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Wide-spread vulnerability of black ash (*Fraxinus nigra* Marsh.) wetlands in Minnesota USA to loss of tree dominance from invasive emerald ash borer

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The emerald ash borer (EAB) has killed ash species (*Fraxinus* L.) in much of eastern North America, but it has yet to reach the vast ash wetlands in northern Minnesota, USA. In these wetlands, a single species, black ash (*Fraxinus nigra* Marsh.) comprises a majority of trees and has a foundational role in controlling ecosystem function. Given the likelihood of wide-spread mortality of black ash from EAB and the likelihood of severe ecosystem impacts, we examined the potential for co-occurring tree species to replace black ash, either through gap filling in the overstory or release from the understory. We addressed this objective by examining woody plant communities in 32 mature black ash sites located across a large geographic region and inclusive of two distinct wetland types as defined by hydrologic regime. Our results indicate a region-wide lack of species capable of replacing black ash in both wetland hydrologic types; thus there is very low existing potential for replacement of black ash from expansion in the overstory or through release in the understory. These results point to an urgent need for silvicultural intervention to identify and establish future-adapted non-ash tree species so as to promote resilience in the face of EAB by maintaining aspects of the foundational role of black ash in controlling ecosystem functions.

Introduction

The invasive emerald ash borer (EAB; *Agriulus planipennis*) is impacting hardwood forests in much of eastern North America where ash (*Fraxinus* L.) is a component of the tree community. EAB has also invaded forests with ash in European Russia, with concerns about spread into central Europe (Valenta *et al*., 2017). For most ash species, EAB causes over 90 per cent mortality of trees over 2.5 cm diameter (at breast height) by a few years after infestation (Klooster *et al*., 2014). There are a number of assessments of the ecosystem impacts of EAB-caused mortality, such as changes in carbon cycles, hydrology and food webs (Gandhi and Herms, 2010; Flower *et al*., 2013; Youngquist *et al*., 2017; Kolka *et al*., 2018). The likelihood that impacts occur depends in part on the abundance of ash compared to other species in a site, and consequently, the ability of other trees to confer resilience of ecosystem function in light of threats (Mitchell *et al*., 2016; Youngquist *et al*., 2017).

Rapid mitigation might occur when ash constitutes a small portion of total abundance within the overstory. In these settings, there should be high potential for other species to replace ash by gap filling (Bowen and Stevens, 2018; Hoven *et al*., 2020); a similar dynamic is predicted in response to fungal-caused dieback of ash in woodlands in the UK (Broome *et al*., 2019). Delayed mitigation may occur when species in a sub-canopy layer are released by the mortality of overstory ash (Smith, 2006), a dynamic that is more likely to occur when ash makes up a large proportion of the overstory layer (Davis *et al*., 2016; Hoven *et al*., 2020). More protracted mitigation may occur when other species occur as advance regeneration that is released by overstory and midstory mortality (Hoven *et al*., 2020).

Much of the research in North America on impacts of EAB has taken place in mixed-species forests, where ash makes up only a portion, often a minority, of the overstory (e.g. Kashian and Witter, 2011; Bowen and Stevens, 2018; Klooster *et al*., 2018; Hoven *et al*., 2020). While loss of ash may be impactful in mixed-species forests, these impacts may pale in comparison to the potential impacts when a single ash species makes up the majority of overstory trees, as in black ash (*Fraxinus nigra* Marsh.) wetlands of the western Great Lakes region of North America (Youngquist *et al*., 2017). For example, in Minnesota, USA, there are nearly 500 000 ha of black ash wetlands, with similarly large amounts in the states of Wisconsin (340 000 ha) and Michigan (270 000 ha) (Youngquist *et al*., 2017). This single species often comprises a majority of overstory trees in this forest (e.g. Palik *et al*., 2011; D'Amato *et al*., 2018) and is considered foundational (*sensu* Ellison *et al*., 2005) for its role in

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modulating the structure and function of these ecosystems through influences on hydrology, litter quality and resource availability (Youngquist *et al*., 2017). Moreover, black ash is considered the most vulnerable of North American ash species to EAB-induced mortality, suggesting these systems have the greatest likelihood of wide-scale mortality following invasion (Cappaert *et al*., 2005). As of spring 2020, EAB has yet to invade the black ash resource in northern Minnesota but has established populations to the east and south of the region.

