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ORIGINAL PAPER

Fourteen years of swamp forest change from the onset, during, and after invasion of emerald ash borer

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Abstract Since beginning its invasion of eastern North America by 2002, the Asian-origin beetle emerald ash borer (EAB; *Agrilus planipennis*) has decimated ash trees (*Fraxinus* spp.). In the Great Black Swamp in northwestern Ohio, USA, 90 km south of the epicenter of EAB invasion, we examined changes in forest communities during a 14-year period spanning EAB's arrival in 2005 through 2018. No green ash (*Fraxinus pennsylvanica*) trees larger than 4 cm in diameter were alive on study sites in 2018, but ash saplings 1–4 cm in diameter (764 stems/ha) and seedlings (1.5% cover) were plentiful. Basal area growth of other tree species did not compensate for ash loss; total basal area averaged 8% lower in 2018 than in 2005. In the understory, non-native plants were negligible (< 2% cover, < 3 species/0.05 ha) among years and did not change significantly after EAB's arrival. Native plant cover was twice as high in 2018 than when EAB arrived in 2005. Changes in understory cover primarily entailed reorganization of species already established when EAB arrived, rather than colonization by new species. New colonizers proportionally comprised only 0.05–0.07 of total cover among years. The shrub spicebush (*Lindera*

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benzoin) and forb Virginia creeper (*Parthenocissus quinquefolia*) dominated understories throughout the study. From a perspective of maintenance of native understories in EAB-aftermath forests, observed changes were probably as favorable as could be expected. Native species already present increased the most, neither floristic quality nor wetland indicator species declined, and non-native plants did not increase.

Keywords *Fraxinus pennsylvanica* · Great Black Swamp · Invasive Insect · *Lindera benzoin* · Understory · Wetland

Introduction

Accumulating invasions of introduced pests are making the demise of dominant tree species increasingly common (Brockerhoff and Liebhold 2017). Accurately forecasting how forest communities respond to losing these dominant trees can have broad implications, such as for modeling and managing changes in forest carbon storage, productivity, biodiversity, invasions by non-native species, and wildlife habitat (Klooster et al. 2018). However, identifying how remaining species respond is challenging owing to limited long-term data inclusive of forest conditions before or at the onset of pest invasion, the diversity of forest types and sites being invaded, variable effects among pests, and numerous interacting factors such as climate, herbivory, and secondary invasions (Flower and Gonzalez-Meler 2015; Looney et al. 2017).

A general model, with a complex array of specific potential outcomes, has been proposed for how forest communities respond to canopy disturbance. The reorganization-colonization model proposes that forests respond to disturbance via reorganization of species present before the disturbance and via colonization of species absent from the pre-disturbance vegetation (Marks 1974; Ehrenfeld 1980; Halpern and Lutz 2013). Illustrating the potential complexity of specific outcomes, reorganization processes could hinge on whether gaps are favorable for shade-tolerant species, while colonization can depend on seed bank persistence, uncertainties of seed dispersal, and reorganization of established species (Collins et al. 1985; Clark et al. 1998; Klooster et al. 2014). Furthermore, changes in understory diversity and species composition can be minimal under several scenarios of canopy gap creation, such as if tall shrubs simply retain dominance or if a pest only affects mature trees and not seedlings or saplings (Huenneke 1983; Kashian 2016). Consequently, a range of responses to pest-related losses of dominant species are possible in forest communities, from minimal change to major alterations in species diversity and composition including secondary biological invasions.

Here, we examined long-term changes in forested wetlands invaded by the emerald ash borer (EAB; *Agrilus planipennis*). Native to Asia, this beetle species was identified in North America in 2002 in southeastern Michigan, USA, and neighboring Ontario, Canada (Klooster et al. 2018). By 2018, EAB had invaded 35 states and 5 Canadian provinces (U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Riverdale, Maryland). All North American species of ash trees (*Fraxinus* spp.) within EAB's range were susceptible to mortality, including the most widely distributed and abundant green (*Fraxinus pennsylvanica*), white (*F. americana*), and black ash (*F. nigra*). The phloem- and cambium-feeding EAB kills ash trees by disrupting water and nutrient flow in the wood, girdling branches and the trunk (Herms and McCullough 2014). Ash canopy dieback occurred within 1–2 years in several studies around the epicenter of EAB invasion, with up to half of trees dead within 3–4 years and over 99% mortality within six years (Knight et al. 2012, 2013; Klooster et al. 2018). Current literature suggests that "orphaned" cohorts of ash seedlings and saplings (< 5 cm in stem diameter at 1.4 m) too small to be colonized by EAB can persist, until the seedlings grow to susceptible sizes and assuming seed and sprout reserves are not exhausted (Klooster et al. 2014; Aubin et al. 2015; Kashian 2016).

Few studies are available on how other species of the forest community respond to EAB invasion and that include data before or upon the arrival of EAB. The sparse existing literature suggests possibilities and uncertainties for how post-EAB plant communities may change with respect to residual species, species invasions, floristic quality (such as shifts in abundance of disturbance-promoted, ruderal species compared with mature-forest species), and wetland- compared to dry site-affinity species. Available studies suggest that responses are primarily via reorganization of existing vegetation, such as from lateral and vertical growth of plants near dead ash (Costilow et al. 2017; Dolan and Kilgore 2018). Two studies further reported that EAB invasion was not associated with new plant invasions but did coincide with accelerating non-native plant growth (Hoven et al. 2017; Dolan and Kilgore 2018). The relative responses of ruderal and mature-forest species could hinge on the proportion of ash in a forest (and subsequent canopy gap creation), potentially with different responses in mixed-species forests as opposed to where ash comprises monospecific forested wetlands (Looney et al. 2017). How EAB could influence forested wetland hydrology and wetland-affinity plants remains uncertain across mixed-species forests. Loss of ash trees could raise water tables if water usage by other species does not compensate, but on the other hand, increased sunlight penetrating more open canopies could increase evaporation (Diamond et al. 2018; Robertson et al. 2018).

