



# Species and landscape variation in tree regeneration and 17 years of change in forested wetlands invaded by emerald ash borer

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## ABSTRACT

Understanding variation in tree regeneration among species and sites, and how well forest size class distribution (seedlings, saplings, and trees) portends long-term species compositional change, may assist managing forests during contemporary global change rapidly altering forests, such as after invasion by introduced pests. In northwestern Ohio, one of the North American regions longest invaded by emerald ash borer (EAB, *Agrilus planipennis*), we 1) examined variation in size class abundance among tree species and sites in 22 forested wetlands in 2018 and 2021; and 2) assessed how closely size class distribution of tree species in 2005, at the onset of EAB invasion before *Fraxinus* trees died, forecasted observed forest change during the next 17 years. In 2018 and 2021, three major groups of tree species emerged with respect to their frequency across size classes: 1) species commonly in all three, or at least two, size classes on a site, 2) species frequent in only one size class, which varied but was often seedlings, and 3) species almost always present only as trees, with little advance regeneration. Shade tolerance correlated with species occurring in all three size classes. Among sites in 2018 and 2021, abundance of regeneration and similarity of species composition across size classes varied between years (largely from fluctuations in seedlings) and with site factors. Sites with the least regeneration had high soil available water capacity and high cover of graminoids. On long-term sites after the onset of EAB invasion in 2005, all seedling-to-sapling and sapling-to-tree advancements recorded through 2021 were from species already present in 2005, and only shade-tolerant species (e.g., *Ulmus americana*) advanced. Results suggest that there is substantial variation in advance regeneration availability among species and sites in forested wetlands across the EAB-invaded landscape. Portions of this variability were structured into well-demarcated groups of similarly responding species and sites, were associated with species traits such as shade tolerance and site factors such as soil texture, and were prognostic of forest changes within the first two decades after EAB invasion.

## 1. Introduction

Tree regeneration is a fundamental component of forest ecology and management with new knowledge of regeneration continually needed as environmental conditions and forest composition changes, such as during contemporary global change including pervasive biological invasions (Miller et al., 2023). At any point in time, a mature forest can have varying quantities and composition of tree species individuals in three main size classes: seedlings (smallest individuals, sometimes including short sprouts), saplings (subcanopy stems), and trees (largest individuals usually in intermediate to dominant canopy positions; Morris et al., 2023). Seedlings and saplings are often termed advance

regeneration, as they are already available for potential growth release if disturbance creates canopy gaps in mature forests (Dolan and Kilgore, 2018; Marshall, 2020). A given tree species in a forest could be present in only one size class, combinations of two size classes, or in all three. Occurrence in all three could indicate continuous recruitment potential if advancements across size classes and replenishments occur (Guyon and Battaglia, 2018). Occurrence of a species in just one or two of the size classes could suggest a bottleneck and potential regeneration failure under status quo conditions, such as if adults occur with seedlings not advancing to saplings (Boyce, 2012). Size class occurrence of tree species in forests can relate to interactions of site conditions with many species traits, such as shade or flood tolerance, seed size affecting

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dispersal or ability to penetrate litter layers, mycorrhizal associations, and susceptibility to herbivory (Clark et al., 1999).

Among sites across a landscape, multiple types of metrics can aid characterizing potential regeneration status based on forest size classes. For example, quantities of seedlings or saplings – without regard to species – can indicate potential for a forest to sustain density of some species or mixtures, albeit potentially deviating from those currently in the canopy (Burr and McCullough, 2014). Focusing on species composition, proportions of a forest's tree species occurring in all three size classes or a combination of them can identify potential regeneration mismatches, such as if a site has different species in the sapling layer than in the overstory (Dollar et al., 1992; Johnson and Waller, 2013; Guyon and Battaglia, 2018).

As with traits of species such as shade tolerance, many site factors could influence a forest's size class distribution and its dynamics. For example, especially dry or wet soil could hinder seed germination and seedling growth, limiting seedling layer formation and potentially making forest regeneration episodic or at risk of failure (Evans et al., 2022). Degree of herbivory or competition from understory plants, such as graminoids or non-native shrubs (Walters and Williams, 1999; Hoven et al., 2022), are examples of additional site factors potentially influencing forest size classes and regeneration.

For assessing potential for regeneration and forest change, the abundance and species composition of seedling and sapling layers are often compared with the tree layer (Miller and McGill, 2019). One of the most widely proposed models of forest change in mature, temperate forests is gap-phase regeneration whereby change occurs in dynamic small gaps from the death of individual or small groups (such as 2–3 individuals) of canopy trees (e.g., Cho and Boerner, 1991; Cook, 2005; Dolan and Kilgore, 2018). In this model, advance regeneration present before canopy gaps form is a driver of change, interacting with species' shade tolerances. Shade-tolerant species are proposed to fill the small gaps, the dominant form of disturbance. Gaps larger than the typical 1–3 trees would be required to support recruitment of light-demanding species, assuming advance regeneration or new colonization occurred (Cowell et al., 2010).

Assessing whether, or for what species and site conditions, size class analyses at a point in time can portend subsequent forest change continues to be a major focus in the contemporary era of often rapid forest change (e.g., Costilow et al., 2017; Saladyga et al., 2020; Evans et al., 2022). One such example is the widespread invasion of forests by introduced pests, such as insects and diseases. In mixed-species forests, introduced pests can selectively remove dominant tree species, creating gaps abruptly or gradually of uncertain similarity to natural patterns (Marks, 2017). Moreover, the pest-afflicted tree species could formerly have had a major role in a forest's regeneration, so loss or alteration (e.g., by affecting certain size classes) of the pest-afflicted tree species could change forest regeneration dynamics (Morris et al., 2023).

Using forested wetlands invaded by emerald ash borer (EAB, *Agrilus planipennis*) as a model system, we examined tree species- and site-focused size class distribution within a landscape (northwestern Ohio, USA) among the first (and thus longest) invaded by EAB in North America (Hausman et al., 2010; Knight et al., 2012a; Costilow et al., 2017). The introduced EAB, a wood-boring beetle originally from Asia, was first described in North America in 2002 in southeastern Michigan and southern Ontario, just north/northeast of our study landscape (Klooster et al., 2018). North American *Fraxinus* species are susceptible by varying degrees to the beetles, which killed up to 90–100% of local populations of the most susceptible species, *Fraxinus pennsylvanica*, over 2 cm in stem diameter at 1.4 m (hereafter diameter) as the initial invasion moved through in the 2000 s (e.g., Aubin et al., 2015; Kreutzweiser et al., 2020; Siegert et al., 2021). We also extended a unique dataset, collected beginning in 2005 at the onset of EAB invasion before *Fraxinus* trees died, to evaluate how well composition of seedling and sapling layers matched actual forest change through 2021. We examined the following questions: 1) Do size class distributions vary among tree

species across the landscape and if so, is the variation correlated with species traits such as shade tolerance? 2) Are certain size classes (e.g., seedlings) more widely distributed across the landscape? 3) Do sites exhibit lack of regeneration or species compositional mismatches across size classes, and is variation associated with site factors such as soils and understory vegetation? and 4) Does similarity of species composition across forest size classes change from the onset through 17 years after EAB invasion?

## 2. Materials and methods

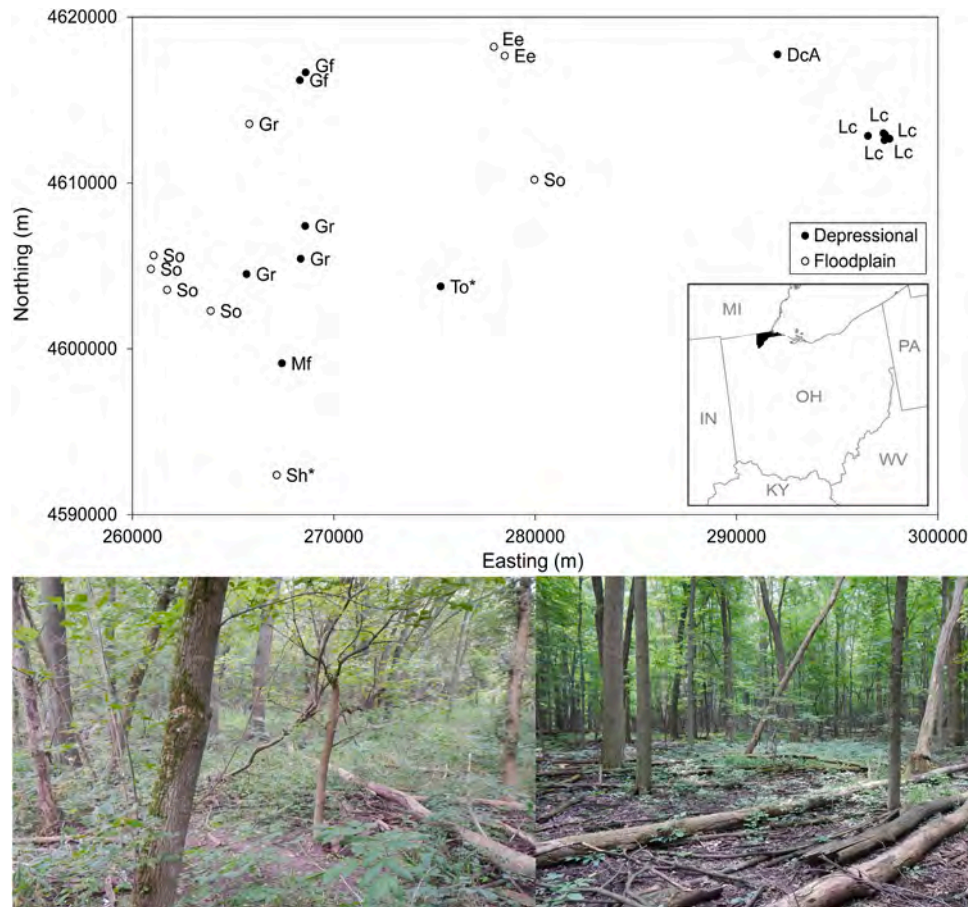
### 2.1. Study area

We performed the study in Lucas County, northwestern Ohio, USA, within a 30 km × 40 km area (Fig. 1). Climate is temperate, averaging 86 cm/yr of precipitation and daily temperature ranges of – 8–0 °C in January and 17–29 °C in July (Toledo Airport station; National Centers for Environmental Information, Asheville, NC). Forested wetlands, the focus of our study, occur in this area along floodplains of rivers and streams (e.g., Maumee River, Swan Creek) and as depressional wetlands in low-lying areas (Abella et al., 2021). The wetlands we studied in protected areas were bordered primarily by upland forest (typically dominated by *Quercus velutina* and *alba*) and mesic, but not flooded, forest with mixed hardwoods such as *Carya* spp. and *Juglans nigra*. The onset of EAB invasion in our study area is considered to be 2005, with most decline and mortality of *Fraxinus pennsylvanica* (the major *Fraxinus* in our study area's wetlands) proceeding from 2006 to 2008 (Hausman et al., 2010; Knight et al., 2012a; Costilow et al., 2017). Each of our study plots described below contained dead *Fraxinus* trees as snags or fallen logs, where *Fraxinus* had been a co-dominant in similar proportion (~10–30% of basal area) in mixed-species forests (Fig. 1).

### 2.2. Data collection

In 2018, 14 years after EAB invasion, we used 1940 aerial photographs and field reconnaissance to identify areas of mature wetland forest ( $\geq \sim$  age 70 years and containing trees  $\geq$  40 cm diameter) in Metroparks Toledo preserves throughout the study area. Metroparks Toledo manages the largest area (5237 ha) of preserves in the study area, and the mature wetland forests we studied had been under protection management (e.g., no timber harvest) since at least Metroparks acquisition of the properties beginning as early as the 1930 s. We randomly established 17 permanent plots in mature forests across the study area in floodplain and depressional wetlands and sampled them in summer (late June through August) in 2018 and again in 2021 (Fig. 1). In summer 2018 and 2021, we also remeasured five long-term plots originally sampled in 2005 (onset of EAB invasion but before *Fraxinus pennsylvanica* mortality) and annually from 2006 to 2008 during tree decline and mortality (Hausman et al., 2010). With the 17 recent and 5 long-term plots, in total we sampled 22 plots all using the same methods consistently through time and with continuity of investigators (authors of this paper).