Understanding the potential for other tree species to assume the ecological role of threatened ash species is important, as this can help stakeholders anticipate likely impacts and managers identify mitigation strategies (Mitchell *et al*., 2014; Smith *et al*., 2015; D'Amato *et al*., 2018), such as preemptive release of co-occurring species or artificial regeneration. To date, for black ash wetlands in eastern North American, there have been limited assessments of woody plant communities conducted with a goal of determining the potential for other species to replace black ash broadly across the landscape and how this potential might vary with differences in underlying environmental factors (e.g. Smith, 2006; Palik *et al*., 2012; Davis *et al*., 2016). For instance, in northern Minnesota landscapes, black ash wetlands are classified into two types based on hydrologic regimes, including wet and very wet swamps (Aaseng, 2003; D'Amato *et al*., 2018). These hydrologic types differ, among other factors, in duration of ponded surface water during the growing season and degree of saturated soil, being longer for very wet than wet swamps (Aaseng, 2003; Palik *et al*., 2011). This variation in hydrology may be an important factor influencing the composition and abundance of woody species capable of replacing black ash after mortality from EAB (Diamond *et al*., 2019). There is a need to develop guidelines for mitigation by wetland hydrologic type, but differences between them have not yet been examined.

We examined black ash wetlands in northern Minnesota, USA across a large geographic area with a goal of assessing replacement potential by other tree species. Specifically, we quantified the composition and abundance of woody species in different vertical layers of woody vegetation in 32 mature black ash sites within the two distinct hydrologic types. We asked (1) how likely is it that black ash will be replaced by other tree species in these ecosystems through expansion in the overstory or successional replacement from the sapling or seedling layers and (2) does replacement potential differ between black ash wetlands that differ strongly in hydrologic regime.

Methods

Study area and site selection

This study was conducted in northcentral and eastern Minnesota, USA, between latitude 47.75–47.55° and longitude −93.60 to −93.80°. Mean annual temperature of the region is approximately 4.0°C. *maximum* summer temperatures can exceed 32°C, while minimum winter temperature can drop below −35°C. Mean annual rain-equivalent precipitation is 50–64 cm (PRISM Climate Group, 2015). In winter, average total snowfall ranges from 1 to 2 m.

Study sites were selected from the two black ash wetland hydrologic types in the region, northern wet ash swamps and northern very wet ash swamps. Soils of both hydrologic types are typically Histosols characterized by mucky peats of varying depths underlain by silty clay horizons (Natural Resource Conservation Service, 2019), but may also include mineral soils of varying composition (Slesak *et al*., 2014). The two wetland types occur in a variety of geomorphic settings, including depressions, which have convex, pool-type geometry with hydrologic isolation from other surface water, lowlands, which are extensive wetland complexes with flat topography, transitions, which are flat to gently sloping linear boundaries between uplands and conifer wetlands, and riverine, which are lowlands with a steeper gradient such that water visibly flows in small channels occasionally (Diamond *et al*., 2019).

We selected a total of 32 black ash sites from a larger pool, identified from inventory records of federal, state, and county ownerships, to be as inclusive as possible of the two hydrologic types in the various geomorphic settings. Of the 32 study sites selected, 14 were identified in inventory records as wet ash swamp and 18 as very wet ash swamp.

Additional criteria for site selection included (1) black ash comprised at least 50 per cent of overstory basal area (trees ≥10 cm diameter at breast height (1.4 m), hereafter dbh); (2) large enough to establish at least one 0.02 ha circular plot (see below); (3) no evidence of recent cutting or mortality of trees; (4) no ditches, roads or trails and (5) dominated by mature trees in the site.

Vegetation sampling

Vegetation was sampled in summer 2017 in one to four plots in each site, depending on wetland size (total sample plots = 130). An initial plot was established in the centre of the site with additional plots added (if size permitted) that were 45–200 m apart. Each plot consisted of a 400 m^2 circular plot, a 200 m^2 centrally nested circular subplot, and three 10 m^2 circular subplots located at a distance of 5.5 m from the centre of the 400 m^2 plot at compass azimuths of 0, 120 and 240°. Species and diameter of overstory trees (dbh ≥ 10 cm) were sampled in the full plot. Sapling sized trees and large shrubs (2.5 cm ≤ dbh < 10 cm) were measured in the 200 m^2 subplot. Seedling trees and smaller woody shrubs (dbh < 2.5 cm and ≥ 0.5 m tall) were tallied in 10 m^2 subplots. For each plot, total basal area or density was determined and scaled to a per ha basis and these values were averaged among plots within each site (if there was more than one plot) for subsequent analyses (see below). Herbaceous species, while not quantitatively sampled, were observed within each plot to verify ecosystem indentity (wet or very wet black ash swamp) using a classification key-based ground layer plant indicators species (following Aaseng, 2003).