Using a tree and understory community data set spanning the onset of EAB invasion through 14 years after, we examined an overarching expectation that post-EAB forest dynamics would emphasize reorganization of species already present before EAB arrived. Specifically, we anticipated that density of small ash trees would not change; density and basal area of non-ash tree species would increase; understory species richness would not change but cover (including of non-native plants) would increase; and no change would occur in functional vegetation measures such as floristic quality and wetland indicator status.

Methods

Study area

Our study area was the 253-ha Pearson Metropark, managed by Metroparks Toledo, and located 10 km east of Toledo, Ohio, USA. Climate is temperate, with cold winters and warm, humid summers. At Toledo Metcalf Field weather station, 10 km southwest of the park, annual precipitation averaged 82 cm/year (range 46–124 cm/year) for the available record (1999–2018; Online Resource 1). Soils were mapped as Latty silty clay, with 0–1% slopes on glacial lake plain, and classified as mesic Typic Endoaquepts (Stone et al. 1980).

The park is among few protected remnants of the historic Great Black Swamp, a 400,000-ha lowland mostly south of the Maumee River and extending from the southwestern shore of Lake Erie to near the Ohio-Indiana border (Kaatz 1955). Before the mid-1800s when timber harvest, installation of drainage ditches to facilitate cultivation, and clearing for agriculture had appreciably altered the region, the swamp was a nearly continuously forested wetland with standing water (often 20–100 cm deep in spring) or saturated soils most of the year (Kaatz 1955). An 1819 U.S. Government land survey recorded a mesophytic forest dominated by ash (*Fraxinus* spp.), American elm (*Ulmus americana*), beech (*Fagus grandifolia*), hickory (*Carya* spp.), basswood (*Tilia americana*), oaks such as swamp white oak (*Quercus bicolor*), silver maple (*Acer saccharinum*), sycamore (*Platanus occidentalis*), and cottonwood (*Populus deltoides*; Good 1961). Pearson Metropark contained mature swamp forest when the park was established in 1934. Mature forest persisted through 2005, when we began the study, with species composition similar to that described in 1819 (Online Resource 2, 3).

Data collection

We studied five sites, randomly located within mature swamp forest containing ash and without tree cutting associated with attempted EAB quarantine (Hausman et al. 2010). In 2005 when the study started, EAB invasion of the study area was beginning, but widespread, acute impacts (e.g., ash canopy dieback) were not yet evident. For example, the Ohio Department of Agriculture identified three EAB-infested trees in spring 2005 in the park, which at the time represented the eastern edge of EAB invasion expanding from the epicenter in southeastern Michigan (Hausman et al. 2010). We collected data at each site in mid-summer (June-July) annually from 2005 to 2008 and in 2018. This schedule spanned the onset of EAB invasion (2005), dieback (2006 and 2007) and mortality of ash trees (2008), and 14 years after EAB arrived (2018).

At each site, we established a 20 m × 25 m (0.05 ha) plot permanently marked with aluminum pipe at each corner. On each of the five plots for each of the five data collection years, we recorded the species and diameter at 1.4 m for each tree species ≥ 1 cm in diameter at 1.4 m. Multiple stems arising from a probable common genet were counted as separate stems. Understory plants, including tree seedlings < 1 cm in diameter at 1.4 m and all other vascular plants, were inventoried by species using visual cover categorization as trace (assigned 0.1%), 0.25%, 0.5%, 1% intervals to 10% cover, and 10% intervals to 100% cover. To aid cover categorizations, we subdivided plots into finer-scale grids. Continuity of investigators throughout the study further assisted consistency of cover categorizations, and cover estimates compared among investigators of the research team on a plot were within one cover class. Cover was aerial coverage of foliage and was recorded separately by species, such that total cover for all species could exceed 100% if foliage of multiple species overlapped. Nomenclature, native or non-native status to the United States, and classification of growth form (e.g., tree, shrub) followed the Natural Resources Conservation Service (2018). Of 93 taxa recorded in the understory during the study, 90 were identified to species and 3 to genus. The taxa identified only to genus (some specimens of *Crataegus*, *Oxalis*, and *Viola*) lacked diagnostic structures, but were taxonomically distinct from other identified species, so we treated all taxa as species for statistical analyses.

Data analysis

We analyzed forest dynamics across the five study years during the 14-year period using repeated measures analysis of variance with Tukey's test for mean separation in SAS 9.4 (PROC MIXED; Online Resource 4). Response variables for trees were density and basal area in the regeneration (≥ 1 < 10 cm in diameter) and large-tree (≥ 10 cm) layers for green ash (the only species of ash recorded on our plots) and non-ash species combined. Understory response variables included: cover and species richness (0.05 ha) of native and non-native species, wetland species indicators, a floristic quality index, and cover of the nine species with the highest average cover. The wetland indicators were the number and cover of facultative wetland and obligate wetland species, and the average wetland index of species (ranging from integers 1 to 5 for each species corresponding with upland, facultative upland, facultative, facultative wetland, and obligate wetland species). Wetland species classifications followed Andreas et al. (2004) for Ohio. We calculated a floristic quality index using species conservatism scores also following Andreas et al. (2004). Increasing floristic quality indicates conservative species with specific habitat requirements. Widespread species typical of many wetland habitats dominated our study's swamp forests, which had floristic quality lower than the "high" values of the index which can exceed 30 when many conservative species are present (Lopez and Fennessy 2002).

To estimate understory community persistence and colonization through time, we calculated means and standard errors of means for the proportion of plot cover and species richness comprised of species already present in 2005 and species colonizing plots after 2005. From a matrix of relative cover (cover of $\text{species}_i/\sum$ all species on a plot) in PC-ORD 6, we calculated Sørensen similarity each plot had for each study year to its 2005 species composition.

Results

Tree layers

From 2005 to 2008 at the onset and early aftermath of EAB invasion, plots contained an average of 32–48 trees/ha of large (≥ 10 cm in diameter) green ash, the only ash species on plots. In 2018, no large ash trees were alive on plots (Fig. 1). Ash comprised 20% of the 33–35 m^2/ha of large-tree basal area from 2005 to 2007, before declining to 14% in 2008 and 0% in 2018. Basal area growth of large non-ash trees did not compensate for losing ash. As a result, total stand basal area in 2018 was 8% lower than in 2005 when EAB arrived.

