Projet de stabilisation de berge et de réparation de structures de soutènement en bordure du fleuve Saint-Laurent par la Ville de Boucherville

6211-02-130

Poliquin, Renée (BAPE)

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Envoyé:	4 août 2016 11:12
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Objet:	RE: Demande d'information de la commission du BAPE concernant le projet de stabilisation de berge et de réparation de structures de soutènement en bordure du fleuve Saint-Laurent par la Ville de Boucherville
Pièces jointes:	Kloosteretal_2013_ash dynamics.pdf

Bonjour Madame Poliquin,

Veuillez trouver ci-après la réponse du MFFP à la question DQ7, reçue le 2 août 2016, en regard du projet cité en objet. L'article joint et cité ci-après fait également partie de la réponse.

Selon Klooster WS, Herms DA, Knight KS, Herms CP, McCullough DG, et al. 2013. Ash (Fraxinus spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (Agrilus planipennis). Biol. Invas. Doi:10.1007/s10530-013-0543-7 45. Knight KS, Brown JP, Long RP. 2012. Factors affecting the survival of ash, à la page 10 :

« The pattern of mortality was similar for all three ash species and across soil hydro-classes, suggesting that eastern North American forests containing white, green, and black ash trees are equally vulnerable to nearly complete EAB [Emerald Ash Borer]-induced ash mortality. »

(Traduction libre) Le patron de mortalité est semblable pour les trois espèces de frêne, quelle que soit la classe de drainage du sol, ce qui laisse croire que les forêts du Nord-est américain qui recèlent des frênes blanc, vert ou noir sont toutes aussi vulnérables à une mortalité associée à l'agrile du frêne.

Ainsi, les frênes ayant « les pieds dans l'eau » ne seraient pas plus résistants que les autres.

En espérant le tout satisfaisant, le Ministère se montre disponible pour répondre à tout complément d'information ou autre question.

Cordiales salutations,

Marie-Hélène Grignon
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ORIGINAL PAPER

Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*)

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Abstract Emerald ash borer (EAB; *Agrilus planipennis*) has killed millions of ash trees and threatens ash throughout North America, and long-term persistence of ash will depend on the potential for regeneration. We quantified ash demography, including mortality and regeneration, of *Fraxinus americana* (white ash), *Fraxinus pennsylvanica* (green ash), and *Fraxinus nigra* (black ash) in mixed hardwood forests near the epicenter of the EAB invasion in southeastern Michigan and throughout Ohio. Plots were established across a gradient of ash densities. Ash was the most important species in hydric sites, and ranked second among all species in mesic and xeric sites. In sites nearest the epicenter in Michigan, ash mortality exceeded 99 % by 2009, and few or no newly germinated ash seedlings were observed, leaving only an "orphaned cohort" of established ash seedlings and saplings. As ash mortality increased, the number of viable ash seeds in soil samples decreased sharply, and no viable seeds were collected in 2007 or 2008. In Ohio sites farther from the epicenter, densities of new ash seedlings were much higher in plots with healthy ash trees compared to plots where trees had died. EAB was still present in low densities in Michigan and Ohio stands in 2012 where average mortality of ash was nearly 100 %. The future of ash at these sites will depend on the outcome of the dynamic interaction between the orphaned cohort of previously established ash seedlings and saplings and low density EAB populations.

Keywords Ash regeneration · Demography · Invasive forest pest · Seedlings

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Introduction

North American forests have experienced multiple invasions by devastating alien pathogens and insects including chestnut blight (*Cryphonectria parasitica* (Murrill) Barr), Dutch elm disease (*Ophiostoma ulmi* (Buism.) Nannf. and *O. novo-ulmi* Brasier), beech bark disease (*Cryptococcus fagisuga* Lind. and its fungal associates), hemlock woolly adelgid (*Adelges tsugae* Annand), and gypsy moth (*Lymantria dispar* L.), all of which have altered forest community composition, structure, and successional trajectories (Orwig 2002; Lovett et al. 2006; Gandhi and Herms 2010a). Effects of invasive organisms on the demography of dominant species can result in a cascade of direct and indirect ecological impacts (Gandhi and Herms 2010a). For example, changes in vertebrate and invertebrate communities (Martin et al. 1951; Faanes 1984; Gandhi and Herms 2010b), and facilitation of invasive plant species (Eschtruth et al. 2006) may occur following extensive tree mortality.

In recent years, emerald ash borer (EAB, *Agrilus planipennis* Fairmaire) has killed tens of millions of ash trees in the north central United States and neighboring Canada since its introduction from Asia, and threatens ash throughout North America as it continues to spread (Cappaert et al. 2005; Poland and McCullough 2006). White (*Fraxinus americana* L.), green (*Fraxinus pennsylvanica* Marsh.), and black (*Fraxinus nigra* Marsh.) ash are widely distributed throughout eastern North America and are highly susceptible to EAB (Poland and McCullough 2006; Smith 2006; Anulewicz et al. 2007; Whitehill et al. 2009). Widespread EAB-induced ash mortality threatens a variety of ecosystems since these tree species occur and are often abundant in diverse habitats (MacFarlane and Meyer 2005). EAB is representative of many invasive species that exhibit stratified dispersal. Infestations in southeastern Michigan near the invasion epicenter where EAB has been established longest are largely representative of natural spread; in contrast, sites in Ohio are largely outlier infestations resulting from human assisted dispersal (Cappaert et al. 2005).

Long-term persistence of ash in forests invaded by EAB will depend on the potential for regeneration. Ash trees reproduce from seeds that are shed in the fall (Griffith 1991; Gucker 2005a). Trees of some species can take up to 60 years to reach reproductive maturity

[20–25 cm diameter at breast height (dbh)] (Kurmis and Kim 1989). Earliest flowering in ash occurs when the trees are 8–10 cm dbh (Kennedy 1990; Schlesinger 1990), whereas EAB can colonize and kill trees as small as 2.5 cm dbh (McCullough et al. 2008; Rebek et al. 2008), which eliminates individuals from the population before they reach reproductive maturity. Seed production varies from year to year, and occasional mast years greatly increase the reproductive potential (Boerner and Brinkman 1996). On the forest floor, the majority of seeds are thought to germinate 2–3 years after seed rain (Clark 1962; Leak 1963), whereas in laboratory collections, seeds have remained viable for 7 years (Kennedy 1990; Bonner 2008). Ash seedlings are moderately shade-tolerant. The potential for ash regeneration will be determined by whether an ash seed bank persists longer than EAB in the forest communities, and/or if populations of seedlings and saplings reach reproductive maturity as EAB populations collapse following elimination of their host plants.