In each 20 m × 25 m (0.05 ha) plot, we recorded the species and measured the diameter of each individual  $\geq$  1 cm diameter for tree species. Using cover categories (0.1, 0.25, 0.5, 1%, 1% intervals to 10%, and 5% intervals to 100% cover, the maximum a species could attain on a plot), we visually recorded areal cover of vascular plant species rooted in plots by species for trees < 1 cm diameter (hereafter referred to as seedling size) and grouped as native or non-native graminoid, forb, shrub, vine, or fern. We followed the taxonomy, growth form, and native/non-native (to North America) classification of the PLANTS Database (NRCS, 2023). Particularly for small seedlings lacking fully developed leaves, we did not always separate *Acer saccharinum* and *rubrum*, which can hybridize into *Acer × freemanii* (Blood et al., 2010), and *Carya* species, so we present these taxa on a genus level. For species traits involving quantitative values described below, we averaged values



**Fig. 1.** Locations of 22 study sites in forested wetlands within a 30 km × 40 km region in northwestern Ohio, USA, where we examined forest changes after invasion by emerald ash borer. Each point denotes a plot, classified according to wetland type and soil series (DcA, Del Rey complex; Ee, Eel loam; Gf, Gilford fine sandy loam; Gr, Granby loamy fine sand; Lc, Latty silty clay; Mf, Mermill loam; Sh, Shoals loam; So, Sloan loam; To, Toledo silty clay). Example photos of plots (\* in the map) in depressional and floodplain wetlands are also included and show fallen *Fraxinus pennsylvanica* trees (photos by S.R. Abella, 2017). A set of five of the plots (all with Lc soils) on the top right of the map had data of forest conditions at the onset (2005), during (2006–2008), and in the second decade after (2018, 2021) *Fraxinus* mortality.

for *A. saccharinum* and *rubrum*. For *Carya*, we used *Carya laciniosa* as this predominated on our plots. From the NRCS Web Soil Survey application incorporating the county soil survey (Stone et al., 1980), for each plot we obtained the soil taxonomic classification (series level), texture (% sand, silt, and clay), organic matter (% weight), available water holding capacity ( $\text{m}^3/\text{m}^3$ ), and pH (1:1 soil:H<sub>2</sub>O) for 0–15 and 15–50 cm mineral soil depths.

We obtained data for tree species traits from published literature (Table S1). From rankings for Ohio flora in Andreas et al. (2004), we obtained species' affinity for wetlands (ranked from 1, upland, to 5, obligate wetland) and coefficient of conservatism, a metric ranking species' habitat specificity (ranging from 1, generalists with broad habitat ranges, to 10, specialists with narrow habitat requirements). We obtained shade, drought, and flood tolerance, each ranked from 1 (intolerant) to 5 (most tolerant), from Ninemets and Valladares (2006). From the Seed Information Database (SER-INSR-RBGK, 2023), we obtained mean seed weight (mg) for each species. From multiple papers, we synthesized seed dispersal vectors (non-mutually exclusive wind, water, gravity, and animal, each coded as 1 for utilized and 0 for not) and timing of seed dispersal as primarily spring (coded as 1), summer (2), or winter (3; McKnight et al., 1980; Battaglia et al., 2002; Bonner and Karrfalt, 2008; Diggins, 2013). We compiled tree species-mycorrhizal associations (arbuscular, ectomycorrhiza, or both for *Populus deltoides*) from Phillips et al. (2013). We classified species on a relative basis as generally preferred, neutral, or non-preferred forage by white-tailed deer (*Odocoileus virginianus*), the study area's major large

herbivore, based on Dahlberg and Guettinger (1956), Abella et al. (2022), and Sample et al. (2023).

### 2.3. Data analysis

For statistical analyses, we subdivided occurrences of tree species by size classes: seedlings (< 1 cm diameter; represented as % cover), saplings ( $\geq 1 < 10$  cm diameter; saplings/ha), and trees ( $\geq 10$  cm diameter; trees/ha). These size classes include those commonly used for regeneration studies in temperate forests, including wetlands, as they are both convenient breakpoints and ecologically significant by representing key transitions during a tree's life history (Cho and Boerner, 1991; Walters and Williams, 1999; Cowell et al., 2010). The 1-cm-diameter cutoff can represent a transition from seedling to sapling, often a bottleneck in growth advancement of temperate trees (Evans et al., 2022). Growth above the 10-cm-diameter cutoff often represents accession above the sub-canopy to at least an intermediate position in the lower canopy of a mature temperate forest (Cowell et al., 2010; Costilow et al., 2017; Morris et al., 2023). An issue arising in regeneration studies by size class is handling small-statured tree species (Miller and McGill, 2019). In our study, such species (e.g., *Crataegus crus-galli*) were infrequent but some did have individuals exceeding 10 cm diameter and thus able to display advancement to the largest size class (Table S2). Consequently, though their infrequency made them only a minor part of the results, we retained these species in the dataset.

Using the size class data from all 22 plots measured in 2018 and 2021

and the earlier years of the long-term plots, we prepared plot  $\times$  tree species matrices on which we performed tree species- and plot-focused ordination and classification multivariate analyses detailed in Table 1. Species-focused analyses ordinated or grouped species relative to their similarity to each other in occurrence or abundance among plots. Complementing this analysis, we tested a null hypothesis of equal frequency of occurrence across all seven size class combinations (each of the three size classes individually and each combination therein) using Chi-square goodness of fit tests for 2018 and 2021. Plot-focused analyses ordinated or grouped the plots relative to their compositional similarity to each other using the metrics in Table 1. The species- and plot-focused analyses concentrated on different features of variation: how similar tree species were in their size class distribution in the species-focused analyses, and how similar groups of plots were in their forest size class distribution with and without regard to their species composition in the plot-focused analyses.

We computed ordinations, cluster analyses, and Sørensen similarity in PC-ORD 7.07 (McCune and Mefford, 1999). For all ordinations, we used Bray-Curtis ordination (variance-regression endpoint selection, Euclidean distance and projection geometry), as this returned solutions representing at least 50–75% of the variance in axes 1–2. We input tree species traits and soil and understory vegetation (e.g., cover of native graminoids) variables in ordinations as potential correlates with community patterns. For cluster analyses, we used Ward's group linkage method (Euclidean distance) with a minimum of four plots per group, typically resulting in stopping splitting at a three-group level.

To analyze the long-term plots, we calculated species compositional similarity (Sørensen index), with and without *Fraxinus* (all *F. pennsylvanica*) included, of seedlings compared with saplings and saplings compared with trees in 2005 (onset of EAB invasion) and of 2005 composition with that of subsequent years (2006–2008, 2018, 2021). We then compared mean similarity across years using repeated measures analysis of variance and Tukey tests, in addition to compiling the number of instances each species advanced across size classes on each

**Table 1**

Summary of data matrices used in statistical analysis of distribution of size classes (seedlings, < 1 cm diameter at 1.4 m; saplings,  $\geq 1 < 10$  cm; and trees,  $\geq 10$  cm) for tree species in 2018 and 2021 and for long-term change spanning the onset of emerald ash borer invasion (2005) through 17 years later (2021) in forested wetlands containing *Fraxinus* trees, Ohio, USA.

Analysis	Data matrix <sup>b</sup>	Figure
2018, 2021 data <sup>a</sup>		
Species-focused size class occurrence	Species $\times$ 7 size class combinations, relativized frequencies	2
Frequency of size class occurrence across all species	Frequency of occurrence in 7 size class combinations	S1
Plot-focused size class occurrence of species	Plot $\times$ 7 size class combinations, relativized frequencies	3
Plot-focused species composition similarity among size classes	Plot $\times$ 3 size class comparisons, ranked Sørensen similarities	4
Plot-focused size class abundance	Plot $\times$ 3 size classes, ranked cover (seedlings) and density (saplings, trees)	5
Long-term 2005–2021 data		
Size class similarity in 2005 and 2005 with later years	Plot-years $\times$ size class abundance, with and without <i>Fraxinus</i> included	6

<sup>a</sup> For analyses of 2018 and 2021 data from 22 plots, only species recorded in at least four plots within a year were included in matrices analyzed using cluster analysis and ordination (all species were included in the analysis of frequency of size class occurrences across all species using Chi-square goodness of fit).

<sup>b</sup> Relativized measures factored out differences in total abundance or frequency within a size class to isolate species composition, by expressing measures as a proportion of species (for the species-focused analysis) or plot totals. For the analysis of plot-focused species composition, seedling cover and sapling and tree density were relativized by plot totals before Sørensen index computation. Ranked measures assigned plots numerical values between 1 and 22 from low to high.

plot.

### 3. Results

#### 3.1. Species-focused analyses: variation in tree species among size classes in 2018 and 2021

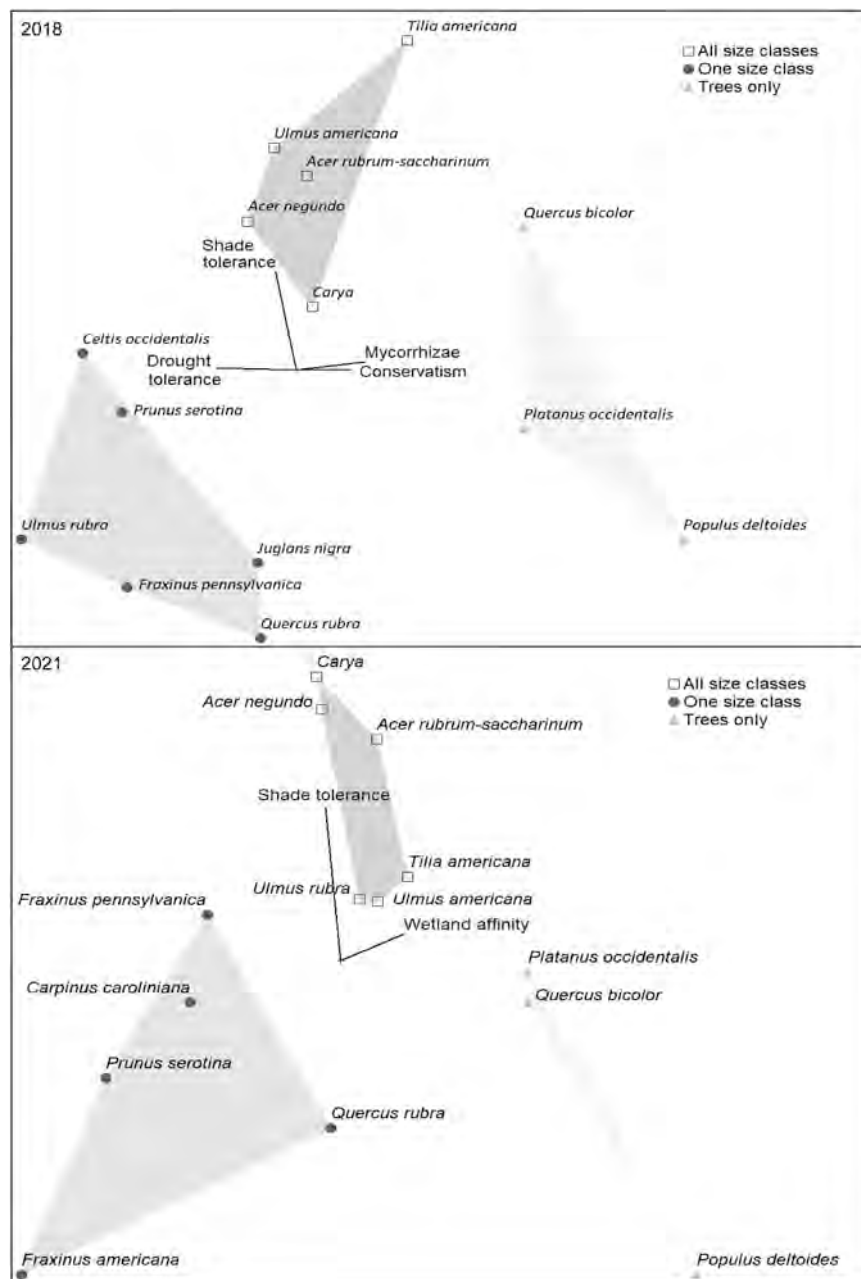
On the 22 plots in 2018 and 2021, three groupings of tree species emerged with respect to their frequency of occurrence among seedling, sapling, and tree size classes: 1) species commonly in all three, or at least two, size classes on a plot (*Acer rubrum*, *saccharinum*, and *negundo*; *Ulmus americana*, *Tilia americana*, and *Carya*); 2) species commonly present in just one of the size classes on any given plot but in any of the three size classes among plots (*Quercus rubra*, *Fraxinus pennsylvanica*, *Juglans nigra*, *Prunus serotina*, *Celtis occidentalis*, and *Carpinus caroliniana*); and 3) species nearly always occurring only as trees, with seedlings and saplings absent (*Platanus occidentalis*, *Populus deltoides*, and *Quercus bicolor*; Fig. 2). In both years, increasing shade tolerance correlated with species occurring simultaneously in all three size classes on a plot. Although not all species arranged on the center and right side of the species ordinations have associations with ectomycorrhizae, the ectomycorrhizal taxa (*Carya*, *Quercus*, *Tilia*, and a species colonized by both types, *P. deltoides*) were concentrated there, the only exception being the ectomycorrhizal *C. caroliniana* (Fig. 2). Increasing coefficient of conservatism, signifying narrower habitat requirements, was associated with species occurring mainly only as trees in the 2018 ordination, notably *Q. bicolor* and *P. occidentalis*, both with coefficients of conservatism of 7.