Data summary and analysis

Non-metric multidimensional scaling (NMS) was used to graphically display and interpret compositional differences within each vegetation layer among sites, as related to hydrologic regime. For NMS, the data matrix consisted of sites (rows) and species (columns) that occurred in at least six sites. Data were square root transformed (basal area for overstory and sapling layers; densities for seedling/shrub layer) to down-weight the influence

of overly abundant species. NMS relaxes assumptions of normality and linear relationships to environmental variables, provides a biologically meaningful view of data and preserves distance properties among sample units (sites, in our case) (Clark, 1993; McCune and Grace, 2002). Ordinations were run using Sørenson (Bray–Curtis) distance measures and a specification of 6 dimensions and 250 iterations (with actual data) for the initial analysis. The significance of dimensional solutions was assessed using Monte Carlo permutation procedures (based on 249 interactions). Final ordinations were restricted to three dimensions based on stress reduction and examination of scree plots (McCune and Grace, 2002).

Multi-response permutation procedure (MRPP; Biondini *et al*., 1988) was used to test for differences in composition between hydrologic types. MRPP is a nonparametric procedure used to compare previously defined groups (McCune and Grace, 2002). MRPP was run using a Euclidean distance measure. Additionally, indicator species analysis (Dufrene and Legendre, 1997) was used to test for affinity of non-ash species with each hydrologic type. Indicator species analysis combines information on abundance and frequency of species occurrence in a group. It produces indicator values for species in each group which are then tested for statistical significance using a Monte Carlo permutation technique. Indicator values range from 0 (no association with a group) to 100 (perfect association). All multivariate procedures were performed using PC–ORD version 5.10 (McCune and Mefford, 2006). For statistical tests associated with multivariate procedures, a *P*-value of 0.10 or less was considered significant.

Basal area and density were summarized by vegetation layer (overstory, sapling, seedling/shrub) and species were classified into one of three groups: ash, non-ash trees (overstory capable), other woody species (small trees, shrubs). After checking assumptions of normality and homogeneity of variances, groups were compared between the hydraulic types using *t*-tests on untransformed or square root transformed data, or Mann–Whitney rank sum tests when data could not be normalized with a transformation. For these tests, a *P*-value of 0.05 was considered significant.

Selected traits were examined to assess the likelihood that a species could replace black ash in abundance. Traits included growth habit, life span, wetland indicator status, known health issues and vulnerability to climate change. Growth habit included overstory tree, small tree or shrub, with overstory trees having the potential to achieve dominant canopy positions and the other two categories found in sub-canopy positions. Life span was categorized as short (<80 years), medium (80-140), medium-long (>140-200), and long (>200-400+), with the assumption that longer-lived species have greater replacement value. Sources for the above traits included Barnes and Wagner (2004), Barnes *et al*. (2016), and the USDA Plants Database (USDA Natural Resource Conservation Service, 2020). Wetland indicator status also came from the USDA Plants Database (USDA Natural Resource Conservation Service, 2020) and included obligate wetland, facultative wetland, facultative, facultative upland and obligate upland, with the assumption that an ideal replacement should be an obligate or facultative wetland species. Health issues were derived from the expert knowledge of the region. Vulnerability to climate change for tree species was based on changes in importance value derived from Tree Atlas modelling (Prasad *et al*., 2007), specifically examining projected 'winners' and 'losers' under a high emissions scenario for the Northern Minnesota Drift and Lake Plains Section of the Laurentian Mixed Forest Province. The vulnerability of species not found in Tree Atlas was assessed by considering the current distribution, with northern latitude species considered vulnerable (likely decreasing habitat) and species with wide geographic distributions considered neutral (minimal change in habitat). We assumed that an ideal replacement species would be one predicted to have either little change or increasing habitat in the region.