Density and basal area of small stems (≥ 1 < 10 cm in diameter) of ash and other species fluctuated temporally (Fig. 1). Ash remained present throughout the study, but only as low-statured individuals or shrub-like thickets. In 2018 by 14 years after EAB's arrival, no ash larger than 4 cm in diameter were alive on plots, 96% of the 191 total ash stems on plots were 1–2 cm in diameter, and cover of ash seedlings (< 1 cm in diameter) averaged 1.5%. Density of small stems of non-ash species did not display a clear directional trajectory through time, and was lower in 2018 than in 2005 and 2008 (Online Resource 4).

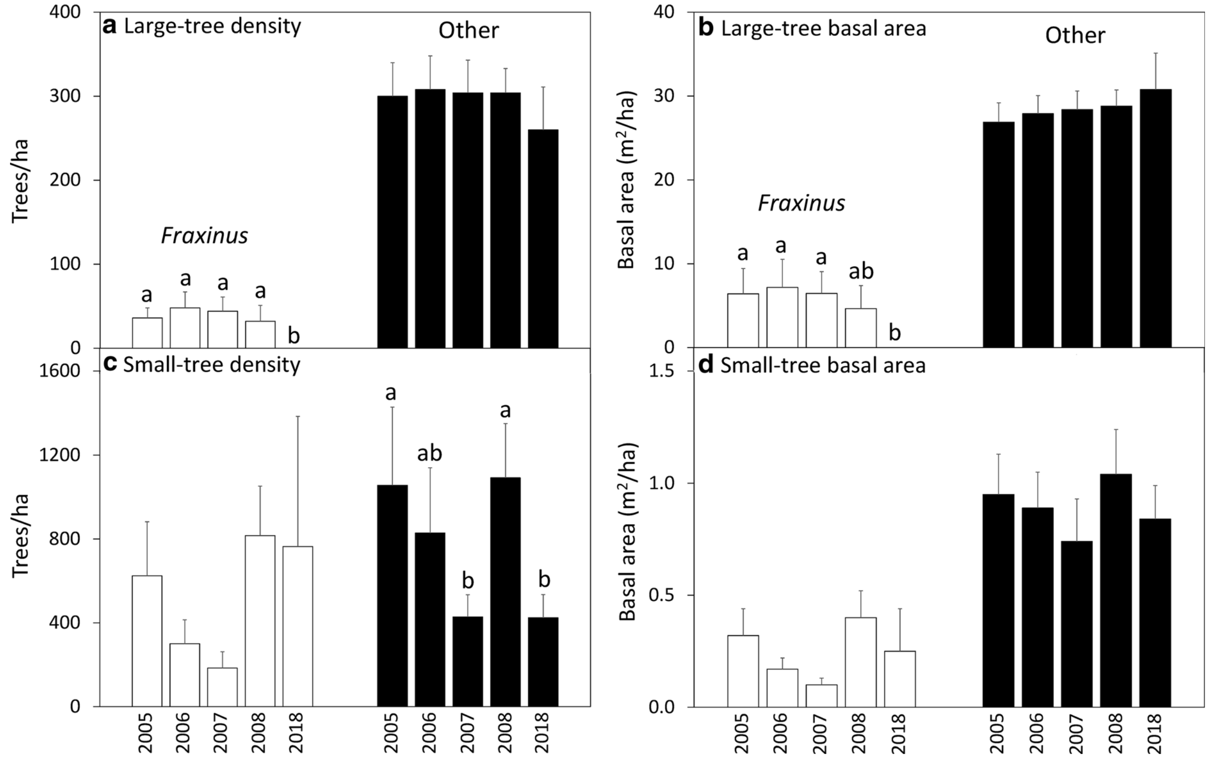


Fig. 1 Changes in large (≥ 10 cm in diameter at 1.4 m) and small (≥ 1 < 10 cm) trees of *Fraxinus pennsylvanica* and other species from the onset of emerald ash borer invasion (2005) to during (2006–2008) and 14 years after (2018) in wetland forests of the Great Black Swamp, northwestern Ohio. For repeated measures analyses of variance significant at $P < 0.05$, letters compare means within a panel at $P < 0.05$ maintained for multiple comparisons. Error bars are standard errors of means. Large *Fraxinus* were absent by 2018. Online Resource 2 contains a full list of tree species

Understory communities

Native species dominated understories throughout the study. Across study years, there was minimal cover (0.2–1.7%) and richness (1–3 species/0.05 ha) of non-native species and no trend for them to increase after EAB invasion (Fig. 2). Except for 2008, native species displayed increasing cover over 2005 levels after EAB arrived. Native species richness temporarily peaked in 2006, one year after EAB arrived, before returning to near 2005 levels. Woody plants dominated understory cover, while woody and herbaceous plants contributed nearly equally to species richness. Although high-quality from a standpoint of dominance by native species, floristic quality was low in terms of plots containing species typifying unique habitats (Table 1).

Wetland community indicators minimally changed through time (Fig. 3). The only significant change was higher richness of facultative-obligate wetland species in 2006 compared to some other years, mostly mirroring the elevated total species richness of communities in 2006.

Three of the nine most dominant understory species displayed significant increases in cover one or more years after EAB arrived (Fig. 4). The forb Jack-in-the-pulpit (*Arisaema triphyllum*) increased in 2007, two years after EAB arrived. The shrub spicebush (*Lindera benzoin*) attained its highest cover in 2018, significantly higher than in 2006 and 2008. The forb Virginia creeper (*Parthenocissus quinquefolia*) had increased cover two (2007) and 14 (2018) years after EAB arrived.