Species occurrence as only seedlings or trees was more frequent in both 2018 and 2021 than under a null distribution of equal occurrence across size class combinations ( $\chi^2 = 38.9$ ,  $P < 0.001$  for 2018;  $\chi^2 = 21.1$ ,  $P = 0.002$  for 2021; Fig. S1). Occurrence simultaneously as both seedlings and trees in 2018 and occurrence as only saplings in 2021 was less frequent.

#### 3.2. Plot-focused analyses: landscape variation in forest size classes in 2018 and 2021

Plots separated into three groups based on size class occurrences of their constituent tree species: 1) plots containing a high proportion of species present as saplings, with or without seedlings and large trees also present depending on the species; 2) plots with few species occurring as saplings and with most species present as seedlings, trees, or both; and 3) plots with many species present mainly as trees and proportionately few as seedlings or saplings (Fig. 3). In the 2018 ordination, plots containing few species as saplings and most present only as seedlings or trees were correlated with high native graminoid cover and soil water holding capacity. Soils with higher pH and clay textures were associated with plots containing many species present only as trees. In the 2021 ordination, native graminoid cover was correlated with plots containing many species present only as trees, while high soil organic matter correlated with subsets of plots containing many species present as saplings or as seedlings as well as trees.

Considering species compositional similarity (Sørensen index) between each pair of size classes (seedlings:saplings, seedlings:trees, and saplings:trees), plots in 2018 formed three groups: 1) high similarity of species composition across all three size classes, 2) dissimilar species composition among size classes or only saplings:trees similar, and 3) dissimilar species composition among size classes or only seedlings:trees similar (Fig. 4). Plots with high species compositional similarity among size classes were associated with sandy soils. Subsets of plots dissimilar in composition across size classes or with only saplings:trees similar were associated with silty soils high in available water capacity, high pH, and high native graminoid cover. In 2021, plots grouped into those with: 1) similar species composition across size classes, 2) high seedling:sapling similarity, and 3) dissimilar size classes or only similarity of either seedlings or saplings with trees. Native graminoid cover was

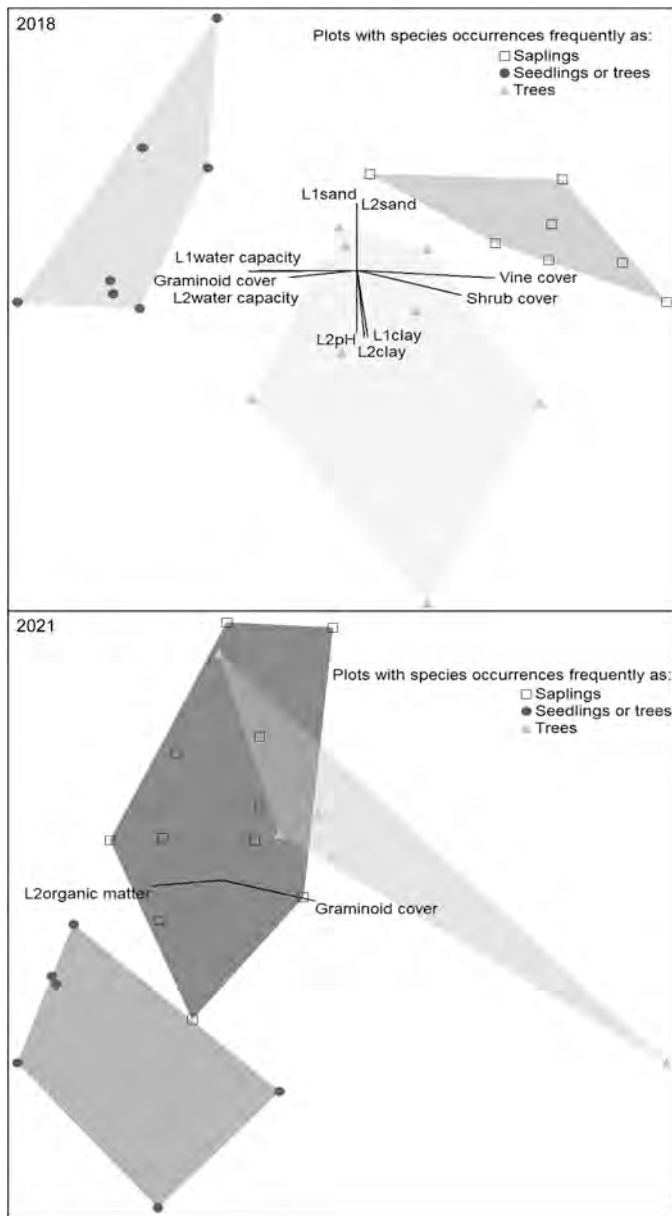


**Fig. 2.** Ordination and classification of tree species according to their frequency of occurrence as seedlings (< 1 cm diameter at 1.4 m), saplings ( $\geq 1$  cm < 10 cm), and trees ( $\geq 10$  cm) 14 (2018) and 17 (2021) years after invasion by emerald ash borer in forested wetlands in Ohio, USA. In the ordinations, species groupings from cluster analysis are shown as convex hulls. Three groups of species were evident, including those mainly occurring in all size classes of seedlings, saplings, and trees on any given plot; in just one of the size classes on any given plot but in any of the three size classes among plots; and as trees only, with seedlings and saplings usually absent. Only species occurring in at least 4 of the 22 study plots are included. Correlations of species traits (e.g., shade tolerance) displaying  $r^2$  values of at least 0.15 with species distributions in the ordinations are shown as vectors. In the 2018 ordination, axis 1 extracted 46% of the variance and axis 2 17% (63% cumulatively). In the 2021 ordination, axis 1 extracted 51% of the variance and axis 2 22% (73% cumulatively).

correlated with a subset of plots dissimilar in species composition among size classes.

Based on total cover of seedlings and quantities of saplings and trees without regard to their species composition, plots in 2018 formed three groups including plots containing: 1) few seedlings and trees but many saplings, 2) many seedlings and trees but few saplings, and 3) especially low amounts in one and often multiple size classes (Fig. 5). Plots containing many saplings were often in depressional wetlands, rather than on floodplains. High soil water holding capacity and native graminoid cover were correlated with plots containing low amounts in one or more size classes. In 2021, average total seedling cover declined to 5% (from

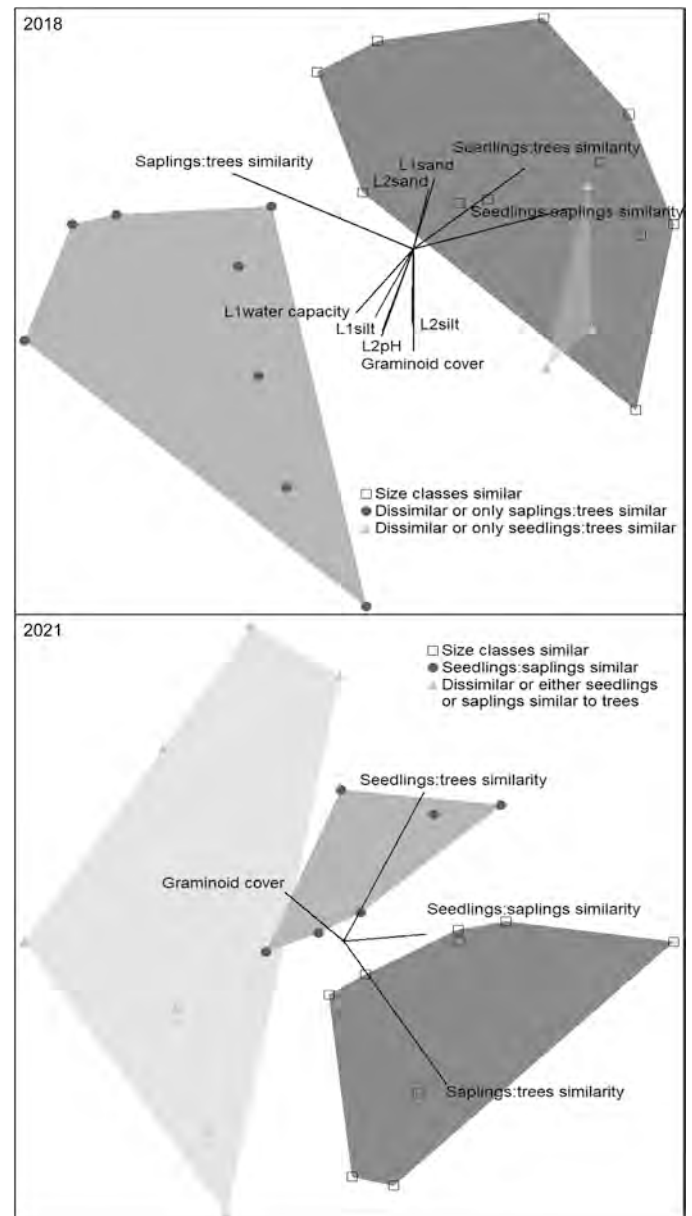
8% in 2018), as some plots that had high (> 20%) seedling cover in 2018 decreased to < 2% cover in 2021. Largely as a result of change in seedling cover, groupings of plots in 2021 shifted to three main groups including plots containing: 1) variable amounts of seedlings and saplings but many trees; 2) moderate seedling cover, many saplings, and few trees; and 3) few seedlings and saplings under low-moderate densities of trees. Similar to in 2018, plots in 2021 with low amounts in all size classes were correlated with high native graminoid cover and soil water holding capacity.



**Fig. 3.** Ordination and classification of 22 study plots according to containing tree species occurring predominately as seedlings (< 1 cm diameter at 1.4 m), saplings (≥ 1 cm < 10 cm), and trees (≥ 10 cm) 14 (2018) and 17 (2021) years after invasion by emerald ash borer in forested wetlands in Ohio, USA. In the ordinations, plot groupings from cluster analysis are shown as convex hulls. Three groups of plots were evident, including those mainly containing species frequently occurring as saplings, just as seedlings and trees, and as trees. Correlations of biophysical variables (e.g., soil available water holding capacity in the 0–15 cm [L1] and 15–50 cm [L2] depths) displaying  $r^2$  values of at least 0.20 with plot distributions are shown as vectors. The understory vegetation variables, such as shrub cover, were all for native species as no non-native understory variables met the  $r^2$  criterion. In the 2018 ordination, axis 1 extracted 36% of the variance and axis 2 24% (60% cumulatively). In the 2021 ordination, axis 1 extracted 29% of the variance and axis 2 21% (50% cumulatively).