Results

Compositional variation among sites

Thirty-six woody species were found in the 32 sites (Table 1). The NMS ordinations by vegetation layer, i.e. overstory, sapling, seedling/shrub, used those species that occurred in that respective layer (Table 1). All three ordinations converged on three axis solutions for each vegetation layer.

The NMS explained 86 per cent of variation in overstory composition. Final stress was 12.50, and instability was less than 0.001. Axes 1 and 3 accounted for most variation (65 per cent; Figure 1a). There was no clear separation of sites based on hydrologic type. This was confirmed by MRPP, finding more heterogeneity of composition within hydrologic types and less between than expected by chance Table 2). Indicator values were generally low for all species in the overstory (Table 3), with only balsam poplar (*Populus balsamifera* L.) having a significant association with the wet hydrologic type.

In the sapling layer, NMS explained 79 per cent of variation in composition among sites. Final stress was 14.50 and instability was less than 0.001. Axes 2 and 3 accounted for most variation (56 per cent; Figure 1b). There was no clear patterning of sites based on hydrologic type. This was confirmed by MRPP, finding more heterogeneity in composition within hydrologic types and less between them than expected by chance (Table 2). Most indicators values were low (Table 3). Only three species had significant association with a hydrologic type in the sapling layer including yellow birch (*Betula alleghaniensis* Britt.) with very wet swamps and balsam poplar and chokecherry (*Prunus virginiana* L.) with wet swamps.

In the seedling/shrub layer, NMS explained 83 per cent of variation in composition among sites. Final stress was 14.00 and instability was less than 0.001. Axes 1 and 2 accounted for most variation (63 per cent; Figure 1c). There was no clear separation of sites between hydrologic types. This interpretation was confirmed by MRPP, finding more heterogeneity of composition within hydrologic types and less between than expected by chance (Table 2). Indicator values were generally low (Table 3), with only two species having significant association with a hydrologic type in the seedling/shrub layer, both with wet swamps, including serviceberry (*Amelanchier* Medik.) and chokecherry.

Species abundance

Overstory layer

Black ash, and some green ash (*F. pennsylvanica* Marsh.), dominated the overstory of all sites (Figure 2a). While sites were chosen to include at least 50 per cent basal area in black ash,

Table 1 Woody species occurrence in different vegetation layers in two types of black ash wetlands as defined by hydrologic regime (wet ash swamp and very wet ash swamp).

Species	Growth Habit	Overstory[1]		Sapling[2]		Seedling/shrub[3]	
		Wet ash swamp	Very wet ash swamp	Wet ash swamp	Very wet ash swamp	Wet ash swamp	Very wet ash swamp
Fraxinus nigra	Lg. tree	100	100	100	100	93	94
F. pennsylvanica	Lg. tree	29	50	29	22	0	0
Acer rubrum	Lg. tree	14	33	21	39	21	33
A. saccharum	Lg. tree	0	22	7	11	0	0
Betula papyrifera	Lg. tree	43	50	29	33	21	0
B. alleghaniensis	Lg. tree	7	28	7	39	7	11
Larix laricina	Lg. tree	0	11	0	0	0	0
Picea glauca	Lg. tree	21	17	21	22	14	22
Populus balsamifera	Lg. tree	36	11	36	6	36	11
P. tremuloides	Lg. tree	50	39	38	17	7	17
Quercus rubra	Lg. tree	0	6	7	6	0	6
Q. macrocarpa	Lg. tree	21	22	21	22	29	28
Thuja occidentalis	Lg. tree	43	61	0	17	0	0
Tilia americana	Lg. tree	14	28	7	22	29	17
Ulmus americana	Lg. tree	57	67	64	78	43	67
Abies balsamea	Sm. tree	43	44	36	61	21	17
Acer negundo	Sm. tree	0	0	21	11	21	17
Amelanchier spp.	Sm. tree	0	0	36	11	57	11
Prunus nigra	Sm. tree	0	0	0	0	21	17
P. virginiana	Sm. tree	0	0	71	33	93	39
Acer spicatum	Shrub	na[4]	na	29	50	57	72
Alnus incana	Shrub	na	na	79	72	79	67
Cornus sericea	Shrub	na	na	0	0	64	50
Corylus cornuta	Shrub	na	na	0	6	88	67
C. americana	Shrub	na	na	7	6	21	17
Crataegus spp.	Shrub	na	na	0	0	7	0
Diervilla lonicera	Shrub	na	na	na	na	14	6
Lonicera hirsuta	Shrub	na	na	na	na	14	0
L. canadensis	Shrub	na	na	na	na	14	0
L. oblongifolia	Shrub	na	na	na	na	0	6
Rhamnus alnifolia	Shrub	na	na	0	0	57	50
Rosa acicularis	Shrub	na	na	na	na	14	11
Salix spp.	Shrub	na	na	29	11	14	0
Viburnum lentago	Shrub	na	na	0	0	21	6
V. rafinesquianum	Shrub	na	na	0	0	7	0
V. trilobum	Shrub	na	na	0	0	14	22

