labile species could provide a mix of high- and low-quality food resources within a given year. We also note that our study does not consider any interactive effects of environment on food quality and invertebrate performance. It is possible that differences in temperature and light could offset changes in initial leaf litter quality.

Our results support the generalization that shredders and other detritivores preferentially use higher quality leaves and that high-quality resources increase growth and survival (Eggert and Wallace 2003; Eggert and Wallace 2007; Marcarelli et al. 2011; Mehring and Maret 2011; Stephens et al. 2013; Santonja et al. 2018). Therefore, our observed responses of *L. indivicus* to changes in litter species could be indicative of responses across some forest-associated macrodetritivorous taxa to the loss of black ash; other species are able to utilize lower quality resources and may not be affected (e.g., Eggert and Wallace 2007). We note that Trichoptera were not abundant within the leaf litter bags. This absence is likely the result of drying within almost all plots. However, limnephilid caddisflies can occur at high densities in depressional black ash wetlands (Batzer et al. 2004, 2005; Youngquist, personal observations) and can be an important shredder in healthy forested wetlands (Richardson and Mackay 1984; Whiles and Wallace 1997; Colburn 2004; Batzer et al. 2005; Batzer and Palik 2007). Ultimately, changes in leaf litter processing by *L. indivicus* may affect multiple food web pathways and other functional feeding groups (Covich et al. 1999; Cross et al. 2005; Jonsson and Malmqvist 2005; Santonja et al. 2018).

Conclusions

Overall, our results indicate that the loss of black ash will alter carbon and nutrient dynamics via two interrelated mechanisms. First, changes in canopy structure will affect environmental factors that influence leaf litter breakdown and decomposition and second, changes in litter quality will affect

biological breakdown via changes in detritivore feeding rates. In addition to altering rates of breakdown, the loss of high quality resources could alter invertebrate communities by reducing growth and survival of shredders and other detritivores; thus, further affecting nutrient and energy flows through the ecosystem. In the face of EAB invasion, replacing black ash with other canopy trees may be the best option to keep these wetlands forested and maintain certain processes, like transpiration; however, managers need to consider the nutritional quality of the leaf litter provided by replacements and should select species that are as functionally equivalent to black ash as possible.

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Compliance with Ethical Standards

Conflict of Interest The authors declare no conflict of interest.

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