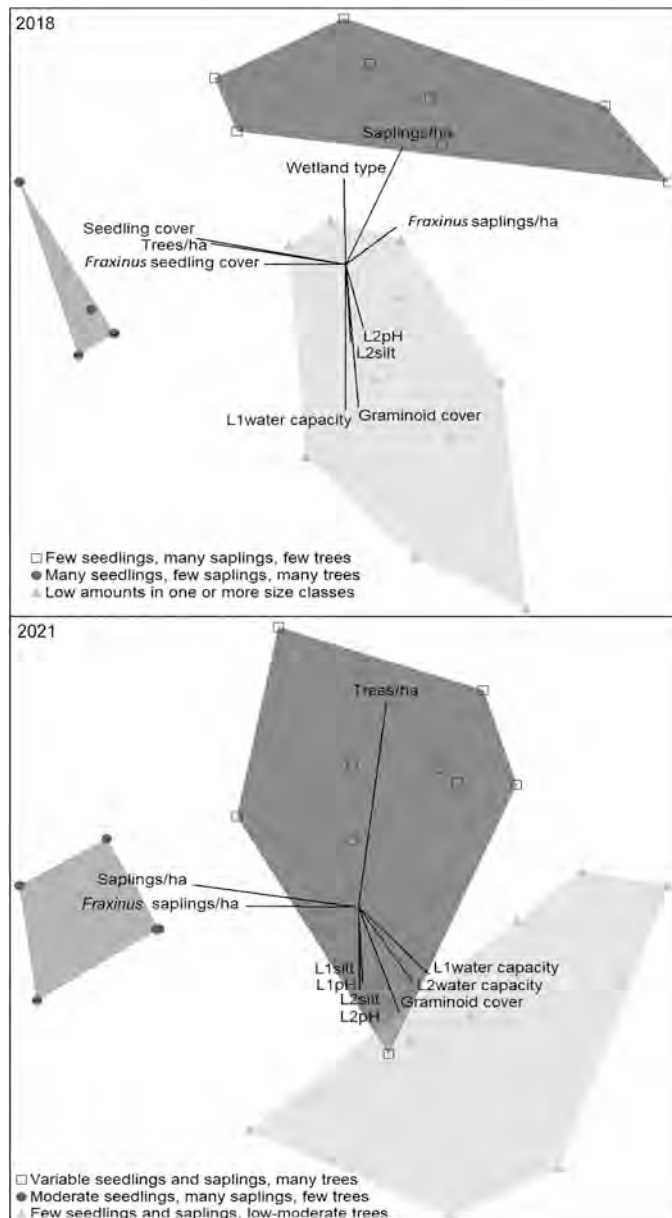
### 3.3. Forest change on long-term plots

Across repeated measures spanning the onset of EAB invasion in 2005 through 17 years later in 2021, there was no statistically significant change in similarity of 2005 species composition with later years between seedlings and saplings and between saplings and trees in the



**Fig. 4.** Ordination and classification of 22 study plots according to their Sørensen similarity of species composition between size classes of tree species for seedlings (< 1 cm diameter at 1.4 m), saplings (≥ 1 cm < 10 cm), and trees (≥ 10 cm) 14 (2018) and 17 (2021) years after invasion by emerald ash borer in forested wetlands in Ohio, USA. In the ordinations, plot groupings from cluster analysis are shown as convex hulls. Three groups of plots were evident each year according to similarity of species composition between size classes, and the characteristics of the groups differed in one or more ways between years. Correlations of biophysical variables (e.g., soil pH in the 0–15 cm [L1] and 15–50 cm [L2] depths) displaying  $r^2$  values of at least 0.20 with plot distributions are shown as vectors. The understory vegetation variable of graminoid cover is for native graminoids. In the 2018 ordination, axis 1 extracted 45% of the variance and axis 2 30% (75% cumulatively). In the 2021 ordination, axis 1 extracted 37% of the variance and axis 2 33% (70% cumulatively).

forest community when *Fraxinus* was excluded from the analysis ( $F_{5, 20} = 0.9$ ,  $P = 0.475$  for seedlings:saplings;  $F_{5, 20} = 1.5$ ,  $P = 0.249$  for saplings:trees; Fig. 6). When *Fraxinus* was included, seedling:sapling similarity of 2005 with later years also did not change through time ( $F_{5, 20} = 0.9$ ,  $P = 0.514$ ). However, sapling:tree similarity declined ( $F_{5, 20} = 5.5$ ,  $P = 0.002$ ). By 2018 and 2021, mortality of all *F. pennsylvanica* trees ≥ 10 cm diameter, but persistence or growth of *F. pennsylvanica* saplings



**Fig. 5.** Ordination and classification of 22 study plots according to their abundance of seedlings (< 1 cm diameter at 1.4 m), saplings ( $\geq 1$  cm < 10 cm), and trees ( $\geq 10$  cm) 14 (2018) and 17 (2021) years after invasion by emerald ash borer in forested wetlands in Ohio, USA. In the ordinations, plot groupings from cluster analysis are shown as convex hulls. Three groups of plots were evident each year according to the relative abundance of size classes of tree species they contained, and the characteristics of the groups differed in one or more ways between years. Correlations of biophysical variables (e.g., soil texture in the 0–15 cm [L1] and 15–50 cm [L2] depths) displaying  $r^2$  values of at least 0.20 with plot distributions are shown as vectors. The understory vegetation variable of graminoid cover is for native graminoids. Wetland type is floodplain or depressional, with plots in depressional wetlands concentrated in the upper part of the 2018 ordination. In the 2018 ordination, axis 1 extracted 38% of the variance and axis 2 35% (73% cumulatively). In the 2021 ordination, axis 1 extracted 38% of the variance and axis 2 34% (72% cumulatively).

from seedlings, sufficed to reduce ( $P < 0.05$ , Tukey's multiple comparisons) the entire community sapling:tree similarity compared with 2005–2008.

The three most major changes on the long-term plots between 2005 and 2021 were that 1) *F. pennsylvanica* went from the third most abundant species (36 trees/ha) in the tree size class in 2005 to having no

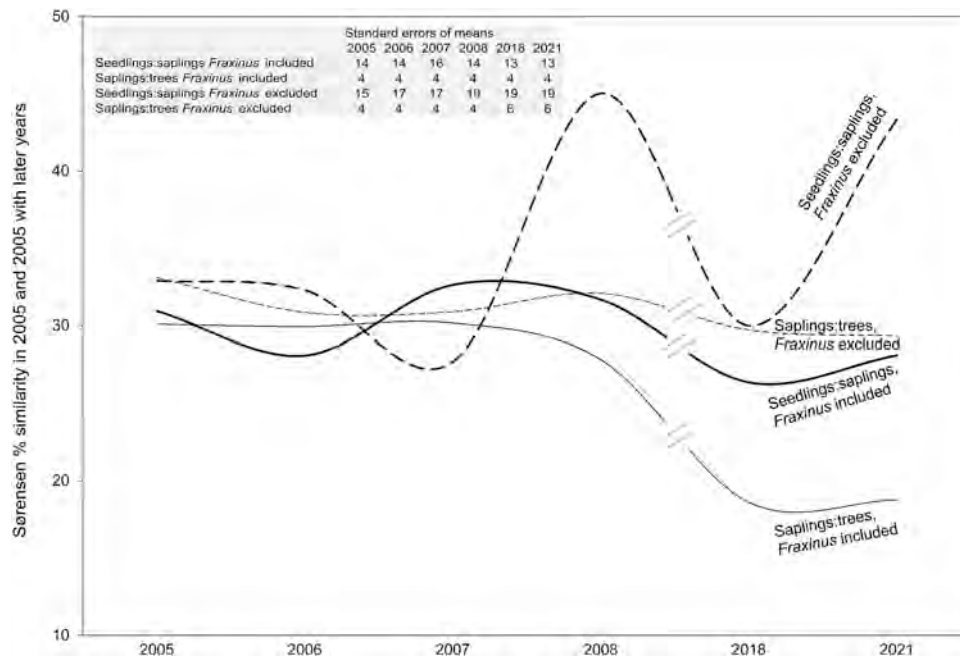
trees in 2021, while its saplings increased in number by 16% as the species remained the most abundant species in the sapling layer in 2021; 2) *Acer negundo* decreased sharply in density, by 79% as saplings and by 44% as trees; and 3) while compositional change was subtle overall (Fig. 6), there were seven instances of seedling-to-sapling transitions of species on plots and five instances of sapling-to-tree transitions between 2005 and 2021 (Table 2). Species making at least one seedling-to-sapling advancement on plots included *Carpinus caroliniana*, *Carya laciniata*, *F. pennsylvanica*, *Acer rubrum-saccharinum*, and *Acer nigrum*. Species making at least one sapling-to-tree advancement were *A. nigrum*, *C. laciniata*, *Ulmus americana*, and *Ulmus rubra*. Of 12 total instances of species advancements on plots between 2005 and 2021, only one was not preceded by recorded presence of the species specifically in the lower size class within the dataset. This instance was *C. caroliniana* on one plot not being recorded as a seedling (likely establishing during the 2009–2017 period for which data were not collected) but having 120 additional saplings/ha present in 2021 not present in 2005.

## 4. Discussion

### 4.1. Groups of species similar in size class occurrence

Across the set of 39 taxa of trees in our study, we found that occurrence as only seedlings or only trees among plots was most frequent compared with occurrence as only saplings or in multiple size classes. Spatial incongruence in distribution of size classes within species could arise from several processes, such as adults becoming established in past forest conditions that have changed unfavorably for the species' regeneration, habitat requirements differing with life stage, or seed dispersal (Collins and Carson, 2004). In our study, *Quercus rubra* was the commonest species that never occurred in all three size classes on any of the 22 plots, instead occurring most often as only trees or as only seedlings. This species is only moderately shade tolerant, which may enable seedlings to persist for varying time periods in shade but limit them from advancing to saplings, without or with mature trees that may have become established under past more open conditions (Collins and Carson, 2004). *Quercus rubra* establishment may also be sensitive to temporal variation in site hydrology, as the species occurred on moderately well to somewhat poorly drained soil but was absent from sites mostly inundated with water during spring and early summer in southeastern Michigan just north of our study area (Knopp, 2012). The species has low flood tolerance, raising the possibility that adults could have become established during a protracted period without inundation (De Jager et al., 2012). As flood tolerance can increase with tree age, adults could persist in site conditions unsuitable for the establishment or growth of seedlings (Evans et al., 2022). Another possibility is that seeds could disperse to site conditions supporting germination and short-term seedling persistence, but not growth to maturity (Clark et al., 1999). Although heavy-seeded species such as *Q. rubra* often disperse a maximum of only tens of meters (Battaglia et al., 2008), within-site heterogeneity in factors such as soil texture and duration of flooding influencing tree regeneration can also occur at these fine scales in forested wetlands (Knopp, 2012; Evans et al., 2022). While untangling the potential mechanisms for disjointed distributions of size class occurrences within species was beyond the scope of our study, our results do indicate that many species most frequently occurred in only one size class compared with multiple size classes.

Like *Q. rubra*, *Fraxinus pennsylvanica* exemplified the group of species typically occurring in only one size class per plot that varied among plots, which for *F. pennsylvanica*, was either seedlings or saplings. In different regions and site conditions, some studies have found that *Fraxinus* regeneration (along with soil seed banks) becomes depleted after EAB invasion (Burr and McCullough, 2014; Klooster et al., 2014), while other studies report that *Fraxinus* regeneration remains abundant (Kashian, 2016; Robinett and McCullough, 2019; Marshall, 2020; Morris et al., 2023). We found that *Fraxinus* seedlings or saplings were common



**Fig. 6.** Average compositional similarity between size classes of tree species for seedlings (< 1 cm diameter at 1.4 m), saplings (≥ 1 cm < 10 cm), and trees (≥ 10 cm) in 2005 (onset of emerald ash borer invasion and before *Fraxinus pennsylvanica* mortality) and of 2005 with the subsequent years of 2006–2008 (during *F. pennsylvanica* decline and mortality) and 14 (2018) and 17 (2021) years after invasion in forested wetlands in Ohio, USA. Average similarities with *F. pennsylvanica* included and excluded are shown.

**Table 2**

Change in abundance across size classes for tree species spanning the onset of emerald ash borer invasion (2005) through 17 years later (2021) in forested wetlands containing *Fraxinus* trees, Ohio, USA. Data are mean ± standard error of mean. Advancements into a larger size class, shown as increases in sapling or tree densities, are in bold. Size classes include seedlings (< 1 cm diameter at 1.4 m, with abundance expressed as % cover), saplings (≥ 1 < 10 cm), and trees (≥ 10 cm).