Values are the frequency of occurrence in sites: 14 for wet and 18 for very wet ash swamps. [1]Overstory trees with dbh $\geq$ 10 cm. [2]Sapling sized trees and larger shrubs (2.5 cm $\leq$ dbh $<$ 10 cm). [3]Seedling sized trees and smaller woody shrubs (dbh $<$ 2.5 cm and $\geq$ 0.5 m tall). [4]na = not applicable.

Table 2 Results of MRPP comparison between black ash wet and very wet hydrologic types based on woody vegetation composition

Structural layer	T[a]	A[b]	*P*
Overstory	-0.32	0.003	0.31
Sapling	-1.01	0.009	0.15
Seedling/shrub	-0.51	0.006	0.23

[a]T denotes degree of separation between groups (wet forest, very wet forest), with higher negative values indicating greater separation. [b]A denotes level of within-group agreement, comparing the distance within and between groups, with higher values indicating greater separation.

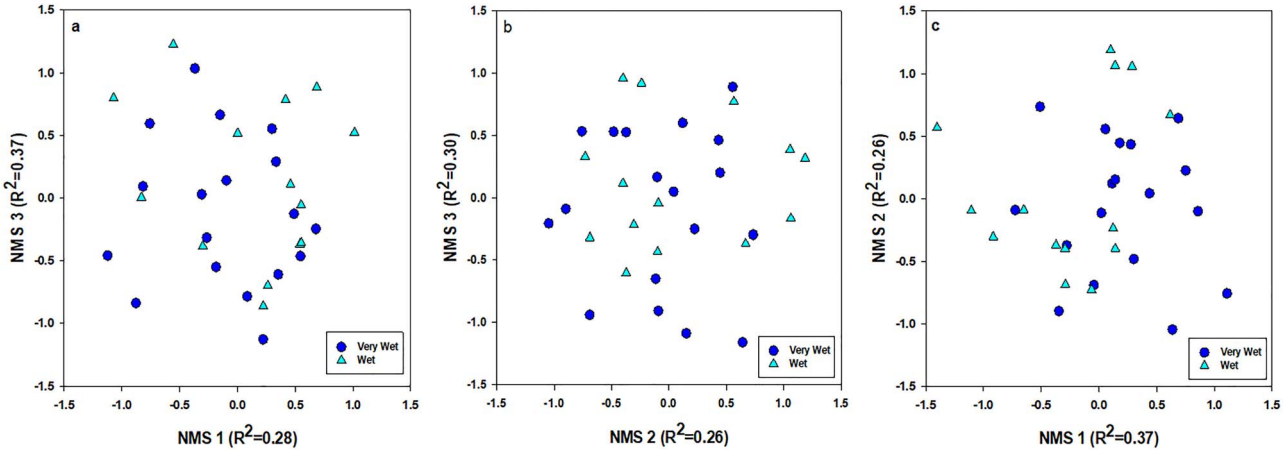

Figure 1 NMS of sites based on (a) overstory trees, (b) sapling layer and (c) seedling/shrub layer, each coded by wetland hydrologic type.

Table 3 Indicator values for non-ash woody species associated with two black ash wetland hydrologic types (wet ash swamp and very wet ash swamp) in Minnesota USA.