The objective of this study was to quantify ash demography, including mortality and regeneration, in mixed hardwood forests that varied in their degree of ash mortality. Specifically, we (1) documented ash mortality over time; (2) characterized the ash seed bank in relation to ash decline; and (3) quantified density of newly germinated ash seedlings, established ash seedlings, and ash saplings within EAB-impacted forests. Ash monitoring plots were established near the epicenter of the EAB invasion in the Upper Huron River Watershed in southeast Michigan where ash mortality was high, and across Ohio where EAB outlier populations of different ages had resulted in varying levels of ash mortality. This allowed us to characterize ash demography and regeneration dynamics across a gradient of EAB-induced ash mortality ranging from zero to 100 %.

Methods

Michigan sites

Beginning in 2004, transects were established through 38 forested stands on public land (Huron River MetroParks and Michigan State Recreation Areas) within the Upper Huron River Watershed in southeastern Michigan (Fig. 1a). Transects were located

28–45 km from the epicenter of the EAB invasion near Westland, Michigan (Siegert et al. 2008), and have experienced the longest duration of EAB infestation in North America. During the initial stages of the study, transects encompassed a gradient of EAB-induced ash mortality ranging from very low to nearly 100 % (Smith 2006). To compare transects with different environmental characteristics, transects were classified according to edaphic conditions and the dominant ash species present. Transects in well-drained upland sites with white ash as the most common ash species were classified as xeric. Transects in sites that were moderately well-drained but with seasonal standing water and green or black ash as the most common ash species were classified as mesic. Transects in marshes or along riparian floodplains, frequently containing standing water and mostly black or green ash, were classified as hydric.

Each transect consisted of three replicate circular plots, each with a radius of 18 m. Within each main plot was a centrally located subplot (8 m radius) surrounded by four microplots (4 m^2) placed 8 m from the plot center in each cardinal direction (Fig. 1b). Plot centers were separated by an average of 77 m. All plots contained at least two mature ash trees ≥10 cm dbh and were established across a gradient of ash densities to encompass a range from low to high (10–413 trees per ha). See Smith (2006) for a detailed description of plot establishment, characterization, and maps.

Ohio sites

Ohio sites included non-infested sites and sites with outlier satellite EAB populations that varied in time since infestation, thus providing a gradient of EAB-induced ash mortality from none to high that can serve as a frame of reference for comparing regeneration with the severely impacted sites in Michigan. Between 2005 and 2008, 62 forested transects were located on public and private lands in 20 counties throughout Ohio (Fig. 2a). Plot design followed that for Michigan except that plots were smaller. Each transect contained three plots, with individual plots separated by ≥20 m. Plots were circular, with an 11.4-m radius main plot, an 8-m radius subplot, and four 4-m^2 microplots 6 m from the plot center in each cardinal direction (Fig. 2b). Plots contained a minimum of two ash trees with dbh ≥10 cm.

Stand characterization (MI sites)

The density of ash in Michigan sites prior to EAB impact was calculated from the living and dead (standing or fallen) ash trees using a modification of the Forest Inventory and Analysis technique (i.e. US Forest Service 2007). Because EAB was already killing ash trees at the beginning of the study, both living and dead ash trees were included to document the pre-invasion state of the community when nearly all ash trees were alive. Total ash density (trees per ha) was calculated for each plot, and then relative density of ash was calculated by dividing the density of ash trees by the densities of all trees in the plot, then multiplying by 100. Relative ash density for each transect was calculated by averaging the relative densities of each of the three replicated plots. Total ash basal area was calculated by summing the basal area (calculated from dbh measurements) of all ash trees per plot. Relative dominance of ash was calculated for each plot by dividing the total basal area of all ash trees by the sum of the basal areas of all trees, then multiplying by 100. Transect-level relative ash dominance was calculated by averaging the three replicate plots within each transect. Transect-level relative frequency of ash was calculated by dividing the absolute frequency of ash (percentage of plots within each transect that contained ash) by the sum of the absolute frequencies of all overstory trees, and multiplying by 100. Relative importance values were calculated for all ash trees ≥12.5 cm dbh by transect by adding together the density, dominance, and frequency of ash relative to all overstory species. The maximum theoretical relative importance value for a single taxa, or the sum of the importance values for all taxa, was 300 for each stand.

Ash decline and mortality (MI and OH sites)

In Michigan, percentage ash mortality at the transect level was quantified annually from 2004 to 2010. Ash trees with dbh ≥2.5 cm were surveyed within the 8-m subplots, and ash ≥12.5 cm dbh were surveyed in the entire 18-m radius main plots, with trees classified as either living or dead. Any root sprouts present were recorded along with their number and condition.

In Ohio, transect-level ash decline was characterized by rating the degree of canopy decline of individual ash trees in plots, and averaging across