Taxa	2005			2021		
	Seedling %	Saplings/ha	Trees/ha	Seedling %	Saplings/ha	Trees/ha
<i>Acer negundo</i>	0.6 ± 0.4	556 ± 203	36 ± 13	0.8 ± 0.4	116 ± 30	20 ± 13
<i>Acer nigrum</i>	0.4 ± 0.4	8 ± 8	–	–	<b>24 ± 15</b>	<b>4 ± 4</b>
<i>Acer rubrum-saccharinum</i>	1.5 ± 1.4	80 ± 55	96 ± 31	0.5 ± 0.4	36 ± 36	88 ± 29
<i>Carpinus caroliniana</i>	– <sup>a</sup>	20 ± 11	–	0.1 ± 0.1	<b>36 ± 27</b>	–
<i>Carya</i> spp.	0.1 ± 0.1	48 ± 19	32 ± 15	0.1 ± 0.1	<b>52 ± 21</b>	<b>40 ± 18</b>
<i>Crataegus</i> spp.	–	8 ± 5	–	–	–	–
<i>Fraxinus pennsylvanica</i>	1.2 ± 0.6	624 ± 258	36 ± 12	2.8 ± 0.7	<b>724 ± 580</b>	–
<i>Malus coronaria</i>	–	4 ± 4	–	–	4 ± 4	–
<i>Populus deltoides</i>	–	–	12 ± 8	–	–	8 ± 5
<i>Quercus bicolor</i>	–	–	4 ± 4	–	–	4 ± 4
<i>Quercus rubra</i>	0.1 ± 0.1	32 ± 32	12 ± 8	0.1 ± 0.1	12 ± 12	12 ± 8
<i>Tilia americana</i>	0.1 ± 0.1	12 ± 5	80 ± 27	0.2 ± 0.1	<b>16 ± 7</b>	60 ± 23
<i>Ulmus americana</i>	–	4 ± 4	–	0.2 ± 0.1	–	<b>8 ± 5</b>
<i>Ulmus rubra</i>	–	44 ± 27	28 ± 15	0.1 ± 0.1	28 ± 17	<b>36 ± 19</b>

<sup>a</sup> Not present that year.

among plots in 2018 or 2021, at least in depressional wetlands, and even increased between 2005 and 2021 on the long-term plots. Given the abundance of *Fraxinus* advance regeneration, our results seem supportive of other studies noting that one of the largest uncertainties in the future dynamics of EAB-aftermath forests is likely to be the fate of current *Fraxinus* seedlings and saplings (e.g., Aubin et al., 2015; Klooster et al., 2018; Morris et al., 2023). It is unclear whether *Fraxinus* saplings can persist at least long enough to reproduce, which can occur by age 20 years (Bonner and Karrfalt, 2008). Further, it is unclear whether some proportion of saplings can grow to more persistent mature trees coexisting with sub-lethal damage from EAB (Siegert et al., 2021). These possibilities may hinge on factors such as adaptation within *Fraxinus* species, whether reduced abundance of mature host trees lowers the habitat carrying capacity for EAB to keep EAB populations sufficiently low for persistence of some mature *Fraxinus* trees for various time periods, and how effective biocontrols for EAB become (Robinett and

McCullough, 2019). Biocontrols have been released in 30 + states and three Canadian provinces, and Duan et al. (2023) noted that *Fraxinus* saplings in several areas are infested by low EAB populations partly regulated by biocontrols. However, Duan et al. (2023) further noted it is not yet clear if biocontrols will persistently improve *Fraxinus* recovery and regeneration. In northwestern Ohio around our study area, parasitoid species intended for EAB biocontrol were released by 2022 (Duan et al., 2023). The fate of the current *Fraxinus* sapling layer could be a driver not only of future *Fraxinus* populations but also of regeneration dynamics of other species where *Fraxinus* dominates the sapling layer and could compete with other species (Morris et al., 2023).

A second group of species occurred almost exclusively as trees, with seedlings and saplings absent or nearly so. Our results for these species – *Populus deltoides*, *Platanus occidentalis*, and *Quercus bicolor* – are consistent with their regeneration failure widely reported in previous research in mature wetland forests in temperate eastern North America (e.g.,



Bowles et al., 2003; Johnson and Waller, 2013; Guyon and Battaglia, 2018). Emerald ash borer invasion does not appear to have changed this situation of regeneration failure of these species, perhaps because the gaps created by death of *Fraxinus* trees in mixed-species forests are too small and discontinuous or fill too rapidly for these species to regenerate even if seed-producing adults are nearby (Costilow et al., 2017; Dolan and Kilgore, 2018). For example, in a wetland forest in Indiana, Cowell et al. (2010) found that *Q. bicolor* did not regenerate in gaps even relatively large (0.6 ha) for those typically forming from periodic multi-tree death in temperate forests.

To reliably regenerate, this group of shade-intolerant species may require openings of one or more hectares, along with minimal competition (Reinhardt Adams et al., 2011), conditions not typical after EAB invasion in mixed-species forests (Dolan and Kilgore, 2018). Historically, major flooding (a process widely altered contemporarily by construction of dams and drainage ditches), tornados and windstorms, potentially fires set by Native Americans during dry periods, and logging by Euro-American settlers may have afforded regeneration opportunities for these species across their broad range in eastern wetland forests (Johnson and Waller, 2013). In an old-growth, depressional wetland forest west of our study area, Cho and Boerner (1995) used dendroecological analysis to conclude that regeneration events for these species may only occur once a century or longer, perhaps linked with tornado activity. Although we recorded few to no seedlings and saplings in 2018 and 2021 and no recruitment of the species within a 17-year period on the long-term plots in mature forests, regeneration of *P. deltoides* and less so *P. occidentalis* is occurring within our study area elsewhere in multi-hectare openings such as abandoned agricultural lands (Fig. S2). Although not regenerating within the mature forests themselves, trees of the species within mature forests could be important seed-producers for regeneration in the broader landscape, particularly for the wind-dispersed *P. deltoides* and *P. occidentalis* with seeds that can disperse hundreds of meters (*sensu* Battaglia et al., 2008).

A third group of species, all of which were shade-tolerant, frequently occurred in all three size classes on a plot. The most common species in this group – *Ulmus americana*, *Acer rubrum*, and *Acer saccharinum* – were reported to have increased in abundance in recent decades in several prior studies. For example, *U. americana* increased in density between the 1970 s and mid-1990 s in two studies in floodplain and depressional forests in Illinois (Bell, 1997; Bowles et al., 2003), increased from the mid-1950 s to the 2000 s in small tree abundance in Wisconsin floodplain forests (Johnson and Waller, 2013), and disproportionately filled gaps relative to other species in a northwestern Ohio depressional wetland (Cho and Boerner, 1991). These and other studies indicate that after invasion of Dutch elm disease (and potentially other pathogens afflicting *Ulmus*) by the mid-1950 s, the density of large *U. americana* trees has declined while the density of small trees often has increased (Marks, 2017). Dutch elm disease disproportionately kills large trees, with mortality sharply increasing for *U. americana* trees > 15 cm diameter (Marks, 2017). Our results suggest that *U. americana* is frequent as seedlings through at least small trees. Future dynamics of this abundant *U. americana* resource may depend on factors such as selection for disease-tolerant individuals and spatial patterns of trees potentially influencing isolation from disease spread (Marks, 2017).

#### 4.2. Seedling dynamics

The seedling layer was highly dynamic between the study years of 2018 and 2021. High between-year variation in the seedling layer is consistent with prior research in forested wetlands. In an Ohio *Fraxinus-Ulmus* wetland forest, the median longevity of seedlings was six months, only 2% of seedlings persisted more than two years, and of 2553 seedlings of 19 taxa tracked, only 2 seedlings grew to exceed 30 cm tall within a 10-year period (Boerner and Brinkman, 1996). Although they were short-lived, seedlings of *Ulmus americana* in that study were more abundant in dry springs when flooding was less limiting to seedling

establishment. In another study, along the Wisconsin River floodplain, different sets of tree species dominated seedling composition each year from 1997 to 2000, and years with high summer floods had few new seedlings appearing and high mortality (Dixon, 2003).

Primary factors that can relate to temporal variation in seedling abundance are periodicity in seed crops and soil seed bank formation and hydrology (Battaglia et al., 2008; Evans et al., 2022; Keller et al., 2023). Many eastern North American temperate trees form only transient or short-term seed banks, living < 1 year or at most a few years, so much of the appearance of new seedlings arises from germination of seed produced the prior or current year (Meadows et al., 2006). Formation and replenishment of at least short-lived seed banks, coupled with high-turnover but regularly appearing seedling layers, could in part explain why *Acer rubrum-saccharinum* and *U. americana* were among the species most successfully occurring in all three size classes in our study. In a forested wetland in New York, *Acer × freemanii* (the *A. rubrum-saccharinum* hybrid) and *U. americana* had both abundant seed banks and seedlings (Blood et al., 2010). In a prior investigation in depressional wetlands within our study area, *A. rubrum* was the tree species most frequently detected in seed banks in winter 2018 (Abella et al., 2020), preceding high *A. rubrum-saccharinum* seedling cover in summer 2018 in the present study.

Hydrological conditions any given year could also influence seedling abundance. Seedling cover was over a third higher in 2018 than in 2021, though precipitation was generally similar in these years. Early spring precipitation was 124% of average (1955–2021 records) in March 2018 and exactly average (6.5 cm) in March 2021 (Toledo Airport station; National Centers for Environmental Information, Asheville, NC). In the early growing season from April through June, precipitation was nearly identical in 2018 (119% of the 26-cm average) and 2021 (116%). Flooding in spring can limit seedling establishment in forested wetlands, and EAB could accentuate flooding by rapidly killing mature *Fraxinus* trees and thus reducing drawdown of soil moisture (Slesak et al., 2014). Whether any EAB-related hydrological changes persist over the longer term may depend on factors such as the degree of *Fraxinus* recovery or infilling by other trees or understory plants (Van Grinsven et al., 2017).

#### 4.3. Species traits

Among species traits, shade tolerance was most consistently correlated with variation in size class distribution among species in 2018 and 2021, and only shade-tolerant species advanced across size classes on the long-term plots. Other traits, such as seed size and dispersal mechanism, did not differentiate species with respect to size class distributions. An example is the group of species exhibiting potential regeneration failure. This group included a species with among the heaviest seeds dispersed by animals (*Quercus bicolor*) and species with the smallest seeds dispersed via wind and water (*Platanus occidentalis* and *Populus deltoides*; McKnight et al., 1980). Instead of seed size and dispersal, the commonality among these species appeared to be shade intolerance limiting occurrence of seedlings and saplings within mature forests despite presence of adults of these species. Experimental plantings support this view. Plantings in small gaps (one or a few trees) below dead *Fraxinus* trees after EAB invasion showed poor survival and growth, even with protection from herbivory and removal of understory competitors (Woods et al., 2019). Similarly, the group of species often occurring in all three size classes spanned a range of seed sizes and dispersal mechanisms from the large, animal-dispersed nuts of *Carya* to the wind-water-animal-dispersed samaras of *Acer* (McKnight et al., 1980). These species instead had in common shade tolerance and participation in gap-phase regeneration using advance regeneration and its ability to transition across size classes (Cho and Boerner, 1991; Cowell et al., 2010; Dolan and Kilgore, 2018).

#### 4.4. Biophysical site factors

As soil texture became finer and water holding capacity increased, seedling cover, sapling density, and species compositional similarity of size classes generally declined. Finer-textured soil (silt and clay) can be associated with longer hydroperiods, which particularly in spring and early summer, can hinder seedling establishment and sapling persistence to decouple their distribution from trees (De Jager et al., 2012).

Although shrubs or vines can increase after EAB invasion on some sites (Dolan and Kilgore, 2018; Abella et al., 2019), we found that native graminoid cover most often correlated with variation in abundance of forest size classes. High graminoid cover was frequently associated with plots containing few seedlings and saplings, lower compositional similarity among tree sizes, and also often lower densities of trees. Several possibilities could relate to this association. For example, plots could have had high graminoid cover before EAB invaded, and graminoid cover subsequently remained high concomitant with little tree recruitment after EAB invasion. Alternatively, graminoids could have increased after EAB invaded and *Fraxinus* trees died. Further, graminoids could directly hinder tree regeneration, or, instead, graminoids could be dominating plots the least environmentally conducive to tree regeneration. In a greenhouse experiment, Reinhardt Adams et al. (2011) reported that grasses reduced the height growth and biomass of *Quercus bicolor* seedlings, consistent with an idea that competition from understory plants can influence tree regeneration after EAB invasion (Hoven et al., 2022). Our graminoid-dominated plots with few trees seem to structurally resemble the open, savanna-like (containing widely spaced trees such as *Acer saccharinum* and *Platanus occidentalis*) sites with grassy understories described by Walters and Williams (1999) in some Pennsylvania floodplains. Walters and Williams (1999) noted it was uncertain whether these open, grassy sites had occurred historically or had formed via hydrological alteration or other anthropogenic disturbances. Further examining these types of grassy areas in our study area for their history, habitat values, and suitability for post-EAB reforestation may help determine whether they are EAB-created artifacts and candidate sites for enrichment tree plantings.