Persistence and colonization

The total number of understory species among years ranged from 45 (2005) to 61 (2006), with 93 total species recorded during the study. On average among plots, 28–47% of species present in later years

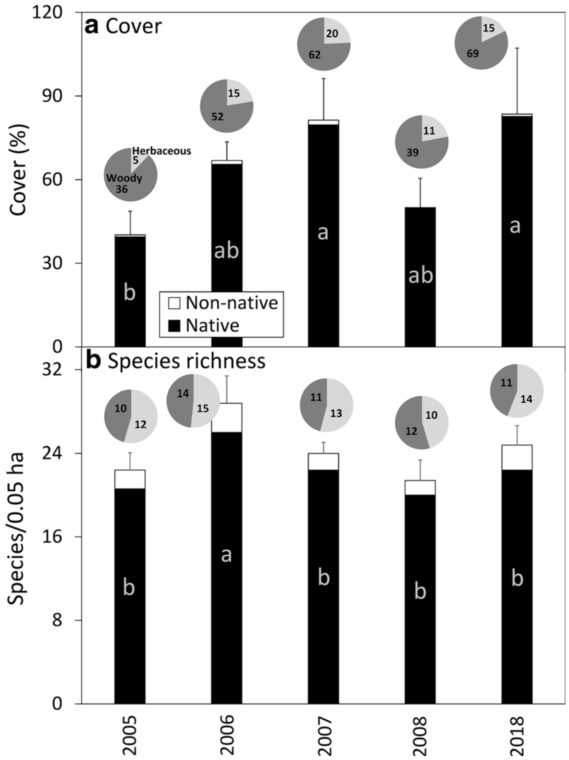


Fig. 2 Changes in understory plant cover and species richness from the onset of emerald ash borer invasion (2005) to during (2006–2008) and 14 years after (2018) invasion in wetland forests of the Great Black Swamp, northwestern Ohio. Non-native species measures did not differ significantly among years in overall repeated measures analyses of variance ($P > 0.05$) so letters for multiple comparisons of means are not shown. Native species cover and richness both differed significantly across years in overall repeated measures analyses of variance. Letters separately for each measure compare means across years at $P < 0.05$ maintained for multiple comparisons. Error bars are standard errors of means for total cover and richness. Pie charts show mean total cover and species richness of herbaceous and woody plants, with numbers listing exact values summing to total mean cover or richness for all plants

(2006–2018) colonized after EAB's 2005 arrival (Table 1). The main new colonizer was the perennial forb eastern waterleaf (*Hydrophyllum virginianum*), present all years after 2005 and averaging 1% cover in two years. Most (85%) of the 47 other species of new colonizers were transient – present only one or two years – and had low cover (< 0.5%) when present. All the colonizing species were capable of perennial life spans, except for one. This was the non-native, annual bristlegrass (*Setaria viridis*), which inhabited one plot in 2006.

While new colonizers were transient, species already present in 2005 when EAB arrived persistently dominated post-EAB understories. Among the 45 species present in 2005, 43 (96%) persisted for multiple future years. Moreover, species already present in 2005 comprised 93–95% of total understory cover in subsequent years (Table 1). As a result, average community compositional similarity to 2005 varied little (range 63–65%) among years after EAB arrived.

Discussion

Ash dynamics

Results were consistent with previous studies of ash dynamics around the epicenter of EAB invasion, including nearly complete mortality of stems over 4 cm in diameter but at least short-term persistence of a seedling and sapling layer (Aubin et al. 2015; Kashian 2016). A working hypothesis in EAB literature is that the ash seedling-sapling layer will gradually decline as stems reach EAB-susceptible diameters of 2–4 cm and the seed bank is exhausted (Burr and McCullough 2014; Klooster et al. 2014). Although the 10-year gap between the 2008 and 2018 measurements in our study precluded identifying fluctuations during that period, the data showed no net significant decline in either ash sapling density (1–4 cm diameter) or seedling cover.

While how long the "orphaned" seedling-sapling layer may persist is unknown, conditions would seem poised for this layer to begin declining (Burr and McCullough 2014; Kashian 2016; Klooster et al. 2018). First, no ash larger than 4 cm in diameter were alive, less than the minimum diameter of 8 cm at which ash produce seed (Aubin et al. 2015). Second, 94% of remaining ash stems were 2–4 cm in diameter (the other 6% were 1 cm in diameter), approaching or at the susceptibility threshold to EAB (Klooster et al. 2018). Third, a demographic study in northeastern Ohio found that only 2% of ash seedlings lived longer than five years, especially under heavy deer herbivory (Boerner and Brinkman 1996). This suggests potential accelerated attrition of seedlings if no new seed inputs occur. Fourth, although forming persistent soil seed banks, ash seed is thought to live only a few years in the soil, consistent with an absence of ash from soil

Table 1 Understory plant community metrics in wetland forests of the Great Black Swamp, northwestern Ohio, from the onset of invasion by emerald ash borer (2005) to during (2006–2008) and 14 years after invasion (2018)

	2005 Mean ± SEM	2006	2007	2008	2018
Cover (%)[a]	40±8	67±7	81±15	50±11	83±24
Proportion cover by original species[b]	1.00±0.00	0.94±0.03	0.95±0.02	0.95±0.03	0.93±0.02
Proportion cover by new species[b]	0.00±0.00	0.06±0.03	0.05±0.02	0.05±0.03	0.07±0.02
Species richness (0.05 ha)	22±2	29±3	24±1	21±2	25±2
Proportion richness by original species	1.00±0.00	0.69±0.01	0.71±0.03	0.72±0.05	0.53±0.05
Proportion richness by new species	0.00±0.00	0.31±0.01	0.29±0.03	0.28±0.05	0.47±0.05
Within-plot similarity with 2005 (%)[c]	–	63±5	65±4	63±3	63±8
Floristic quality index	16±1	18±2	17±1	17±1	16±1

[a]Aerial cover of herbaceous plants, shrubs, and tree seedlings (stems < 1 cm in diameter at a height of 1.4 m)

[b]Original species were those present in 2005; new species were those absent in 2005 and that colonized plots in later years

[c]Sørensen similarity of 2005 species composition on plots compared with later years