Fig. 1 a Location of Michigan plots within the Upper Huron River Watershed in southeastern Michigan and **b** detail of plot design. To allow for different sampling intensities, plots were composed of an *18-m* radius main plot, *8-m* radius subplot, and four *4-m²* microplots
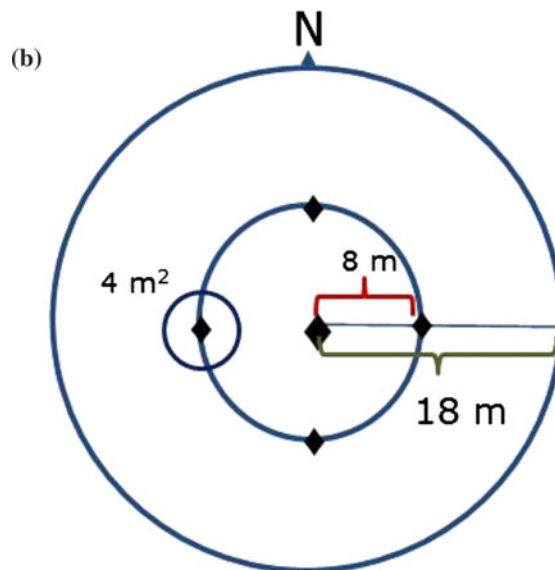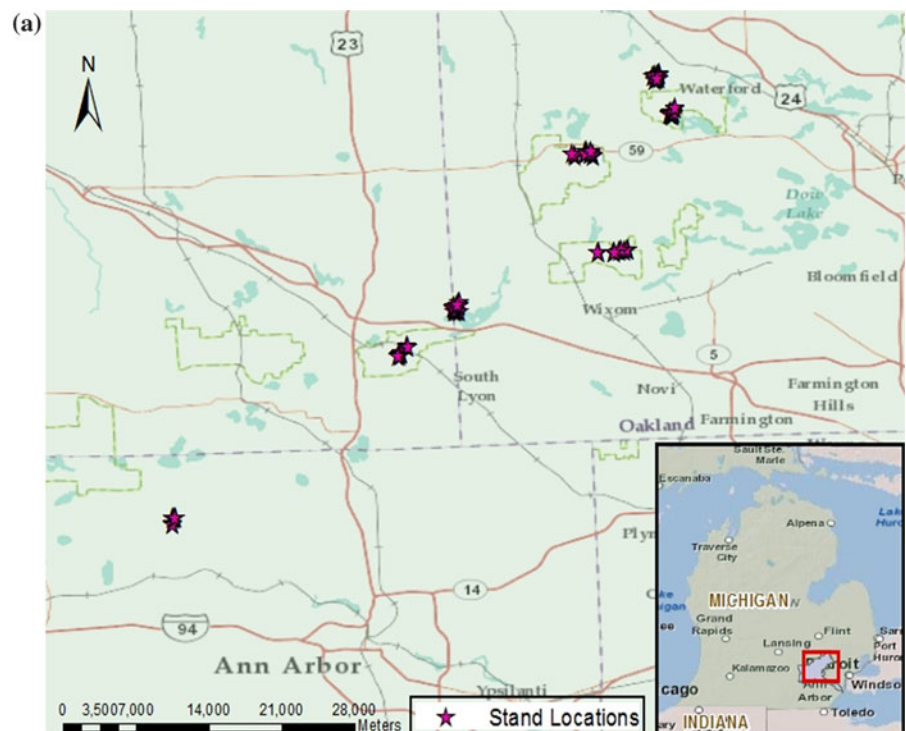
transects. Ash trees with dbh ≥10 cm were rated on a scale of 1–5 based on the amount of leaf area, since ash decline associated with EAB is typically indicated by a thinning canopy. A rating of 1 represented a healthy tree showing no symptoms of canopy thinning, 2–4 corresponded to light, intermediate, and severe canopy thinning, respectively, and 5 represented a completely dead canopy (Smith 2006) (Fig. 3). This rating scale has been shown to be strongly correlated with EAB larval density (Flower et al. 2013). Stand-level ash decline was calculated as the average of the individual tree ratings. Percentage of ash mortality (based on number of trees with canopy ratings of 5) was quantified annually from 2005 to 2010.
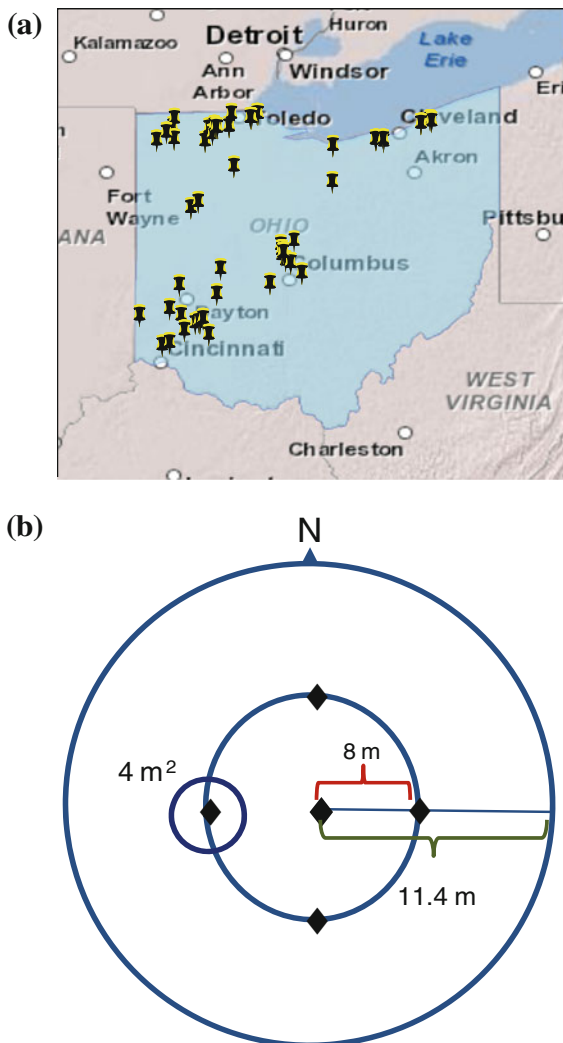
(a)

(b)

Fig. 2 **a** Location of Ohio plots and **b** detail of plot design. To allow for different sampling intensities, plots were composed of an *11.4-m* radius main plot, *8-m* radius subplot, and four *4-m²* microplots

Seed bank dynamics (MI sites)

To characterize the ash seed bank in Michigan sites, soil samples were collected annually in August from a subset of the 38 transects from 2005 to 2008. Transects were selected to represent gradients of ash density, time since EAB infestation, and soil hydrological condition (hydric, mesic, and xeric). In 2005, samples were collected in nine transects (27 plots) with four pairs of replicate soil cores taken per plot at two depths (see below) (16 cores per plot), for a total of 432 samples. Paired samples were taken in each of the four cardinal

directions at a random distance from the plot center, with pairs taken 1 m apart. In 2006–2008, efforts were expanded to sampling in 18 transects (54 plots) per year, but only from one depth (see below) (8 cores per plot). As in 2005, replicate samples were taken, for a total of 432 soil samples collected each year from 2006 to 2008.

Soil samples were extracted using an AMS® slide hammer (Forestry Suppliers, Inc., Jackson, MS); soil cores were 5 cm diameter × 10 cm deep for a volume of 200 cm³ and a surface area of 20 cm². In 2005, paired soil cores were collected at two depths (0–10 cm and 10–20 cm). Because there were only 9 viable seeds (out of 63 total seeds) in the deeper cores in 2005, samples were taken only at a depth of 0–10 cm from 2006 to 2008.

To determine their viability, seeds were analyzed using pressure and tetrazolium tests, or were germinated. One soil sample from each pair was dried and sieved for ash seeds and seed fragments. Ash seeds and seed fragments were counted, and the presence of an embryo was determined using pressure tests (Sawma and Mohler [2002]). Seeds containing embryos were further tested using tetrazolium stain to check for viability (Peters [2005]). The other soil sample from each pair was cold stratified at 4 °C for 5–6 months, andseed viability was determined by greenhouse germination (Cardina and Sparrow [1996]). Prepared soil samples were sieved and placed in 11 × 11 × 7 cm trays in a greenhouse set at 24 °C day/20 °C night for three months, and the number of germinated ash seedlings was recorded. Any ash seeds or seed fragments detected while sieving were recorded.