Species	Overstory		Sapling		Seedling/shrub	
	Wet swamp	Very wet swamp	Wet swamp	Very wet swamp	Wet swamp	Very wet swamp
Acer rubrum	4	28	8	24	10	21
Betula papyrifera	19	28	10	21	na	na
B. alleghaniensis	2	24	2	30*	na	na
Picea glauca	13	7	12	10	6	12
Populus balsamifera	28*	2	32*	1	28	2
P. tremuloides	31	14	23	6	na	na
Q. macrocarpa	8	14	10	12	9	19
Thuja occidentalis	16	38	na	na	na	na
Tilia americana	3	22	na	na	19	6
Ulmus americana	33	29	35	35	17	40
Abies balsamea	25	19	16	34	12	9
Acer negundo	na	na	na	na	14	6
Amelanchier spp.	na	na	3	27	42*	3
P. virginiana	na	na	49*	10	70*	9
Acer spicatum	na	na	13	26	25	41
Alnus incana	na	na	37	39	46	28
Cornus sericea	na	na	na	na	45	15
Corylus spp.	na	na	na	na	53	23
Rhamnus alnifolia	na	na	na	na	34	21
Salix spp.	na	na	17	5	na	na
V. trilobum	na	na	na	na	7	11

Indicator values range from 100 (perfect association with a group) to 0 (no association with a group). An indicator value was considered significant (denoted by *) at $P \leq 0.10$. Na denotes that the species did not occur in that structural layer.

the species was more abundant, comprising on average 85 per cent of basal area. There were no statistical differences between wetland hydrologic types in ash basal area or basal area of non-ash species (Table 4). Non-ash tree species were diverse (Table 1), but in total occurred in low abundance in both hydrologic types (Figure 2a) and frequency of occurrence was generally 50 per cent or less, except for American elm (*Ulmus americana* L.) and northern white cedar (*Thuja occidentalis* L.), which were found in over 60 per cent of very wet ash swamps (Table 1).

Sapling layer

Ash (mostly black ash) comprised the majority of sapling layer basal area, although values were variable among sites (Figure 2b). Non-ash, overstory-capable, trees and other woody species (small trees, shrubs) were less abundant, but generally less variable in abundance among sites. There were no significant differences in basal area between wetland hydrologic types for any of these groups (Table 4).

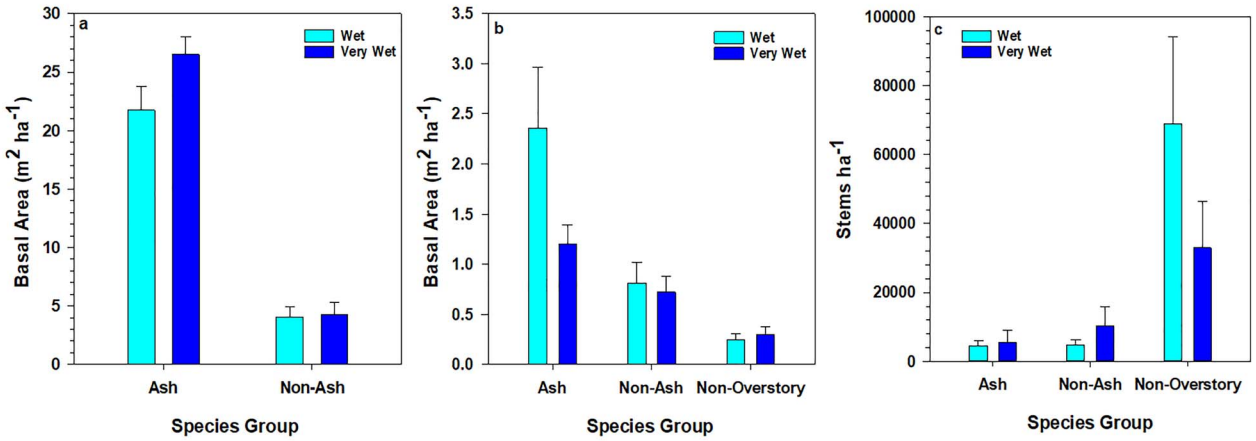

Figure 2 Abundance of woody species in (a) overstory (m^2 ha^{-1}), (b) sapling layer (m^2 ha^{-1}) and (c) seedling/shrub layer (stems ha^{-1}) in black ash sites, each coded by wetland hydrologic type. Ash includes black ash and green ash. See Table 1 for non-ash species.