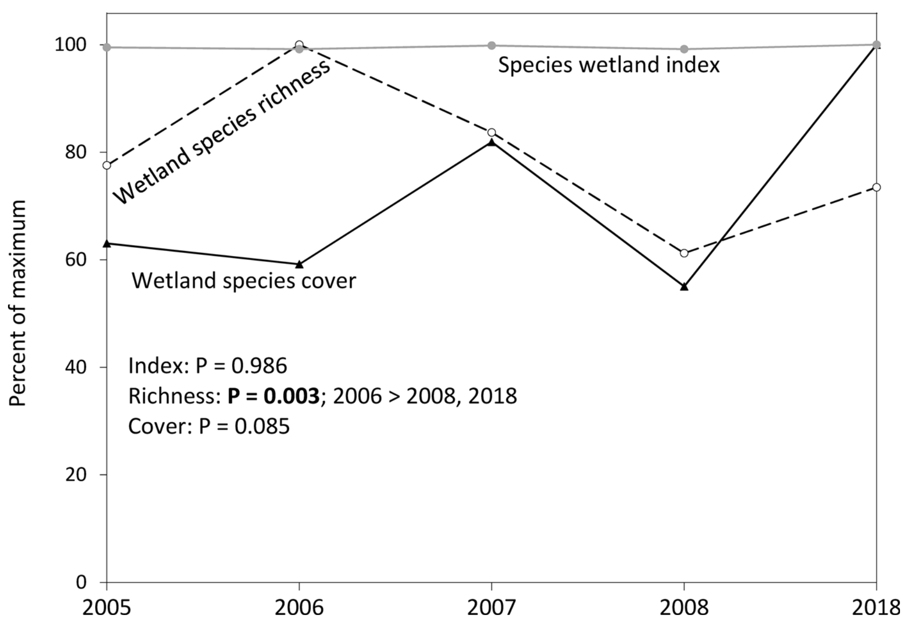
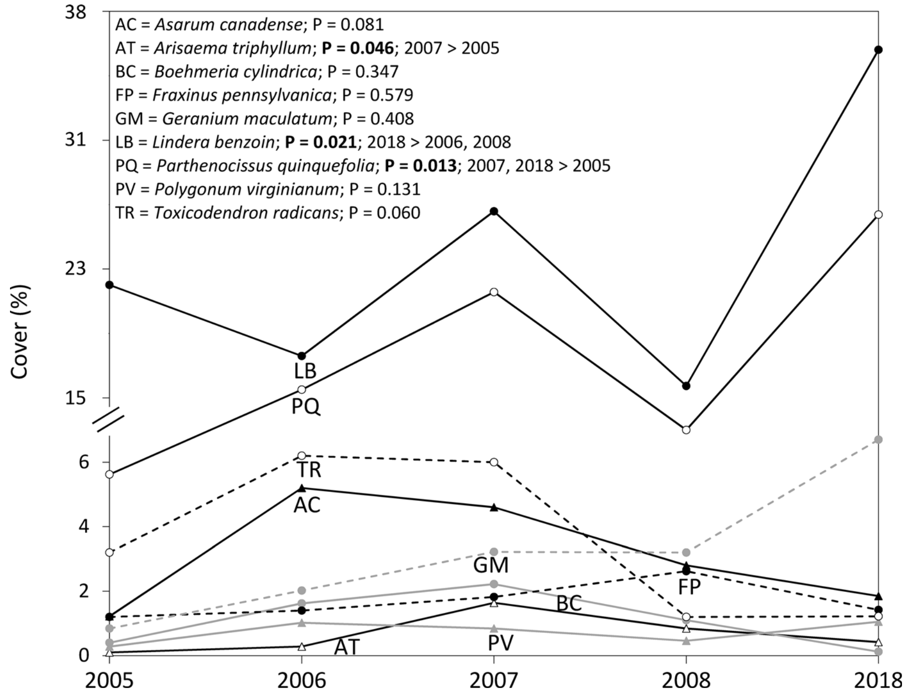


Fig. 3 Indicators of wetland vegetation status for forest understories from the onset of emerald ash borer invasion (2005) to during (2006–2008) and 14 years after (2018) invasion in the Great Black Swamp, northwestern Ohio. Measures include the average value of wetland indices (ranging from 1 for upland to 5 for obligate wetland species) constituent species had among plots within a year, and the richness (per 0.05 ha) and cover of species with wetland scores of 4–5 (facultative wetland and obligate wetland species). Wetland species richness differed significantly among years, with year comparisons listed after the *P* value. All measures are expressed as the percent of the maximum value each measure attained among years

seed banks within a few years of adult tree mortality (Klooster et al. 2014). Although this evidence seems to portend an inevitable decline or elimination of the seedling-sapling layer, future dynamics could hinge on unknowns such as the possibility of biological control reducing EAB density, population crashes of EAB after removal of mature ash enabling a window for some small ash to grow to reproductive size, or

Fig. 4 Changes in cover of nine dominant understory plant species from the onset of emerald ash borer invasion (2005) to during (2006–2008) and 14 years after (2018) invasion in wetland forests of the Great Black Swamp, northwestern Ohio. For species with mean cover differing significantly across years, year comparisons significant at $P < 0.05$ are shown



persistence of some lingering, reproducing trees (Klooster et al. 2018). Additionally, closure of canopy gaps could slow growth of ash saplings, delaying reaching EAB-susceptible size, enabling suppressed ash thickets to persist owing to ash's moderate shade tolerance (Bartlett and Remphrey 1998).