Ash seedling and sapling demography (MI and OH sites)

Densities of ash seedlings and saplings (plants per ha) were characterized in Michigan and Ohio sites between June and September from 2008 to 2010. Newly germinated ash seedlings (as indicated by the presence of cotyledons) and established ash seedlings (lacking cotyledons up to 1.37 m tall) were counted in the 4-m² microplots in Michigan and Ohio. To detect changes in density at a finer scale, established ash seedlings were further separated into seedlings ≤25 cm tall and those >25 cm tall but <2.5 cm dbh in 2009 and 2010 in Michigan. Newly germinated seedlings were also counted in 2011 in Michigan plots. Ash saplings (>1.37 m tall and <2.5 cm dbh) were counted in 8 m subplots in Michigan and Ohio from 2008 to 2010.
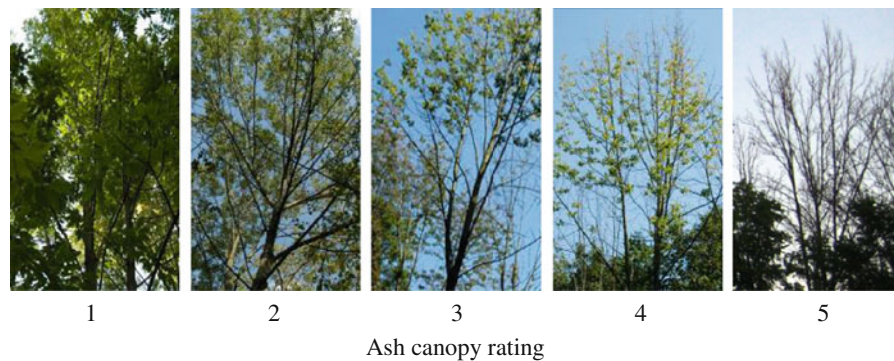
Fig. 3 Pictorial representation of the *1–5* ash decline rating scale, with *1* indicating a healthy tree, *5* indicating a dead tree, and *2–4* representing increasing stages of tree decline (as evidenced by canopy thinning and dieback) (Smith 2006)

Data analyses

The unit of replication was transect-level. All data were checked for assumptions of normality and heterogeneity of variance. Ash density, basal area, and dominance values were log transformed, and established seedling densities were log transformed to satisfy normality assumptions. Analysis of variance (ANOVA) was used to test for differences in characteristics among three hydrological classes (xeric, mesic, and hydric) for: (1) ash characteristics including density, basal area, dominance, and importance value; and (2) number of viable seeds in the seed bank. Following a significant F-test, means were separated using a multiple comparisons procedure (pdiff); data are presented as mean ± SE. New and established ash seedling, sapling, and tree densities in Michigan and Ohio sites were zero-inflated and therefore analyzed using the nonparametric Kruskal–Wallis test. The relationship between ash mortality and number of viable seeds in the seed bank was quantified using Spearman's correlation coefficients. All analyses were performed using SAS 9.3 (SAS Institute Inc. 2011, Cary, NC, USA).

Results

Site characteristics and ash mortality in Michigan sites

In Michigan, ash density (stems per ha) for trees ≥12.5 cm dbh was highest in hydric transects, intermediate in mesic transects, and significantly lower in xeric transects ($F = 18.27$; $df = 2, 111$; $p < 0.0001$; Table 1). A similar trend was observed for relative density ($F = 17.95$; $df = 2, 111$; $p < 0.0001$), relative dominance (percentage of total basal area that was ash species) ($F = 6.23$; $df = 2, 111$; $p = 0.0027$), and relative importance values ($F = 8.96$; $df = 2, 35$; $p = 0.0007$), which were also greater in hydric transects than in xeric or mesic transects (Table 1). Total ash basal area (m^2 per ha) followed a similar pattern, but the differences were not significant (Table 1).

Ash was the most important tree species in hydric transects, whereas it ranked second among all species in mesic and xeric transects. Within hydric transects, ash had a mean importance value of 79, followed by *Acer* (61) and *Ulmus* species (35). Within mesic transects, importance value was highest for *Quercus* species (65), while ash ranked second (58) and *Acer* species ranked third (46). A similar pattern was found in xeric transects, where the mean importance value was greatest for *Quercus* species (66), followed by ash (51) and *Acer* species (40).

In Michigan, cumulative ash mortality (trees ≥2.5 cm dbh in subplots and ≥12.5 cm dbh in main plots) more than doubled from 40 % in 2005 to 99.7 % in 2009, before declining slightly to 97 % in 2010 (Fig. 4). Percentage ash mortality decreased slightly in 2010 as the number of ash saplings entering the ≥2.5 cm dbh size class increased and were subsequently included in the mortality assessment. In Ohio, average transect-level ash mortality for trees ≥10 cm dbh ranged from 0 to 100 %, with sites infested longer exhibiting greater mortality (data not shown).

Table 1 Density (stems per ha), relative density (% ash stems per ha), total basal area (BA; m² per ha), relative dominance (% ash BA per ha), and importance value for all ash species (white, green, and black) in xeric, mesic, and hydric stands within the Upper Huron River Watershed in southeastern Michigan

Ash characteristic	Xeric N = 45	Mesic N = 36	Hydric N = 33
Density (stems ha^{-1})	77.1 ± 7.6 b	124.7 ± 9.6 a	174.5 ± 17.1 a
Relative density (% ash stems ha^{-1})	18.6 ± 1.6 c	25.3 ± 1.9 b	36.5 ± 2.6 a
Total BA (m² ha^{-1})	5.3 ± 0.5 a	6.3 ± 0.6 a	7.5 ± 0.8 a
Relative dominance (% ash BA ha^{-1})	19.4 ± 1.8	22.7 ± 2.1 b	30.7 ± 2.8 a
Importance value	54.2 ± 4.8 b	62.5 ± 5.1 b	85.8 ± 6.3 a

Values (given as lsmeans ± se) represent all living and dead ash trees ≥12.5 cm dbh identified during plot establishment. Means within a row followed by different letters are significantly different (ANOVA, $p = 0.05$)