Table 4 Statistical results of comparisons in species group abundance between black ash wet and very wet hydrologic types by structural layer

Structural layer	Species group	*t* value	Mann–Whitney U	*P*
Overstory	Ash basal area	−1.918	–	0.065
	Non-ash basal area	−0.131	–	0.897
Sapling	Ash basal area	–	85.0	0.124
	Non-ash basal area	–	115.5	0.704
	Non-overstory basal area	–	124.0	0.955
Seedling/shrub	Ash density	–	93.5	0.223
	Non-ash density	–	101.5	0.361
	Non-overstory density	–	81.0	0.091

There were nine non-ash overstory tree species that occurred in measureable abundance in the sapling layer (Table 1) and four species that occurred sporadically. The frequency of occurrence of non-ash trees was generally low (6–50 per cent of sites), except for American elm, which occurred in 64–78 per cent of sites (Table 1). There were nine non-overstory species (small trees, shrubs) that collectively had higher abundance than many of the individual tree species (Table 1). However, individually, they were infrequent, except for speckled alder (*Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) R.T. Clausen), which occurred in over 70 per cent of all sites, and chokecherry, which occurred in 71 per cent of wet swamps (Table 1).

Seedling/shrub layer

Overstory-capable trees, including ash and other species, were minor components of the seedling/shrub layer in both wetland hydrologic types (Figure 2c). There were no differences in densities of these two groups between hydrologic types (Table 4). Non-ash species were diverse (Table 1), but they were found inconsistently, occurring in generally less than 30 per cent of sites, except for American elm, which was found in 43-67 per cent of the sites (Table 1).

Non-overstory woody species (small trees and shrubs) collectively were more abundant on average than ash or other trees (Figure 2c), but densities were highly variable among sites. There was no significant difference between wetland hydrologic types in density of this species group (Table 4). There were 21 small tree and shrub species found in the seedling/shrub layer, but the frequency of occurrence was highly variable, ranging from 0 to 93 per cent of the sites (Table 1).

Species traits

Selected traits of non-ash woody species were assessed and compared with a hypothetical ideal replacement species. Traits of an ideal species include: facultative wetland or obligate wetland status, no significant regional health issues, long life span and stable or increasing habitat with climate change (Supplementary Table 1). As summarized below, no sampled species compared favourably with the idealized replacement species.

Of the 36 species sampled (Table 1), 13 were tree species with the potential to achieve canopy dominance (Supplementary Table 1). One additional species, balsam fir (*Abies balsamea* L.) is generally a smaller statured tree, but does have the potential to be abundant in terms of stem density and basal area in the lower canopy layer. All other woody species were either small trees or shrubs (Supplementary Table 1) and have limited or no potential

to be abundant in terms of basal area or stem densities in the overstory.

Of the 14 overstory-capable species, five are facultative wetland species, including tamarack (*Larix laricina* (Du Roi) K. Koch), balsam poplar, northern white cedar, American elm, and balsam fir (Supplementary Table 1). The first four have long potential life spans, while balsam fir is short-lived (Supplementary Table 1). Of these five species, four have significant regional health issues, including tamarack, northern white cedar, American elm and balsam fir. All of the species except American elm are considered climate change vulnerable (Supplementary Table 1).

Discussion

In this study, we asked how likely is it that black ash will be replaced by other tree species in black ash ecosystems after widespread mortality from EAB through expansion in the overstory or successional replacement from the sapling or seedling/shrub layers, and we asked if replacement potential varies between black ash wetland types that differ in hydrologic regime, as this thought to be a primary driver of black ash ecosystem differences in the study region (Aaseng, 2003; D'Amato *et al*., 2018).

We found that generally there is very low potential that other tree species will readily replace black ash naturally from either expansion in the overstory or through release of advance regeneration from lower vegetation layers. Similar conclusions were reached by Palik *et al*. (2012) after examining a different suite of black ash sites in northeastern Minnesota, USA, in a study that pre-dated the threat from EAB. Similarly, researchers in southern Michigan, USA concluded that sites with high ash dominance are likely to degrade to shrub communities after EAB mortality (Bowen and Stevens, 2018). Moreover, there are minimal differences in replacement potential between the two hydrologically defined black ash wetland types, at least in the mature, pre-disturbance forest; that is, they both lack potential resilience to the threat from EAB. This finding is notable, because the wetland types are classified based on differences in hydrology (Aaseng, 2003), which has been shown to influence plant community composition and richness (Diamond *et al*., 2020) and microtopography development (i.e. amount of suitable growing space; Diamond *et al*., 2019). Apparently, these differences do not result in large differences in tree composition between the two wetland hydrologic types.