Gap dynamics and loss of ash in mixed-species forests

Results seem consistent with the idea that post-EAB understory dynamics in mixed-species forests, where ash comprises 15–50% of the overstory, follow a transient small-gap dynamics model. In this model, canopy gaps from ash mortality are neither sufficiently large nor persistent to produce major changes in understories or eventual overstories (Dolan and Kilgore 2018). Removal of an individual mature ash created typical canopy gaps of 25–30 m^2, and at most approximately 200 m^2 of gap area in total normally discontinuous across our 500-m^2 plots (Hausman et al. 2010). These estimates agree with average single-tree gaps of 26 m^2 in a mature swamp forest in northwestern Ohio subject to blowdowns and natural disturbance (Cho and Boerner 1991). They also are consistent with the largest canopy areas of 130–170 m^2 estimated for the largest ash trees of 60–70 cm in trunk diameter at 1.4 m (the maximum diameters on our plots) for closed-canopy, mixed-species stands (Lamson 1987). Removal of ash on our plots corresponded with a measured 50% increase in sunlight reaching the forest floor for two years after ash removal, also about proportional to an average loss of 150 m^2 of ash canopy area per plot (Hausman et al. 2010). Based on a lateral branch growth of 0.10–0.15 m/year for eastern deciduous trees bordering canopy gaps (Runkle 1998), a typical 28-m^2 canopy gap created by loss of an ash tree with a 6-m crown diameter would theoretically fill completely within 20–30 years. With decreasing light availability during gap closure, Moore and Vankat (1986) found that understory cover stopped increasing by six years after gap creation in a mesophytic deciduous forest, seemingly consistent with our finding that understory cover in 2018 was similar to cover in 2007 during ash defoliation. While measuring canopy-gap closure rate was beyond our study's scope, we did note that small canopy gaps remained identifiable above fallen ash in 2018 (e.g., Online Resource 3). These observations are consistent with the slow and not statistically significant increase in basal area of non-ash trees on plots anticipated to infill canopies vacated by ash (Costilow et al. 2017). While understory changes occurred under these canopy conditions, our findings reinforced the idea that changes in mixed-species forests after EAB invasion are likely to be relatively subtle compared to an expectation for type conversions – such as between herbaceous- and shrub-dominated understories – anticipated for monospecific ash wetland forests afflicted with EAB (e.g., Looney et al. 2017). Moreover, our results for EAB-associated gaps concur with findings that individual gaps must exceed 60 m^2 in swamp forests to produce major shifts in species composition (Anderson and Leopold 2002).

Understory species persistence mechanisms

Nearly all understory cover through the 14th year after EAB's arrival was supplied by perennial species already present when EAB arrived and that rely primarily on local regeneration processes, rather than on long-distance dispersal or germination from seed banks where species are absent from existing vegetation. For example, three of the most dominant species – false nettle (*Boehmeria cylindrica*), poison ivy (*Toxicodendron radicans*), and Virginia creeper – have persistent soil seed banks where the species also dominate aboveground (Blood et al. 2010). Another dominant, wild geranium (*Geranium maculatum*), expands via rhizomatous growth, with a southern Ohio study finding that the species responded to canopy gaps *in situ* by doubling rhizome mass and length (Schutte Dahlem and Boerner 1987). Seeds of this species typically disperse a maximum of 5 m (Whigham 2004). Wild ginger (*Asarum canadense*), which we found had 5% cover the year after EAB arrived, has seeds with minimal dormancy and apparently lacks persistent seed banks, but genets are theoretically immortal while expanding via clonal growth and local seed dispersal (Cain and Damman 1997). Wild ginger clones expanded vegetatively 16 cm^2/year, corresponding with an estimated spread of 0.7 m/century in a Canadian forest (Cain and Damman 1997). With ants sometimes dispersing seeds 35 m, the seed dispersal capability of wild ginger was estimated to average 15 m/century (Cain and Damman 1997). The tall shrub spicebush responds to canopy gaps by lengthening branches laterally and vertically, with a study in Pennsylvania reporting that branch lengthening rate doubled up to 4 cm/year upon canopy gap creation (Niesenbaum 1992). The traits of species that maintained or increased their cover after EAB's arrival – including formation of persistent soil seed banks, expansion via clonal reproduction, and ability to accelerate growth below small canopy gaps – were consistent with the observed trend for reorganization of established species as the primary community response to EAB invasion.

Factors coinciding with invasion

Weather, soils, and herbivory are three factors that could have affected forests independently of or interactively with EAB. Current literature suggests that green ash mortality in mixed-species forests ultimately occurs independently of climatic variation (Herms and McCullough 2014). It remains unclear if weather in years at the onset or after invasion is a contingency for how the rest of the forest community responds. The first year of our study (2005) when EAB arrived was dry. This was followed by a dry, warm spring (9.2°C average daily high in February through April, 1.5–2.6°C warmer than any other study year) and wet summer in 2006 and near average precipitation in 2007 (Online Resource 1). After increasing during these weather conditions in the first three years of EAB establishment (2005–2007), understory plant cover declined in the fourth year (2008), which had a wet spring and summer. Flooded conditions that year likely limited understory plant cover owing to standing water (Kozlowski 1984). Although plant cover fluctuated through time, collectively climate and hydrological conditions apparently did not change sufficiently to produce shifts in floristic quality or composition of plants indicative of wetland conditions.

It is possible but uncertain that changes in soil properties could accompany EAB invasion and subsequent vegetation changes. Green ash foliage is higher in lignin and lower or similar in nitrogen compared to many replacement tree species such as red maple (*Acer rubrum*; Ricklefs and Matthew 1982). Removal of ash could thus theoretically correspond with long-term increases in litter quality and soil nitrogen mineralization (Scott and Binkley 1997). However, nutrient cycling could also be affected by shifts in soil fungal composition. *Fraxinus* is associated with arbuscular mycorrhizal fungi while residual tree genera such as *Carpinus*, *Fagus*, and *Tilia* are associated with ectomycorrhizal fungi (Phillip et al.

2013). Additionally, nutrient immobilization from decomposing coarse woody debris from dead ash could affect soil processes in EAB-aftermath forests (Higham et al. 2017).

Herbivory by densely populated white-tailed deer (*Odocoileus virginianus*) is known to be affecting eastern North American forests (e.g., Asnani et al. 2006; Jenkins et al. 2015) and could have influenced forests before and after EAB's arrival. While estimates of deer populations were not available for our study area, deer density ranged from 8–22/km^2 from 2010 to 2018 in floodplain forests at Swan Creek Metropark, 17 km west of our study area (Metroparks Toledo, Toledo, Ohio, USA). Surveys there found that 57% of ash seedlings, 12% of red maple, and 43% of shrubs showed evidence of browsing. Several of the understory species in our study – such as poison ivy, wild ginger, and spicebush – that were abundant after EAB arrived were also ones that increased by 12 years after protection from deer herbivory in a northeastern Ohio study (Asnani et al. 2006). Similarly, across state parks in Indiana, the density of native shrubs (e.g., spicebush) and tree saplings (including ash) quadrupled between 1997 and 2010 after deer density declined (Jenkins et al. 2015). Following EAB invasion in our study, we did not observe increases of this magnitude in small-tree density ($\geq 1 < 10$ cm in diameter) or cover of tree seedlings and shrubs. It is uncertain but possible that deer herbivory tempered understory response to EAB canopy disturbance, including for measures such as species richness or floristic quality if sensitive species were limited by herbivory or already removed from local species pools.