Seed bank dynamics in Michigan sites

Total number of viable ash seeds in the soil samples declined from 2005 to 2008, and no viable seeds were collected in 2007 or 2008 in any of the hydrological classes (Fig. 5; Table 2). In 2005 and 2006, the majority (88 %) of seeds collected (n = 106) were from mesic transects with about equal numbers in xeric and hydric transects (Table 2). In 2005, 56 % of the seeds found were viable (11 of 11 seeds germinated, and 24 of 52 seeds were found chemically viable). The main cause of non-viability was lack of an embryo, although some seeds were non-viable due to insect or fungal damage. In 2005, most seeds (73 %; n = 63) were found within 10 cm of the soil surface (data not shown), leading to the decision to sample only this layer in subsequent years. Although we doubled the number of transects sampled in 2006, fewer seeds were collected than in 2005, and only 30 % were viable (2 of 3 seeds germinated, and 11 of 40 seeds were found chemically viable). Density of viable seeds declined by more than an order of magnitude from 2005 to 2006 in mesic sites (Fig. 5); ash seed density was much lower in hydric and xeric transects compared to mesic transects in 2005 and 2006.
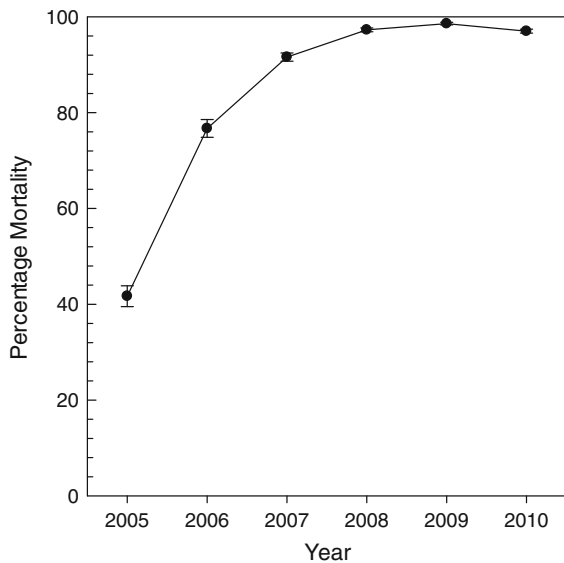
Ash seedling and sapling demography in Michigan sites

In 2008, no new ash seedlings were found in hydric transects, only a few were found in xeric transects, and
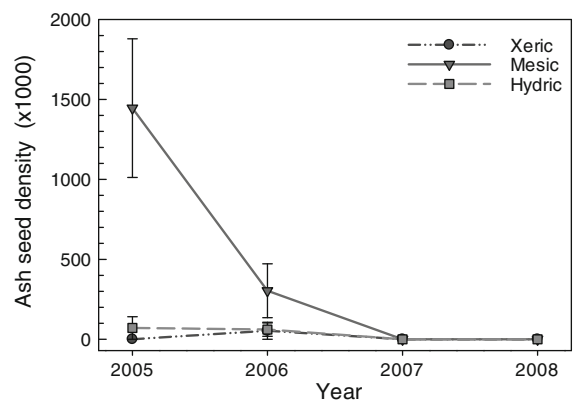

Fig. 4 Percentage ash mortality of trees ≥2.5 cm dbh in subplots and ≥12.5 cm dbh in main plots from 2005 to 2010 in 38 forested stands within the Huron River Watershed in southeastern Michigan

Fig. 5 Density of viable ash seeds in 18 forested stands across three hydrological classes within the Upper Huron River Watershed in southeastern Michigan

significantly more were found in mesic transects (Table 3). A similar trend for new seedling density was observed in 2009. In 2010, density of new seedlings did not differ among hydrological classes. Density of new seedlings, averaged across all hydrological classes, was about 10 times higher in 2008 compared to 2009 or 2010 ($\chi^2 = 34.78$; $df = 2$; $p < 0.0001$).

Across all years, established seedlings (<1.37 m tall) was the most abundant demographic class of ash (Table 3). In 2008–2010, average density of established seedlings was lowest in hydric transects, intermediate in xeric transects, and greatest in mesic transects (Table 3). Differences among years were not significant. In 2009 and 2010, most of the established ash seedlings were ≤25 cm tall (Table 4), and density was lowest in hydric transects, intermediate in xeric transects, and greatest in mesic transects. Ash seedlings >25 cm tall were less abundant, presumably due to natural self-thinning (Franklin et al. 2002). Density of established seedlings > 25 cm tall did not vary by hydrological class for either year.

Density of ash saplings (>1.37 m tall and dbh <2.5 cm) was greater in hydric and mesic transects compared to xeric transects for all 3 years (Table 3). Density of ash trees >2.5 cm was greatest in hydric transects compared to mesic or xeric transects for 2008–2010 (Table 3). No living root sprouts were observed on ash trees with dead canopies.

Ash seedling and sapling demography in Ohio sites

In Ohio, density of new ash seedlings, averaged across hydrological classes, was significantly lower in 2008 than in 2009 and 2010 ($\chi^2 = 167.13$; $df = 2$; $p < 0.0001$). In 2008, density of new ash seedlings averaged 1,401 ± 633 per ha, and was lowest in mesic transects, intermediate in hydric transects, and highest in xeric transects (Table 5). In 2009, after a 2008 mast year for ash seeds (KSK, personal observation), density of newly germinated ash seedlings increased to 28,787 ± 4,751 per ha, and mesic sites had higher seedling densities than hydric or xeric transects. In 2010, density of new seedlings averaged 44,539 ± 7,278 per ha, and was greater in xeric transects than in hydric or mesic sites.

Averaged across hydrological classes, density of established ash seedlings was greater in 2010 than in 2008 and 2009 ($\chi^2 = 57.98$; $df = 2$; $p < 0.0001$); however, there was a significant interaction between year and hydrological class ($F = 15.2$; $df = 4$; $p < 0.0001$). In 2008 and 2009, density of established seedlings did not vary between hydrological class; however, in 2010, density of established seedlings was lowest in hydric transects, intermediate in mesic transects, and highest in xeric transects (Table 5).