#### 4.5. Long-term change

After EAB invasion in 2005, mortality of *Fraxinus pennsylvanica* trees was 100% on the long-term plots. This is consistent with previous research reporting that the species is among the most vulnerable *Fraxinus* to EAB and commonly incurs 90–100% mortality (Knight et al., 2012a; Klooster et al., 2018; Robinett and McCullough, 2019). However, *F. pennsylvanica* showed an increase in sapling density from 2005 to 2021 and remained the most abundant species in the sapling layer. Whether EAB invasion will have “downsized” *F. pennsylvanica* from a canopy tree to only persisting in the subcanopy could largely depend both on whether saplings can advance to trees potentially concomitant with lower EAB density and on whether soil seed banks and seedlings can be replenished and grow to saplings to maintain the sapling layer (Kashian, 2016; Morris et al., 2023). *Fraxinus* appears to form only short-term soil seed banks, likely usually persisting no more than 1–3 years (Meadows et al., 2006; Klooster et al., 2014). In Michigan, *Fraxinus* soil seed banks became nearly depleted after two years without *Fraxinus* seed production, and the appearance of new seedlings ceased (Klooster et al., 2014). *Fraxinus* is a prolific seed producer, though, so some lingering *Fraxinus* trees persisting through EAB invasion for unknown reasons or some saplings producing seed could partly replenish seed banks (Knight et al., 2012a; Aubin et al., 2015; Steiner et al., 2019).

Along with loss of *F. pennsylvanica* trees, the other major change on the long-term plots was *Acer negundo*'s decline in the sapling and tree size class between 2008 and 2018. The causal factors of this decline are unclear but could include factors such as spring freezes, lengthened early summer hydroperiods associated with increased rainfall, competition from tall shrubs that increased after EAB invaded, forest

maturation, or other factors such as disease. *Acer negundo* is among the earliest tree species to leaf out, often by early April (Yu et al., 2016). Small trees that leaf out early, like *A. negundo*, are particularly susceptible to spring freezes (Augsburger, 2013), such as a severe freeze in April 2007 causing widespread tree damage across eastern North America (Meiners and Presley, 2015). Climatic records show that our study area also experienced the extreme April 2007 freeze as well as less severe, but multi-day freezes in April 2013, 2016, and 2018, which are within the 2008–2018 period when the *A. negundo* mortality occurred (Toledo Airport station; National Centers for Environmental Information, Asheville, NC). Early growing season (April through June) precipitation also exceeded the 1955–2021 average in 10 of 14 (71%) years from 2008 to 2021. Moreover, curtailed uptake of soil moisture by *Fraxinus* trees after their death could accentuate this moisture availability (Robertson et al., 2018). Although a moist-site species, *A. negundo* can be susceptible to extended inundation during the growing season (Friedman and Auble, 1999). The tall shrub *Lindera benzoin* increased in cover after EAB invasion (Abella et al., 2019), and whether competition from tall shrubs or perhaps increasing *F. pennsylvanica* sapling density contributed to *A. negundo*'s decline is unclear. Another factor could be forest maturation, as Maeglin and Ohmann (1973) reported that *A. negundo* is a relatively short-lived tree, typically only living 60+ years and reaching peak growth around 15–20 years old. Many damaging agents such as diseases can afflict *A. negundo* (Maeglin and Ohmann, 1973) and also warrant evaluation.

Although analysis of Sørensen similarities of 2005 (onset of EAB invasion) species composition with those of later years across size classes did not reveal statistically significant change at  $P < 0.05$  because of a combination of high variability among plots and relatively modest change, some notable patterns occurred. With *Fraxinus* excluded, there was a rise in similarity of 2005 seedling composition with 2008 sapling composition. The rise in 2008 on some plots resulted from cumulative seedling-to-sapling transition (increasing 2005 seedling:2008 sapling similarity) derived from limited instances of transitions (typically only 20/ha) among species. The increase in 2008 saplings was often transient among species, however, as the number of saplings (and their similarity with seedling composition) declined by 2018. There was another non-statistically significant rise in 2005 seedling with 2021 sapling compositional similarity. This resulted from a combination of new saplings of species that had been present in 2005 as seedlings and from attrition of the saplings (which in some cases could be from their advancement to trees) of species that had not been present as seedlings in 2005. Both of those processes increased similarity.

#### 4.6. Conclusions and considerations for forest management

Our results suggest that in mature, mixed-species forests invaded by EAB, tree recruitment will be derived from on-site pools of shade-tolerant species. In wetland forests in our study area, these species are likely to commonly include *Acer rubrum* and *saccharinum*, *Ulmus americana* and *rubra*, *Carya* spp., *Tilia americana*, and less frequently, species that are relatively uncommon among sites such as *Acer nigrum*. *Acer negundo* and *Fraxinus pennsylvanica* are also possibilities as shade-tolerant species abundant as seedlings and saplings, but their future role in forest recruitment dynamics is uncertain. We found that *A. negundo* sapling and tree density sharply declined between 2008 (shortly after the 2005 onset of EAB invasion) and 2018, and the future fate of currently abundant *F. pennsylvanica* saplings may hinge on EAB population dynamics. Our long-term data spanning 17 years suggest that with due consideration to high variability among years in the seedling layer and uncertainty in some individual species like *A. negundo*, forest managers can use forest size class analyses to identify the pool of species on-site from which recruitment is most likely to arise. Our findings suggest that while not all species found in all three (seedlings, saplings, and trees) or at least two size classes will advance across size classes, trees that do establish are most likely to originate from on-site pools of

shade-tolerant species already found in multiple size classes.

Species less tolerant of shade, specifically *Populus deltoides*, *Platanus occidentalis*, and *Quercus bicolor*, had few to no seedlings or saplings and no tree recruitment on our long-term plots and appear poised for regeneration failure in the mature, EAB-invaded forests. These species can offer unique forest structure and wildlife habitat (Romano, 2010). If managers wish to promote these species in mature, EAB-invaded forests, strategies such as cutting to enlarge or create openings perhaps coupled with planting may be necessary (Knight et al., 2012b). Variability in factors such as degree of competition and soil conditions may preclude a universally applicable minimum size of gap needed for these species to regenerate (McNab et al., 2021). Rather than concentrating on regenerating these shade-intolerant species in mature forests, a different approach could be improving understanding of identifying the types of disturbed sites and landscape configurations (e.g., distance to and dispersal feasibility of seed sources) where shade-intolerant species are likely to recruit. For example, as we noted earlier, profuse recruitment has occurred of wind-dispersed *P. deltoides* on abandoned agricultural lands acquired by conservation organizations, so providing opportunities for these species to recruit could be more feasible using a landscape context. Additionally, our results suggest that a subset of primarily floodplain sites with finer soil textures, high graminoid cover, and open savanna-like structure after *Fraxinus* trees died following EAB invasion, are most likely to have few tree seedlings and saplings. Further evaluating these sites for their appropriateness and suitability for reforestation, including for the shade-intolerant species not otherwise regenerating in mature, EAB-invaded forests, is also supported by our results.

#### CRedit authorship contribution statement

**Abella Scott R.:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Menard Karen S.:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Data curation. **Schetter Timothy A.:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Hausman Constance E.:** Writing – review & editing, Methodology, Investigation, Conceptualization.

#### Declaration of Competing Interest

The authors declare no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data Availability

Data will be made available on request.

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#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.121750](https://doi.org/10.1016/j.foreco.2024.121750).

#### References

- Abella, S.R., Hausman, C.E., Jaeger, J.F., Menard, K.S., Schetter, T.A., Rocha, O.J., 2019. Fourteen years of swamp forest change from the onset, during, and after invasion of emerald ash borer. *Biol. Invasions* 21, 3685–3696.
- Abella, S.R., Hodel, J.L., Schetter, T.A., 2020. Unusually high-quality soil seed banks in a Midwestern U.S. oak savanna region: variation with land use history, habitat restoration, and soil properties. *Restor. Ecol.* 28, 1100–1112.
- Abella, S.R., Menard, K.S., Schetter, T.A., Hausman, C.E., 2021. Co-variation among vegetation structural layers in forested wetlands. *Wetlands* 41, 3.
- Abella, S.R., Schetter, T.A., Gallaher, T.D., 2022. Rapid increase in sensitive indicator plants concurrent with deer management in an oak forest landscape. *Wildl. Soc. Bull.* 46, e1377.
- Andreas, B.K., J.J. Mack, and J.S. McCormac. 2004. Floristic quality assessment index (FQAI) for vascular plants and mosses for the State of Ohio. Ohio Environmental Protection Agency, Wetland Ecology Group, Columbus, Ohio.
- Aubin, I., Cardou, F., Ryall, K., Kreuzweiser, D., Scarr, T., 2015. Ash regeneration capacity after emerald ash borer (EAB) outbreaks: some early results. *For. Chron.* 91, 291–298.
- Augspurger, C.K., 2013. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. *Ecology* 94, 41–50.
- Battaglia, L.L., Minchin, P.R., Pritchett, D.W., 2002. Sixteen years of old-field succession and reestablishment of a bottomland hardwood forest in the lower Mississippi alluvial valley. *Wetlands* 22, 1–17.
- Battaglia, L.L., Pritchett, D.W., Minchin, P.R., 2008. Evaluating dispersal limitation in passive bottomland forest restoration. *Restor. Ecol.* 16, 417–424.
- Bell, D.T., 1997. Eighteen years of change in an Illinois streamside deciduous forest. *J. Torre Bot. Soc.* 124, 174–188.
- Blood, L.E.H.J., Putoniak, Titus, J.H., 2010. Seed bank of a bottomland swamp in western New York. *Castanea* 75, 19–38.
- Boerner, R.E.J., Brinkman, J.A., 1996. Ten years of tree seedling establishment and mortality in an Ohio deciduous forest complex. *Bull. Torre Bot. Club* 123, 309–317.
- Bonner, F.T., and R.P. Karrfalt (eds.). 2008. The woody plant seed manual. Agriculture Handbook 727. U.S. Department of Agriculture, Forest Service, Washington, D.C.
- Bowles, M., Jones, M., Dunn, C., McBride, J., Bushey, C., Moran, R., 2003. Twenty-year woody vegetation changes in northern flatwoods and mesic forest at Ryerson Conservation Area, Lake County, Illinois. *Erigenia* 19, 31–51.
- Boyce, R.L., 2012. Size structure of *Fagus grandifolia*, *Liriodendron tulipifera*, and *Celtis occidentalis* populations in a wetland forest in Campbell County, Kentucky. *J. Ky. Acad. Sci.* 73, 83–89.
- Burr, S.J., McCullough, D.G., 2014. Condition of green ash (*Fraxinus pennsylvanica*) overstory and regeneration at three stages of the emerald ash borer invasion wave. *Can. J. For. Res.* 44, 768–776.
- Cho, D.-S., Boerner, R.E.J., 1991. Canopy disturbance patterns and regeneration of *Quercus* species in two Ohio old-growth forests. *Vegetatio* 93, 9–18.
- Cho, D.-S., Boerner, R.E.J., 1995. Dendrochronological analysis of the canopy history of two Ohio old-growth forests. *Vegetatio* 120, 173–183.
- Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRisLambers, J., Lichter, J., McLachlan, J., Mohan, J., Wyckoff, P., 1999. Interpreting recruitment limitation in forests. *Am. J. Bot.* 86, 1–16.
- Collins, R.J., Carson, W.P., 2004. The effects of environment and life stage on *Quercus* abundance in the eastern deciduous forest, USA: are sapling densities most responsive to environmental gradients? *For. Ecol. Manag.* 201, 241–258.
- Cook, J.E., 2005. Vegetation changes in a central Wisconsin floodplain from pre-settlement to the mid-21st century. *J. Torre Bot. Soc.* 132, 492–504.
- Costilow, K.C., Knight, K.S., Flower, C.E., 2017. Disturbance severity and canopy position control the radial growth response of maple trees (*Acer* spp.) in forests of northwest Ohio impacted by emerald ash borer (*Agrilus planipennis*). *Ann. For. Sci.* 74, 10.
- Cowell, C.M., Hoalst-Pullen, N., Jackson, M.T., 2010. The limited role of canopy gaps in the successional dynamics of a mature mixed *Quercus* forest remnant. *J. Veg. Sci.* 21, 201–212.
- Dahlberg, B.L., and R.C. Guettinger. 1956. The white-tailed deer in Wisconsin. Technical Wildlife Bulletin 14. Wisconsin Conservation Department, Madison, WI. 282 pp.
- Diggins, T.P., 2013. A 300-year successional sequence in an eastern United States riparian hardwood forest. *J. Torre Bot. Soc.* 140, 65–88.
- Dixon, M.D., 2003. Effects of flow pattern on riparian seedling recruitment on sandbars in the Wisconsin River, Wisconsin, USA. *Wetlands* 23, 125–139.
- Dolan, B., Kilgore, J., 2018. Forest regeneration following emerald ash borer (*Agrilus planipennis* Fairemaire) enhances mesophication in eastern hardwood forests. *Forests* 9, 353.
- Dollar, K.E., Pallardy, S.G., Garrett, H.G., 1992. Composition and environment of floodplain forests of northern Missouri. *Can. J. For. Res.* 22, 1343–1350.
- Duan, J.J., Gould, J.R., Quinn, N.F., Petrice, T.R., Slager, B.H., Poland, T.M., Bauer, L.S., Rutledge, C.E., Elkinton, J.S., Van Driesche, R.G., 2023. Protection of North American ash against emerald ash borer with biological control: ecological premises and progress toward success. *BioControl* 68, 87–100.
- Evans, J., McCarthy-Neumann, S., Pritchard, A., Cartwright, J., Wolfe, B., 2022. A forested wetland at a climate-induced tripping-point: 17-year demographic evidence of widespread tree recruitment failure. *For. Ecol. Manag.* 517, 120247.
- Friedman, J.M., Auble, G.T., 1999. Mortality of riparian box elder from sediment mobilization and extended inundation. *Regul. River.: Res. Manag.* 15, 463–476.
- Guyon, L.J., Battaglia, L.L., 2018. Ecological characteristics of floodplain forest reference sites in the upper Mississippi River system. *For. Ecol. Manag.* 427, 208–216.
- Hausman, C.E., Jaeger, J.F., Rocha, O.J., 2010. Impacts of the emerald ash borer (EAB) eradication and tree mortality: potential for a secondary spread of invasive plant species. *Biol. Invasions* 12, 2013–2023.