Maintenance of vegetation functional integrity

From a perspective of native ecosystem conservation under EAB invasion, the observed understory changes were probably as favorable as could be hoped for. Instead of possible dramatic changes from increases of non-native or invasive native plants as has occurred in forests after other recent pests such as hemlock woolly adelgid (*Adelges tsugae*; e.g., Abella 2018), in forests dominated by non-native plants when introduced insects arrive (Wavrek et al. 2017), and in forests disturbed by cutting for attempted EAB quarantine (Hausman et al. 2010), changes in our study predominately were increases in native species already present. This translated into no loss of wetland species nor declines in floristic quality. Nevertheless, the loss of ash basal area has yet to be replaced by other tree species even 14 years after EAB invasion.

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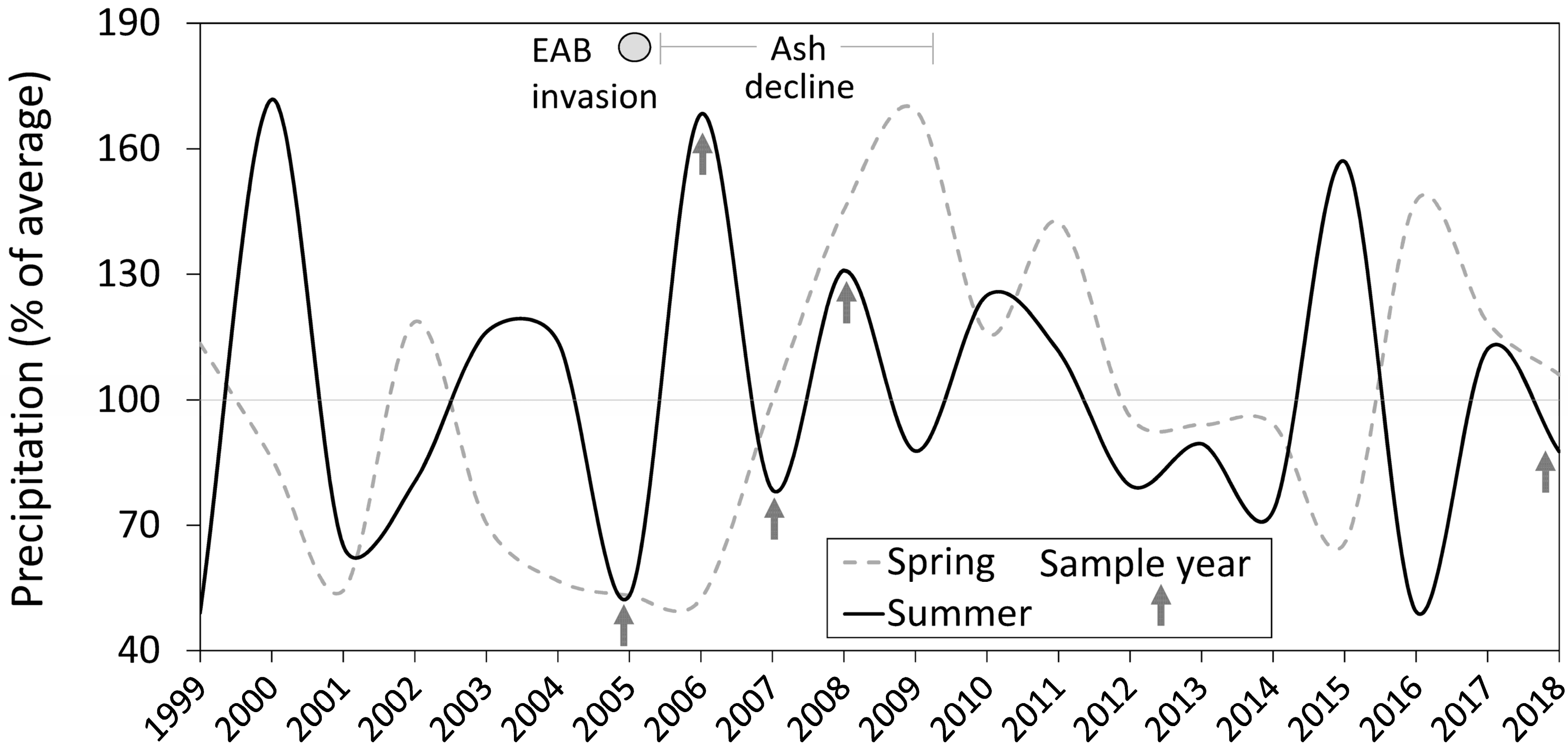
Online Resource 1 Precipitation and key events during a 14-year study of forest dynamics from the onset of emerald ash borer invasion in 2005 through the most recent measurement year of 2018 in the Great Black Swamp, northwestern Ohio, USA. After 2-5 years of decline, mature green ash (*Fraxinus pennsylvanica*) on plots were dead by 2010. Precipitation, separated into spring (February through April) and summer (May through July, preceding or during sampling), is expressed as a percent of the average spring (18 cm/year) and summer (26 cm/year) precipitation for the available period of record (1999-2018). Total annual precipitation averaged 82 cm/year for the period of record. Precipitation was recorded at the Toledo Metcalf Field, 190 m in elevation and 10 km southwest of the study area (National Oceanic and Atmospheric Administration, Washington, D.C., USA)



Online Resource 2 Means and standard errors of means for basal area (m^2/ha) of 22 taxa of live trees recorded in five study years from the onset of emerald ash borer invasion (2005) to 14 years later (2018) in the Great Black Swamp, northwestern Ohio, USA