The density of new ash seedlings was correlated with average stage of ash canopy decline in 2008 ($N = 50$; $p = 0.0089$; rho $= -0.37$) and 2009

Table 2	Years	Hydrological class	# of stands	# of samples	Nonviable	Viable
Total number of nonviable and viable seeds in two replicate soil cores (5 cm diam, 10 cm deep) sampled from forested stands within the Upper Huron River Watershed in southeastern Michigan from 2005 to 2008	2005	Hydric	3	144	1	1
		Mesic	5	240	27	34
		Xeric	1	48	0	0
		Total	9	432	28	35
	2006	Hydric	7	168	5	2
		Mesic	7	168	22	10
		Xeric	4	96	3	1
		Total	18	432	30	13
Viability of seeds was determined by germination analysis for one replicate and pressure and tetrazolium (TZ) analysis for the other. In 2005, soil cores were taken at two depths (0–10 cm and 10–20 cm), but only the upper layer was sampled in 2006–2008	2007	Hydric	7	168	3	0
		Mesic	7	168	5	0
		Xeric	4	96	1	0
		Total	18	432	9	0
	2008	Hydric	7	168	3	0
		Mesic	7	168	5	0
		Xeric	4	96	1	0
		Total	18	432	9	0

Table 3 Density of living ash seedlings, saplings, and trees per ha (±SE) within the Upper Huron River Watershed in southeastern Michigan from 2008 to 2010, organized by size and hydrological class

Size class	Hydrological class	2008 Ash ha^{-1}	2009 Ash ha^{-1}	2010 Ash ha^{-1}
New seedlings	Hydric	0 ± 0 b	21 ± 21 b	21 ± 21 a
	Mesic	2,266 ± 869 a	143 ± 43 a	0 ± 0 a
	Xeric	57 ± 57 b	0 ± 0 b	0 ± 0 a
Kruskal–Wallis test		$\chi^2 = 12.19; p = 0.0023$	$\chi^2 = 11.42; p = 0.0033$	$\chi^2 = 2.70; p = 0.2592$
Established seedlings	Hydric	18,229 ± 8,069 b	11,354 ± 3,333 c	9,250 ± 2,783 c
	Mesic	272,500 ± 40,744 a	239,857 ± 31,023 a	202,370 ± 26,559 a
	Xeric	102,102 ± 40,551.4 b	65,928 ± 15,885 b	43,542 ± 10,785 b
Kruskal–Wallis test		$\chi^2 = 16.32; p = 0.0003$	$\chi^2 = 54.42; p < 0.0001$	$\chi^2 = 57.58; p < 0.0001$
Saplings <2.5 cm dbh	Hydric	357 ± 147 a	458 ± 159 a	486 ± 180 a
	Mesic	75 ± 31 a	287 ± 164 a	274 ± 139 a
	Xeric	9 ± 9 b	72 ± 57 b	133 ± 109 b
Kruskal–Wallis test		$\chi^2 = 7.99; p = 0.0184$	$\chi^2 = 11.74; p = 0.0028$	$\chi^2 = 7.67; p = 0.0216$
Trees ≥2.5 cm dbh	Hydric	11.1 ± 3.5 a	11.8 ± 6.0 a	16.7 ± 6.0 a
	Mesic	3.1 ± 1.4 b	1.6 ± 0.8 b	1.4 ± 0.9 b
	Xeric	3.6 ± 2.3 b	0.6 ± 0.4 b	2.7 ± 1.7 b
Kruskal–Wallis test		$\chi^2 = 12.95; p = 0.0015$	$\chi^2 = 9.60; p = 0.0082$	$\chi^2 = 14.29; p = 0.0008$

Size classifications: new (first-year seedlings with cotyledons) and established seedlings (<1.37 m tall) counted in four 4-m^2 microplots per plot; saplings (≥1.37 m tall, <2.5 cm dbh) counted in each 8-m radius subplot; and trees ≥2.5 cm dbh counted in each 8-m radius subplot and ≥12.5 cm dbh counted in each 18-m radius main plot

Means within year and size class followed by different letters are significantly different (ANOVA, $p = 0.05$)

Table 4 Density of established ash seedlings per ha (±SE) in forested stands within the Upper Huron River Watershed in southeastern Michigan in 2009 and 2010, classified into two size classes: established seedlings ≤25 cm tall, and established seedlings >25 cm tall

Size class	Hydrological class	2009 Ash ha^{-1}	2010 Ash ha^{-1}
≤25 cm tall	Hydric	8,229 ± 2,976 c	6,813 ± 2,467 c
	Mesic	235,104 ± 31,038 a	197,787 ± 26,515 a
	Xeric	62,614 ± 15,928 b	40,019 ± 10,689 b
Kruskal–Wallis test		$\chi^2 = 57.22; p < 0.0001$	$\chi^2 = 58.89; p < 0.0001$
>25 cm tall	Hydric	3,125 ± 832 a	2,438 ± 603 a
	Mesic	4,753 ± 1,031 a	4,583 ± 873 a
	Xeric	3,314 ± 923 a	3,523 ± 935 a
Kruskal–Wallis test		$\chi^2 = 2.65; p = 0.2653$	$\chi^2 = 2.13; p = 0.3440$

Means within year and size class followed by different letters are significantly different (ANOVA, $p = 0.05$)

($N = 50; p = 0.0002;$ rho $= -0.50$). In 2008, density of newly germinated ash seedlings ranged from 3,000 per ha in sites with an average ash canopy rating of 1 (healthy canopy), to zero in sites with average canopy ratings of 4 (severe dieback) and 5 (dead) (Fig. 6). In 2009, following a mast year, density of new ash seedlings increased dramatically in all plots with living ash trees (average ash canopy ratings of 1–4), with density ranging from 24,000 to 40,000 seedlings per ha. In comparison, plots in which all ash trees had died (average canopy rating of 5) had just over 1,300 new ash seedlings per ha in 2009. Density of ash saplings was relatively consistent across all years and did not vary by hydrological class (Table 5).

Table 5 Density of ash seedlings and saplings per ha (±SE) in Ohio from 2008 to 2010 according to size and hydrological class

Size class	Hydrological class	2008 Ash ha^{-1}	2009 Ash ha^{-1}	2010 Ash ha^{-1}
New	Hydric	1,354 ± 1,101 ab	23,998 ± 5,572 b	8,495 ± 2,117 b
	Mesic	85 ± 44 b	40,818 ± 17,970 a	20,767 ± 6,964 b
	Xeric	2,050 ± 1,130 a	28,286 ± 3,771 b	76,714 ± 13,787 a
Kruskal–Wallis test		$\chi^2 = 10.25; p = 0.0059$	$\chi^2 = 7.29; p = 0.0261$	$\chi^2 = 52.39; p < 0.0001$
Established	Hydric	6,111 ± 1,547 a	3,840 ± 854 a	6,736 ± 1,140 c
	Mesic	5,298 ± 1,422 a	3,253 ± 968 a	10,639 ± 4,471 b
	Xeric	6,801 ± 1,960 a	3,999 ± 754 a	19,120 ± 2,260 a
Kruskal–Wallis test		$\chi^2 = 0.62; p = 0.7338$	$\chi^2 = 2.60; p = 0.2719$	$\chi^2 = 38.83; p < 0.0001$
Saplings	Hydric	39 ± 15 a	36 ± 16 a	32 ± 16 a
	Mesic	54 ± 28 a	45 ± 24 a	40 ± 21 a
	Xeric	81 ± 45 a	77 ± 41 a	80 ± 43 a
Kruskal–Wallis test		$\chi^2 = 2.33; p = 0.3118$	$\chi^2 = 1.44; p = 0.4867$	$\chi^2 = 0.22; p = 0.8961$