- Hoven, B.M., Knight, K.S., Peters, V.E., Gorchov, D.L., 2022. Woody seedling community responses to deer herbivory, introduced shrubs, and ash mortality depend on canopy competition and site wetness. *For. Ecol. Manag.* 523, 120488.
- De Jager, N.R., Thomsen, M., Yin, Y., 2012. Threshold effects of flood duration on the vegetation and soils of the upper Mississippi River floodplain, USA. *For. Ecol. Manag.* 270, 135–146.
- Johnson, S.E., Waller, D.M., 2013. Influence of dam regulation on 55-year canopy shifts in riparian forests. *Can. J. For. Res.* 43, 159–170.
- Kashian, D.M., 2016. Sprouting and seed production may promote persistence of green ash in the presence of the emerald ash borer. *Ecosphere* 7, e01332.
- Keller, G.J., Slesak, R.A., Bronson, D., Windmuller-Campione, M.A., McGraw, A., 2023. Effects of flood duration on seedling survival and growth of potential replacement species in black ash (*Fraxinus nigra* Marshall) forests threatened by emerald ash borer. *Trees, For. People* 11, 100367.
- Klooster, W.S., Gandhi, K.J.K., Long, L.C., Perry, K.I., Rice, K.B., Herms, D.A., 2018. Ecological impacts of emerald ash borer in forests at the epicenter of the invasion in North America. *Forests* 9, 250.
- Klooster, W.S., Herms, D.A., Knight, K.S., Herms, C.P., McCullough, D.G., Smith, A., Gandhi, K.J.K., Cardina, J., 2014. Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). *Biol. Invasions* 16, 859–873.
- Knight, K.S., D. Herms, R. Plumb, E. Sawyer, D. Spalink, E. Pisarczyk, B. Wiggin, R. Kappler, E. Ziegler, and K. Menard. 2012a. Dynamics of surviving ash (*Fraxinus* spp.) populations in areas long infested by emerald ash borer (*Agrilus planipennis*). Pp. 143–152 in Sniezko, R.A., A.D. Yanchuk, J.T. Kliejunas, K.M. Palmieri, J.M. Alexander, and S.J. Frankel (tech. coords). Proceedings of the fourth international workshop on the genetics of host-parasite interactions in forestry: disease and insect resistance in forest trees. General Technical Report PSW-GTR-240. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.
- Knight, K.S., J.M. Slavicek, R. Kappler, E. Pisarczyk, B. Wiggin, and K. Menard. 2012b. Using Dutch elm disease-tolerant elm to restore floodplains impacted by emerald ash borer. Pp. 317–323 in Sniezko, R.A., A.D. Yanchuk, J.T. Kliejunas, K.M. Palmieri, J. M. Alexander, and S.J. Frankel (tech. coords). Proceedings of the fourth international workshop on the genetics of host-parasite interactions in forestry: disease and insect resistance in forest trees. General Technical Report PSW-GTR-240. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.
- Knopp, P.D., 2012. The distribution of *Quercus rubra* in the Maumee lake plain of southeastern Michigan. *Am. Midl. Nat.* 168, 70–92.
- Kreutzweiser, D., Dutkiewicz, D., Capell, S., Sibley, P., Scarr, T., 2020. Changes in streamside riparian forest canopy and leaf litter nutrient flux to soils during an emerald ash borer infestation in an agricultural landscape. *Biol. Invasions* 22, 1865–1878.
- Maeglin, R.R., Ohmann, L.F., 1973. Boxelder (*Acer negundo*): a review and commentary. *Bull. Torre Bot. Club* 100, 357–363.
- Marks, C.O. 2017. The ecological role of American elm (*Ulmus americana* L.) in floodplain forests of northeastern North America. Pp. 74–98 in Pinchot, C.C., K.S. Knight, L.M. Haugen, C.E. Flower, and J.M. Slavicek (eds.). Proceedings of the American elm restoration workshop 2016. General Technical Report NRS-P-174. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA.
- Marshall, J.M., 2020. Forest compositional changes after a decade of emerald ash borer. *Forests* 11, 949.
- McCune, B., and M.J. Mefford. 1999. PC-ORD: multivariate analysis of ecological data. User's guide. MjM Software Design, Gleneden Beach, Oregon.
- McKnight, J.S., D.D. Hook, O.G. Langdon, and R.L. Johnson. 1980. Flood tolerance and related characteristics of trees of the bottomland forests of the southern United States. Pp. 29–69 in Proceedings of a workshop on bottomland hardwood forest wetlands of the Southeast. U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, LA.
- McNab, W.H., Kilgo, J.C., Blake, J.L., Zarnoch, S.J., 2021. Effect of gap size on composition and structure of regeneration 19 years after harvest in a southeastern bottomland forest, USA. *Can. J. For. Res.* 51, 380–392.
- Meadows, J.S., Bonner, F.T., Haywood, J.D., 2006. Soil-seed bank survival in forests of the southern United States. *N. For.* 32, 335–345.
- Meiners, S.J., Presley, G.N., 2015. Differential damage of a late frost to Ozark tree species. *J. Torre Bot. Soc.* 142, 12–17.
- Miller, K.M., McGill, B.J., 2019. Compounding human stressors cause major regeneration debt in over half of eastern US forests. *J. Appl. Ecol.* 56, 1355–1366.
- Miller, K.M., Perles, S.J., Schmit, J.P., Matthews, E.R., Weed, A.S., Comiskey, J.A., Marshall, M.R., Nelson, P., Fischelli, N.A., 2023. Overabundant deer and invasive plants drive widespread regeneration debt in eastern United States national parks. *Ecol. Appl.* 33, e2837.
- Morris, T.D., Gould, J.R., Drake, J., Fierke, M.K., 2023. Status of ash forests and regeneration a decade after first detection of emerald ash borer infestation in New York State. *For. Ecol. Manag.* 549, 121464.
- Niinemetts, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecol. Monogr.* 76, 521–547.
- Phillips, R.P., Brzostek, E., Midgley, M.G., 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. *N. Phytol.* 199, 41–51.
- Reinhardt Adams, C., Kauth, P.J., Sorenson, J.W., 2011. Assessing competition between reed canary grass (*Phalaris arundinacea*) and swamp white oak (*Quercus bicolor*). *Ecol. Restor.* 29, 332–338.
- Robertson, W.M., Robinett, M., McCullough, D.G., 2018. Soil moisture response to white ash mortality following emerald ash borer invasion. *Environ. Earth Sci.* 77, 356.
- Robinett, M.A., McCullough, D.G., 2019. White ash (*Fraxinus americana*) survival in the core of the emerald ash borer (*Agrilus planipennis*) invasion. *Can. J. For. Res.* 49, 510–520.
- Romano, S.P., 2010. Our current understanding of the Upper Mississippi River system floodplain forest. *Hydrobiologia* 640, 115–124.
- Saladyga, T., Vanderhorst, J., Cline, J., 2020. Successional dynamics of an Appalachian pin oak (*Quercus palustris* Münchh.) swamp forest. *J. Torre Bot. Soc.* 147, 22–37.
- Sample, R.D., Delisle, Z.J., Pierce, J.M., Swihart, R.K., Caudell, J.N., Jenkins, M.A., 2023. Selection rankings of woody species for white-tailed deer vary with browse intensity and landscape context within the central hardwoods forest region. *For. Ecol. Manag.* 537, 120969.
- SER [Society for Ecological Restoration]-INSR [International Network for Seed Based Restoration]-RBKG [Royal Botanic Gardens Kew]. 2023. Seed Information Database. Available from: <https://ser-sid.org/> (February 2023).
- Siebert, N.W., Engelken, P.J., McCullough, D.G., 2021. Changes in demography and carrying capacity of green ash and black ash ten years after emerald ash borer invasion of two ash-dominated forests. *For. Ecol. Manag.* 494, 119335.
- Slesak, R.A., Lenhart, C.F., Brooks, K.N., D'Amato, A.W., Palik, B.J., 2014. Water table response to harvesting and simulated emerald ash borer mortality in black ash wetlands in Minnesota, USA. *Can. J. For. Res.* 44, 961–968.
- Steiner, K.C., Graboski, L.E., Knight, K.S., Koch, J.L., Mason, M.E., 2019. Genetic, spatial, and temporal aspects of decline and mortality in a *Fraxinus* provenance test following invasion by the emerald ash borer. *Biol. Invasions* 21, 3439–3450.
- Stone, K.L., McConoughey, E.H., Bottrell, G.D., Crouner, D.J., 1980. Soil survey of Lucas county, Ohio. U.S. Department of Agriculture, Soil Conservation Service. U.S. Government Printing Office, Washington, D.C.
- Van Grinsven, M.J., Shannon, J.P., Davis, J.C., Bolton, N.W., Wagenbrenner, J.W., Kolka, R.K., Pypker, T.G., 2017. Source water contributions and hydrologic responses to simulated emerald ash borer infestations in depressional black ash wetlands. *Ecology* 10, e1862.
- Walters, G.L., Williams, C.E., 1999. Riparian forest overstory and herbaceous layer of two upper Allegheny River islands in northwestern Pennsylvania. *Castanea* 64, 81–89.
- Woods, M.J., Cobb, M., Hickie, K., McEwan, R.W., 2019. Assessing the efficacy of seedling planting as a forest restoration technique in temperate hardwood forests impacted by invasive species. *Forests* 10, 699.
- Yu, R., Schwartz, M.D., Donnelly, A., Liang, L., 2016. An observation-based progression modeling approach to spring and autumn deciduous tree phenology. *Int. J. Biometeorol.* 60, 335–349.

Supplemental Material

Abella, S.R., K.S. Menard, T.A. Schetter, and C.E. Hausman. Species and landscape variation in tree regeneration and 17 years of change in forested wetlands invaded by emerald ash borer. *Forest Ecology and Management*.

**Table S1**

Traits of tree species inhabiting at least four plots (out of 22) in 2018 and 2021 in forested wetlands invaded by emerald ash borer, Ohio, USA.