		2005		2006		2007		2008		2018	
Scientific name	Common name	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Acer negundo	boxelder	1.953	0.815	1.749	0.870	1.638	0.828	1.783	0.784	0.903	0.471
Acer nigrum	black maple	0.019	0.019	0.038	0.026	0.037	0.027	0.046	0.032	0.105	0.070
Acer rubrum/saccharinum	red/silver maple[a]	15.362	4.680	15.833	4.846	16.160	4.925	16.349	4.867	16.705	5.984
Acer saccharum	sugar maple	0.007	0.007	0.025	0.017	0.027	0.018	0.011	0.011	-	-
Aesculus glabra	Ohio buckeye	0.003	0.003	0.006	0.006	0.006	0.006	0.007	0.007	0.011	0.011
Asimina triloba	pawpaw	0.114	0.114	0.114	0.114	0.036	0.036	0.130	0.130	0.094	0.094
Carpinus caroliniana	musclewood	0.026	0.020	0.029	0.025	0.018	0.013	0.035	0.018	0.036	0.021
Carya cordiformis	bitternut hickory	0.004	0.004	0.034	0.032	0.077	0.074	0.031	0.024	0.066	0.060
Carya glabra	pignut hickory	0.738	0.406	0.577	0.377	0.652	0.440	0.742	0.526	1.048	0.573
Carya laciniosa	shellbark hickory	-[b]	-	-	-	-	-	-	-	0.038	0.038
Carya ovalis	red hickory	-	-	-	-	-	-	-	-	0.005	0.005
Carya ovata	shagbark hickory	0.261	0.165	0.337	0.231	0.378	0.266	0.379	0.259	-	-
Cornus amomum	silky dogwood	-	-	0.002	0.002	0.002	0.002	0.018	0.010	-	-
Crataegus spp.		0.023	0.021	0.024	0.022	0.026	0.019	0.021	0.021	-	-
Fraxinus pennsylvanica	green ash	6.734	2.935	7.353	3.311	6.563	2.589	5.059	2.640	0.248	0.193
Malus coronaria	sweet crab apple	-	-	-	-	-	-	-	-	0.020	0.020
Populus deltoides	eastern cottonwood	2.354	1.759	2.411	1.788	2.508	1.850	2.546	1.870	2.906	2.303
Quercus bicolor	swamp white oak	0.181	0.181	0.193	0.190	0.197	0.194	0.200	0.197	-	-
Quercus rubra	red oak	2.888	1.956	3.111	2.105	3.231	2.211	3.257	2.216	4.556	3.078
Tilia americana	American basswood	3.309	1.324	3.636	1.569	3.417	1.446	3.624	1.728	3.845	2.114
Ulmus americana	American elm	0.008	0.008	0.251	0.239	0.279	0.266	0.274	0.260	0.436	0.373
Ulmus rubra	slippery elm	0.586	0.316	0.421	0.255	0.436	0.258	0.400	0.236	0.844	0.722

[a]Individuals displayed morphological characteristics of both species and could have been *Acer* × *freemanii* hybrids. The species were combined as one entity for calculating species richness and statistical analyses

[b]Absent from all five plots that year

Online Resource 3 Left column: repeat photos at a study plot from the onset (2005, top), during (2006, middle), and 14 years after (2018, bottom) invasion of emerald ash borer (EAB) in Great Black Swamp forests, Pearson Metropark, Ohio. The large *Fraxinus pennsylvanica* tree in the upper center of the 2005-2006 photos is dead and down by 2018, and the plot lost 18 m^2/ha of *Fraxinus* basal area between 2005 and 2018. The major increaser in the understory was the forb-vine *Parthenocissus quinquefolia*, which expanded from 20% cover in 2005 to 55% cover in 2018. Right column: example plot photos in 2018 showing a post-EAB forest with (top) an overstory of *Quercus rubra-Acer rubrum-Acer saccharinum-Tilia americana* and 3,220/ha *Fraxinus* saplings (1-2 cm in diameter at 1.4 m); (middle) *Fraxinus* downed logs and a forest understory dominated by *Lindera benzoin*, *Toxicodendron radicans*, *Parthenocissus*, and *Acer* seedlings; and (bottom) tall shrub layer of *Lindera* (45% cover) and herbaceous layer of *Parthenocissus*, *Hydrophyllum virginianum*, and *Geranium maculatum* below a residual overstory of *Acer*, *Carya glabra*, and *Ulmus rubra* after losing 6 m^2/ha basal area of *Fraxinus* after 2008. Photos by J.F. Jaeger (2005, 2006) and S.R. Abella (2018)

Online Resource 4 Statistical results for change in forest vegetation response variables across five years in which measurements were made during a 14-year period spanning the onset of emerald ash borer invasion (2005) to 14 years later (2018) in the Great Black Swamp, northwestern Ohio, USA. Statistics are for repeated measures analysis of variance (degrees of freedom: 4, 16), with $P < 0.05$ in bold

	F-statistic	P-value
Large trees (≥ 10 cm diameter)		
Fraxinus pennsylvanica trees/ha	4.86	**0.009**
Other species trees/ha	1.82	0.174
Fraxinus pennsylvanica basal area	4.05	**0.019**
Other species basal area	0.83	0.525
Small trees (≥ 1 < 10 cm diameter)		
Fraxinus pennsylvanica trees/ha	0.78	0.552
Other species trees/ha	5.02	**0.008**
Fraxinus pennsylvanica basal area	1.21	0.345
Other species basal area	1.96	0.149
Understory cover		
Native	3.89	**0.022**
Non-native	2.47	0.087
Understory species richness		
Native	8.46	**<0.001**
Non-native	1.48	0.255
Understory wetland indicators		
Wetland species cover	2.49	0.085
Wetland species richness	6.43	**0.003**
Species wetland index	0.09	0.989
Floristic quality		
Floristic quality index	2.58	0.077
Cover of individual understory species		
Arisaema triphyllum	3.09	**0.046**
Asarum canadense	2.53	0.081
Boehmeria cylindrica	1.21	0.347
Fraxinus pennsylvanica	0.74	0.579
Geranium maculatum	1.06	0.408
Lindera benzoin	3.90	**0.021**
Parthenocissus quinquefolia	4.48	**0.013**
Polygonum virginianum	2.08	0.131
Toxicodendron radicans	2.82	0.060