Size classifications: new (first-year seedlings with cotyledons), established seedlings (<1.37 m tall), and saplings (≥1.37 m tall and <2.5 cm dbh). Values are averaged across all percent mortality levels within each hydrological class

Means within year and size class followed by different letters are significantly different (ANOVA, $p = 0.05$)

Discussion

Analysis of patterns of EAB-induced ash mortality, ash seed bank dynamics, and seedling and sapling demography revealed that new ash regeneration ceased as ash mortality approached 100 %, suggesting that the future of ash at these sites will depend on survival and reproduction of an "orphaned cohort" of previously established ash seedlings and saplings. As mortality of ash trees greater than 2.5 cm dbh exceeded 90 % by 2007 in Michigan, the ash seed bank was rapidly depleted. By 2009 in the Michigan sites, ash mortality exceeded 99 % and no newly germinated ash seedlings were observed, leaving only previously established ash seedlings and saplings. This sharp decline in ash density in southeast Michigan in response to the EAB invasion stands in stark contrast to increased ash density observed throughout much of the rest of its range (Pugh et al. 2011). Similar patterns were observed in Ohio, with ash regeneration decreasing sharply as EAB-induced ash mortality increased.

The pattern of mortality was similar for all three ash species and across soil hydro-classes, suggesting that eastern North American forests containing white, green, and black ash trees are equally vulnerable to nearly complete EAB-induced ash mortality. Density
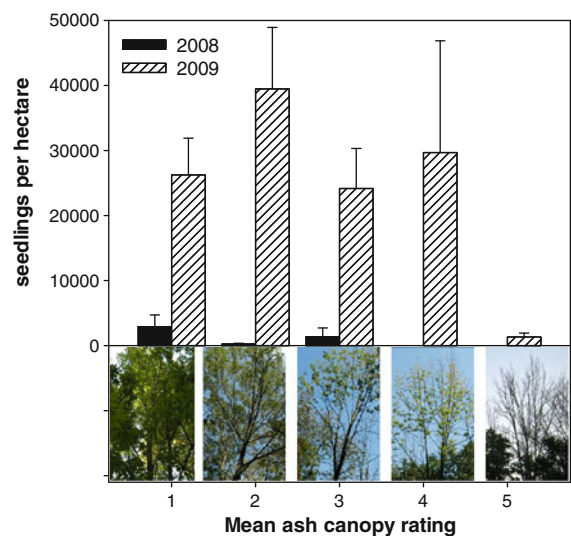

Fig. 6 Density of newly germinated ash seedlings (as indicated by the presence of cotyledons) in ash stands in varying degrees of EAB-induced decline in Ohio. Mean ash canopy condition for each site was calculated in 2008 from individual tree ratings of canopy decline on a scale of *1–5*, with 1 representing a healthy tree, *5* representing a completely dead tree, and *2–4* representing increasing levels of thinning and dieback

of ash seeds in the soil seed bank was initially highest in mesic sites, as was density of ash seedlings and saplings. However, since ash was more dominant in

hydric than in mesic or xeric stands, the impacts of EAB-induced ash mortality on successional trajectories will ultimately be most dramatic in hydric stands (D'Amato 2010). Whereas white ash may comprise only 3–4 % of stand volume in xeric sites, black ash can form pure stands in swamps and hydric sites, and is even considered a climax species in sites with poorly drained peat or muck soil (MacFarlane and Meyer 2005). Black ash stands, which often form in standing water, may have low densities of other canopy-replacing tree species (Klooster 2012; Palik et al. 2012), suggesting the possibility for major shifts in stand structure and composition.

In Michigan sites, percentage mortality of ash trees greater than 2.5 cm dbh decreased slightly in 2010 to about 97 % as smaller saplings grew enough to reach that size class. As we and others (Rebek et al. 2008; McCullough et al. 2008) have observed, once saplings reach 2.5 cm dbh, they can be readily colonized and killed by EAB. This is much smaller than the size at which ash generally reaches reproductive maturity (20–25 cm dbh) (Kurmis and Kim 1989), which further contributes to the precarious future of ash. This finding is contrary to the assumption of the EAB spread models of BenDor et al. (2006) that trees do not become susceptible to EAB until they reach 5 cm dbh.

Previous studies have found root sprouting to be a significant source of ash regeneration, even affecting gap dynamics (Dietze and Clark 2008). Additionally, ash growing in open and urban environments have been observed to sprout vigorously in response to EAB infestation (Poland and McCullough 2006). However, ash killed by EAB in the forest stands we studied did not exhibit that response as we observed sprouting to be uncommon. Sprouts that were present exhibited low vigor and died with the canopy. We observed no trees killed by EAB in which root sprouts served as a viable mechanism for regeneration.

The ash seed bank was depleted rapidly as ash mortality increased. In 2005, when only 42 % of ash trees were dead, the density of viable ash seeds in soil samples was about 500,000 per ha. However, by 2006, as ash mortality reached 77 %, the density of viable seeds dropped to about 130,000 per ha, and by 2007, no viable ash seeds were found.

The lack of viable ash seeds after 2006 in Michigan sites indicates that ash species do not form a persistent and viable seed bank. In Pennsylvania, white ash seed density ranged from 0 to 9,000 per ha (Marquis 1975),

which was substantially less than we observed in the present study. However, by design, our sampling protocol probably overestimated the density of ash seeds at the scale of the entire forest since we specifically selected our plots based on the presence of living ash trees, the density of which ranged initially from 10 to 413 trees per ha.

The Oleaceae family, which includes ash, generally exhibits orthodox storage behavior of seeds that can tolerate desiccation and/or freezing (Ellis et al. 1985; Bonner 2008), and some Oleaceae species do form persistent seed banks (Baskin and Baskin 1998). Viability of ash seeds can be maintained in controlled environments for up to 7 years (Bonner 2008), and viable ash seeds have been detected in soil seed banks after three to 8 years (Clark 1962; Leak 1963; Wright and Rauscher 1990; BenDor et al. 2006). However, our results are consistent with other studies showing that white, green, and black ash seeds do not persist on the forest floor or in the soil (Griffith 1991; Gucker 2005a, b). The lack of a persistent seed bank is somewhat unusual for early- to mid-successional tree species (Hyatt and Casper 2000), and is more consistent with the typical behavior of seeds of dominant late-successional canopy trees (Pickett and McDonnell 1989).