Taxa	Wetland	Shade	Drought	Flood	SeedWt	Wind	Water	Gravity	Animal	Timing	Mycorrhizae	Deer	Conservatism
<i>Acer negundo</i>	3	3.5	3	2.8	35.98	1	0	0	1	3	1	3	3
<i>Acer rubrum-saccharinum</i>	3	3.5	2.3	3.3	112.61	1	1	0	1	1	1	1	2.5
<i>Carpinus caroliniana</i>	3	4.6	2	2.3	15.7578	1	0	0	1	3	2	3	5
<i>Carya spp. (laciniosa)</i>	3	4.4	2	1.5	15141.07	0	0	1	1	3	2	3	7
<i>Celtis occidentalis</i>	2	3.2	3.9	2.7	126.44	1	0	0	1	3	1	1	4
<i>Fraxinus americana</i>	2	2.5	2.4	2.6	37.3	1	1	0	0	3	1	2	6
<i>Fraxinus pennsylvanica</i>	4	3.1	3.9	3	32.32	1	1	0	0	3	1	2	3
<i>Juglans nigra</i>	2	1.9	2.4	1.8	11302.54	0	0	1	1	3	1	2	5
<i>Platanus occidentalis</i>	4	2.9	2.3	2.7	2.85	1	1	0	0	1	1	3	7
<i>Populus deltoides</i>	3	1.8	1.6	3	1.15	1	1	0	0	2	1.5	2	3
<i>Prunus serotina</i>	2	2.5	3	1.1	83.9	0	0	1	1	2	1	2	3
<i>Quercus bicolor</i>	4	3	3.4	2.6	3459.14	0	0	1	1	3	2	2	7
<i>Quercus rubra</i>	2	2.8	2.9	1.1	3143.26	0	0	1	1	3	2	2	6
<i>Tilia americana</i>	2	4	2.9	1.3	108.14	1	1	0	0	3	2	2	6
<i>Ulmus americana</i>	4	3.1	2.9	2.5	5.04	1	1	0	0	1	1	2	2
<i>Ulmus rubra</i>	3	3.5	2.4	2	9.98	1	1	0	0	1	1	2	3

Wetland status ranges from 1 (upland) to 5 (obligate wetland). Shade, drought, and flood tolerance range from intolerant (1) to most tolerant (5). SeedWt (seed weight) is mg/seed. For seed dispersal vectors (wind, water, gravity, animal), 1 signifies that a species can be predominately dispersed by the vector. Predominant timing of seed dispersal includes spring (1), summer (2), and autumn/winter (3). Mycorrhizal associations include arbuscular (1), ectomycorrhizae (2), and both (1.5). Deer preference for a species' foliage and twigs ranges from generally preferred (1), neutral (2), and non-preferred (3). The coefficient of conservatism ranges from generalist (1) to specialist (10). Citations for each trait are provided in the Methods.

**Table S2**

Average abundance of 39 tree taxa in 2018 and 2021 on 22 plots in forested wetlands invaded by emerald ash borer, Ohio, USA. Size classes are as follows: seedlings (< 1 cm diameter at 1.4 m), saplings ( $\geq 1$  cm < 10 cm), and trees ( $\geq 10$  cm).

Taxa	2018			2021		
	Seedlings <sup>a</sup> Cov % (freq %)	Saplings /ha (freq %)	Trees /ha (freq %)	Seedlings Cov % (freq %)	Saplings /ha (freq %)	Trees /ha (freq %)
<i>Acer negundo</i>	0.286 (50)	75 (32)	27 (32)	0.239 (27)	51 (32)	29 (27)
<i>Acer nigrum</i>	– <sup>b</sup>	5 (9)	1 (5)	–	5 (9)	1 (5)
<i>Acer rubrum-saccharinum</i>	3.066 (73)	54 (45)	125 (77)	0.289 (64)	30 (36)	116 (82)
<i>Acer saccharum</i>	–	–	–	–	1 (5)	–
<i>Aesculus glabra</i>	0.023 (5)	23 (9)	15 (5)	0.118 (18)	22 (9)	15 (5)
<i>Asimina triloba</i>	0.455 (5)	28 (5)	–	0.682 (5)	28 (5)	–
<i>Carpinus caroliniana</i>	–	5 (14)	–	0.032 (14)	8 (9)	–
<i>Carya spp. (laciniosa)<sup>c</sup></i>	0.014 (14)	12 (18)	14 (23)	0.130 (32)	17 (27)	15 (23)
<i>Catalpa speciosa</i>	0.050 (9)	4 (5)	–	0.023 (5)	4 (5)	–
<i>Celtis occidentalis</i>	0.032 (14)	3 (9)	2 (9)	0.050 (9)	4 (5)	2 (5)
<i>Crataegus crus-galli</i>	–	3 (5)	11 (5)	–	–	11 (5)
<i>Crataegus spp.</i>	–	1 (5)	4 (5)	–	1 (5)	3 (5)
<i>Fagus grandifolia</i>	–	–	1 (5)	–	–	–
<i>Fraxinus americana</i>	–	2 (5)	–	0.055 (23)	–	–
<i>Fraxinus nigra</i>	0.023 (5)	8 (9)	–	0.005 (5)	7 (5)	–
<i>Fraxinus pennsylvanica</i>	3.307 (82)	235 (41)	1 (5)	3.377 (86)	238 (50)	1 (5)
<i>Fraxinus profunda</i>	0.023 (5)	–	–	–	–	–
<i>Fraxinus quadrangulata</i>	–	2 (9)	–	–	–	–
<i>Gleditsia triacanthos</i>	0.009 (9)	–	–	0.009 (9)	–	–
<i>Gymnocladus dioicus</i>	–	1 (5)	–	0.005 (5)	1 (5)	–
<i>Juglans nigra</i>	0.009 (9)	2 (5)	1 (5)	0.011 (5)	2 (5)	3 (9)
<i>Liriodendron tulipifera</i>	0.091 (5)	–	–	0.005 (5)	4 (5)	–
<i>Malus coronaria</i>	–	1 (5)	–	–	1 (5)	–
<i>Nyssa sylvatica</i>	–	1 (5)	–	–	–	–

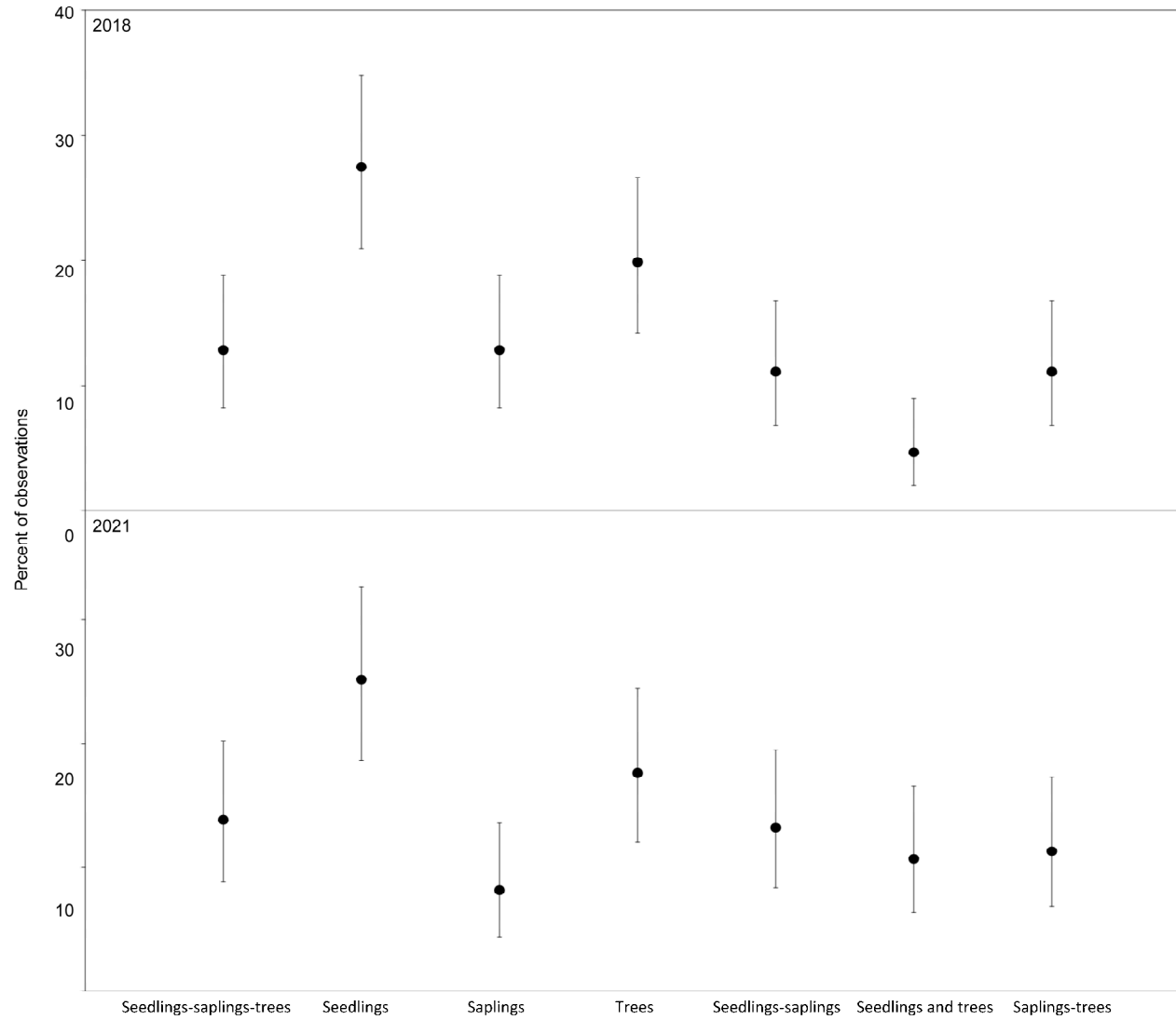
<i>Platanus occidentalis</i>	0.050 (9)	8 (5)	3 (14)	0.027 (9)	5 (5)	3 (14)
<i>Populus deltoides</i>	0.045 (5)	–	12 (36)	–	–	11 (36)
<i>Prunus nigra</i>	0.091 (5)	–	–	–	–	–
<i>Prunus serotina</i>	0.032 (14)	13 (14)	1 (5)	0.048 (18)	5 (5)	1 (5)
<i>Prunus virginiana</i>	–	11 (5)	–	–	13 (9)	–
<i>Quercus bicolor</i>	–	4 (9)	3 (9)	0.023 (5)	5 (9)	3 (9)
<i>Quercus macrocarpa</i>	0.005 (5)	–	–	–	–	–
<i>Quercus palustris</i>	0.023 (5)	3 (5)	4 (9)	0.009 (9)	1 (5)	4 (9)
<i>Quercus rubra</i>	0.089 (41)	4 (9)	9 (27)	0.039 (32)	7 (9)	9 (27)
<i>Robinia pseudoacacia</i>	–	–	1 (5)	0.005 (5)	–	1 (5)
<i>Sassafras albidum</i>	0.011 (5)	3 (5)	4 (5)	0.005 (5)	1 (5)	3 (5)
<i>Tilia americana</i>	0.027 (9)	6 (18)	15 (23)	0.043 (18)	5 (18)	15 (23)
<i>Ulmus americana</i>	0.061 (36)	58 (55)	40 (59)	0.073 (36)	71 (41)	38 (68)
<i>Ulmus pumila</i>	–	–	–	0.005 (5)	–	–
<i>Ulmus rubra</i>	0.030 (23)	10 (14)	8 (14)	0.009 (9)	9 (14)	7 (18)

<sup>a</sup>Cov is % cover; freq is % frequency (based on % of plots a species inhabited, out of 22 possible).

<sup>b</sup>Not present in that size class on any plot that year.

<sup>c</sup>Most *Carya* were *C. laciniosa*.

**Fig. S1.** Percent of total occurrences (with lower and upper 95% confidence limits) in size classes combined for all taxa in 2018 and 2021 on 22 plots in forested wetlands invaded by emerald ash borer, Ohio, USA. One occurrence represents presence of one species on one plot in one size class combination (e.g., a species occurring as a seedling, sapling, and tree simultaneously on the same plot) or individual size class if a species only occurred in one size class on a plot. Percentages are out of 858 total occurrences in 2018 and also 858 occurrences in 2021.





**Fig. S2.** Examples of profuse natural regeneration of *Populus deltoides* on abandoned agricultural lands within the study area, Ohio, USA. Top: seedlings of *P. deltoides* up to 2 m tall on land that had been last disturbed three years earlier (Moseley Trail, Metroparks Toledo). Bottom: young *P. deltoides* trees (~ 10-20 years old) establishing on land that had been cultivated until about 2000 and further disturbed until 2003 (Sylvan Prairie Park, Outdoor Sylvania Community Parks). Photos by S.R. Abella, August 2023.