There are several factors that further complicate replacement potential by non-ash tree species in these wetlands. Of the 36 woody species sampled, less than half (14) are species capable of achieving dominant positions in the overstory. Of these 14, only five are facultative wetland species and physiologically capable of establishing abundant populations in wetland settings. However, even these five species, including tamarack, balsam poplar, northern white cedar, American elm and balsam fir, have specific constraints that may limit the potential for expansion in abundance in the wake of black ash mortality.

Tamarack is being decimated by the eastern larch beetle in northern Minnesota (Minnesota Department of Natural Resources, 2020), ostensibly due to climate warming (McKee and Aukema, 2015). Northern white cedar is preferred browse of white-tailed deer (*Odocoileus virginianus*) throughout the Great Lakes region, which greatly limits the trees ability to establish and recruit into larger size classes (White, 2012). Balsam fir is a small-statured tree and is also relatively short-lived (USDA Natural Resource Conservation Service, 2020), characteristics that likely limit its desirability as a replacement for larger statured, long-lived black ash. It also is periodically severely impacted by spruce budworm outbreaks (Wolter *et al*., 2008). Moreover, all three of these non-ash species, along with balsam poplar, are predicted to have large reductions in habitat in the region by the end of the 21st century due to climate change (Iverson *et al*., 2016). Given that balsam poplar's primary limitation is from climate change, with no other immediate threats, and it occurs with some frequency in the 'drier' wetland type, the species might be a near-term replacement to consider. The final species, American elm, possesses characteristics that are desirable in a replacement species, including potentially long-lived and large-statured, and likely to have increased habitat suitability in the future with climate warming (Iverson *et al*., 2016). However, the species ability to develop and maintain populations of overstory trees is greatly limited by its susceptibility to Dutch elm disease (Knight *et al*., 2012). This introduced fungal disease typically kills trees before they reach larger size, thus limiting the species to sub-canopy positions.

The case for active management

Our results point to a need for silvicultural actions to establish regeneration of non-ash trees species in sites threatened by EAB, so as to promote resilience of ecosystem function. Potentially, with silvicultural treatment in mature forests, such as those examined, natural regeneration of non-ash species might increase in abundance (D'Amato *et al*., 2018). However, our results indicate that this regeneration will be largely from new individuals, rather than advance regeneration, since the latter is largely non-existent in the forests examined. This result also points to a likely need to supplement natural regeneration with artificial regeneration.

In other work, we have evaluated a suite of tree species planted in similar black ash wetlands. These include several native species found in the ecosystem in small numbers, as well as several novel species predicted to be adapted to these sites given a warming climate (Looney *et al*., 2015, 2017). Early results indicate that survival and growth is best for species that meet the criteria of the ideal replacement (Supplementary Table 1), including swamp white oak (*Quecus bicolor* Willd.), hackberry (*Celtis occidentalis* L.) and a Dutch elm disease tolerant variety of American elm. Moreover, growth and survival was generally best in treatments that employed partial cutting, such as group selection, which prevents excessive hydrologic changes or development of aggressive ground layer and shrub competition (Diamond *et al*., 2018; D'Amato *et al*., 2018). Similar trials are underway in Michigan and Wisconsin, USA to evaluate the potential for using regeneration harvests in conjunction with natural regeneration and planting of replacement species to sustain forested habitats after EAB infestations (Bolton *et al*., 2018; Wisconsin Department of Natural Resources, 2015).

Conclusions

Accumulating evidence points to a general lack of sufficient co-occurring woody species to replace black ash after anticipated wide-spread mortality from EAB in Minnesota, USA. Impacts to ecosystem function from loss of tree dominance may be severe. Given the large area of these ecosystems in the region, there is a growing sense of urgency to work proactively to establish site appropriate tree species through silvicultural treatment, potentially including native non-ash, as well as non-native species, that are future climate adapted.

Our results focusing on potential replacement tree species in black ash wetlands impacted by EAB can have wider relevance for considering how to manage for resilient ecosystems in other types of forests facing threats from invasive pest. For example, similar changes in ecosystem processes and community composition have been observed following the selective removal of eastern hemlock (*Tsuga canadensis* (L.) Carrière) by the introduced hemlock woolly adelgid (*Adelges tsugae*) in the eastern USA (Ellison *et al*., 2005). The reality is that it is becoming increasingly difficult to stop these major threats to foundational tree species, suggesting that active management to establish replacement species that are functionally similar and better adapted to the threat will become a common management goal.

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest statement

None declared.

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