We observed a high density of established seedlings, but density of newly germinated seedlings was initially very low and ultimately became nonexistent. Quadrat surveys covering over 2,000 m^2 of the forest floor yielded 13 new seedlings (averaging 65 per ha for all hydrological classes) in 2009, only 1 new seedling in 2010, and no new seedlings in 2011. These values are extremely low compared to sites in Ohio with healthy ash trees (Fig. 6), and suggest that the lack of ash seeds in soil samples was not due to annual germination, but is consistent with our conclusion that ash trees do not form a persistent seed bank.

In Ohio plots in 2008 and 2009, greater densities of new ash seedlings were present in plots with healthy ash trees (average ash canopy rating of 1) compared to plots in later stages of decline (average ratings of 4 and 5). The similarly low densities of new seedlings in Michigan and Ohio plots with extensive ash mortality support our conclusions that the ash seed bank is rapidly depleted and regeneration effectively ceases. The highest seedling densities in Michigan occurred in mesic stands, which is consistent with previous studies of ash recruitment in forests (Lesica 2001), and with

seed density, which was also highest in mesic stands. In Ohio, seedling density did not vary across hydrological class.

In fall of 2008, many ash trees throughout Michigan and Ohio experienced a mast year, with high levels of seed production (DAH, personal observation), and studies have found that density of ash seedlings increases in years following masts (Boerner and Brinkman 1996). In Ohio, the density of newly germinated seedlings in plots with living ash trees (average ash canopy ratings of 1–4) increased by an order of magnitude from 2008 to 2009. However, where ash mortality approached 100 % (average ash canopy rating of 5) very few or no new seedlings were observed. This is contrary to the suggestion that ash trees will increase seed production in response to stress caused by EAB colonization (BenDor et al. 2006), and also is consistent with rapid depletion of the seed bank following ash mortality.

Given the nearly 100 % EAB-induced ash mortality that we observed, and the complete cessation of new ash regeneration, the fate of ash in these forests will depend on the long-term survival of the orphaned cohort of established ash seedlings and saplings and their dynamic interaction with EAB. However, since ash trees with dbh as small as 2.5 cm are susceptible to EAB infestation (McCullough et al. 2008), they are likely to be eliminated before reaching reproductive maturity (20–25 cm dbh) if EAB populations can persist at low densities following nearly complete elimination of their host material.

It is reasonable to predict that as EAB continues to spread, similar patterns of ash decline and seed bank depletion will be observed at other locations. Hence, the population-level changes described here have important implications for the future of white, green, and black ash species throughout eastern North American forests, and potentially other ash species endemic to North America. If the orphaned cohort of ash is extirpated by EAB before reproducing, green, black, and white ash will be functionally extirpated from our study sites, and potentially over much of their range.

Not all ash species are equally susceptible to EAB and the resistance of most North American species has yet to be assessed. In southeastern Michigan, blue ash was found to be less vulnerable to EAB infestation, with up to 60 % of blue ash trees surviving in stands where nearly 100 % of white or green ash had been killed by EAB (Tanis and McCullough 2012).

As comprehensive ash mortality in southeastern Michigan forests has resulted in over-exploitation of its food supply, the carrying capacity for EAB has been dramatically reduced, resulting in a self-induced population crash. However, traps placed in our study sites revealed that EAB was still present in low densities in Michigan and Ohio stands in 2012 even where the average mortality of ash trees was nearly 100 % (DAH and KSK, unpublished data). The orphaned cohort of established seedlings and saplings currently too small to be colonized by EAB, as well as the very small number of surviving ash trees (Knight et al. 2012), represent the only remaining individuals capable of sustaining an EAB population in the Upper Huron River Watershed in southeastern Michigan. Hence, the future of ash and EAB there will be determined by the outcome of the dynamic interaction between ash saplings and low density EAB populations.

Three Asian parasitoid species have been released in North America, including in the vicinity of some of our Michigan and Ohio sites, to provide classical biological control of EAB (Liu et al. 2003; Bauer et al. 2010; Duan et al. 2012). Native parasitoids, particularly *Atanycolus* spp. have also been observed to parasitize EAB (Cappaert and McCullough 2009). However, it remains unclear what long-term impact natural enemies will have on EAB population dynamics and ash survival. If they are able to regulate EAB populations at low densities, then some ash saplings may survive long enough to produce seeds, and thus facilitate persistence at low densities as a dynamic equilibrium develops between ash, EAB, and its natural enemies.

The Michigan sites were severely impacted by Dutch elm disease in the 1960s and 1970s (Barnes 1976), after which ash increased in importance. Since then, American elm (*Ulmus americana* L.) has continued to persist in these mixed hardwood forests, but typically as smaller diameter individuals, while other species, including sugar maple (*Acer saccharum* Marsh.) and white ash, replaced elm in the canopy (Parker and Leopold 1983). We think it is unlikely that ash will continue to persist as elm has, given that the life history strategies of ash and elm interact differently with the respective invasive organisms, resulting in contrasting patterns of demography. Elm flowers at a younger age (Burns and Honkala 1990) and can reproduce before succumbing to Dutch elm disease (Richardson and

Cares 1976), whereas ash as small as 2.5 cm dbh are killed by EAB, and mortality therefore occurs before reproduction, resulting in cessation of recruitment.

The patterns of ash demography and seed bank dynamics that we observed near the epicenter of the EAB infestation support the conclusion that as mortality of ash approached and then exceeded 99 %, the seed bank was rapidly depleted and ash regeneration ceased. If this pattern is replicated as EAB spreads to other regions, it has the potential to functionally extirpate most ash species from eastern North American forests. Other regions, however, may not experience the same pattern of EAB dynamics and ash mortality that we observed. EAB typically overwinter as prepupal larvae, which are intolerant to freezing, but have been shown to survive temperatures as low as -30 °C (Crosthwaite et al. 2011). EAB survival may decrease at northern latitudes (towards the northern limits of the distribution of ash) where winter temperatures frequently fall below this threshold, potentially resulting in lower or slower rates of ash mortality (Crosthwaite et al. 2011).

As a component of diverse forest communities, ash species contribute to ecosystem services such as mediating nutrient and water cycling (Reiners and Reiners 1970), serving as a host for many arthropods (Gandhi and Herms 2010b), and providing food and shelter for birds and mammals (Martin et al. 1951). Furthermore, canopy gaps created when ash die may alter microenvironmental conditions, and change forest structure, which could increase the potential for invasion by nonnative species (Gandhi and Herms 2010a). Monitoring changes in species composition over time will help forest managers develop strategies to mitigate the downstream effects caused by wide-spread ash mortality and the potential extirpation of ash from forested ecosystems.

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