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ORIGINAL PAPER

The effect of emerald ash borer-caused tree mortality on the invasive shrub Amur honeysuckle and their combined effects on tree and shrub seedlings

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Abstract Invasive insects and plants are major threats to the health and viability of North American forests. Emerald ash borer (*Agrilus planipennis*) (EAB) may cause extensive changes to forest composition due to rapid ash (*Fraxinus* spp.) mortality. Invasive shrubs like Amur honeysuckle (*Lonicera maackii*) may benefit from EAB and have negative effects on woody seedlings. We predict that ash mortality has positive effects on seedling abundance, recruitment, and survival, but that these effects are influenced by *L. maackii* basal area and/or cover. We sampled 16 sites, representing a chronosequence of ash mortality throughout western Ohio. We tested whether *L. maackii* growth and fecundity varied in relation to ash decline. We also investigated effects of ash decline, stand basal area (BA), *L. maackii* BA and percent cover on woody seedling abundance, recruitment, and survival using linear mixed models evaluated with Akaike's Information Criterion. These same responses were also investigated for four seedling groups: *L. maackii*, invasive plants (excluding *L. maackii*), shade tolerant natives, and shade intolerant natives. We found a significant positive relationship between ash decline and *L. maackii* BA growth. Lower seedling species richness corresponded with greater *L. maackii* BA and better ash condition. Greater *L. maackii* BA was also associated with lower seedling abundance and recruitment, as well as abundance and recruitment of shade-tolerant species, and recruitment of shade-intolerant species. Sites with poorer ash condition and greater *L. maackii* BA had more *L. maackii* seedlings. These findings indicate that the negative effects of *L. maackii* are more important to future forest composition than ash decline; however ash decline increases *L. maackii* growth, hence exacerbating the effects of this invasive shrub.

Keywords Tree fall gap · Facilitation · *Fraxinus* · *Agrilus planipennis* · *Lonicera maackii* · Seedling recruitment · Chronosequence · Shade tolerance

Abbreviations

BA	Basal area
EAB	Emerald ash borer
DBH	Diameter at breast height
ADI	Ash Decline Index
AMI	Ash Mortality Index

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Introduction

Non-native insects and pathogens continue to pose great economic and ecological threats to the forests of North America (Liebhold et al. 1995; Simberloff 2000; Allen and Humble 2002; Aukema et al. 2010). In the United States there are at least 455 non-indigenous insect species that inhabit forest ecosystems (Aukema et al. 2010), and those that are invasive can have serious impacts on native biodiversity (reviewed by Kenis et al. 2009). Wood and phloem-boring insects have the greatest impact; costing an estimated $1.7 billion to US municipalities, and an additional $830 million is lost annually in property values in urban areas alone (Aukema et al. 2011).

Invasive plants may benefit from the spread of invasive forest insects that attack canopy trees (Orwig and Foster 1998; Herms et al. 2008); improving understory light availability and lowering interspecific competition (Gandhi and Herms 2010). Invasive plants have deleterious effects on community structure and ecosystem processes (Levine et al. 2003; Vila et al. 2011). Since, both non-native woody plants (Johnson et al. 2006; Webster et al. 2006) and exotic insect pests (Lovett et al. 2006) have become major components of Eastern US forests, we must gain a better understanding of their combined impacts.

Emerald ash borer (*Agrilus planipennis*) (EAB) is an invasive insect currently killing tens of millions of ash (*Fraxinus* spp.) trees in North America (Kovacs et al. 2010; Liebhold et al. 2013). Since being inadvertently introduced in the early 1990s (Siegert et al. 2007), it has successfully established in 28 states and two Canadian provinces as of 2016 (www.aphis.usda.gov 2016).

All 16 native US species of ash are viable hosts (Herms et al. 2004) and currently there is little evidence of resistance among North American populations (Anulewicz et al. 2008). During the larval stage EAB is a phloem-borer, disrupting translocation and girdling mature ash trees within 1–4 years (Poland and McCullough 2006). Because mortality rates for several ash species near the invasion epicenter are nearly 100% (Herms and McCullough 2014), it is expected that progression of this invasion will result in widespread ash loss that could have devastating ecological impacts (Poland and McCullough 2006; Gandhi and Herms 2010; Herms and McCullough 2014).

Widespread defoliation and gap formation by tree-feeding insects can lead to extensive forest changes (Kenis et al. 2009; Gandhi and Herms 2010). Researchers have proposed that an increase in light availability from ash mortality could fundamentally alter community composition and enable the spread of invasive understory plants (Hausman et al. 2010; Gandhi and Herms 2010), consistent with the Fluctuating Resource Hypothesis (Davis et al. 2000). But because ash mortality is gradual, its effects on understory light availability, and hence invasive plants, may differ from the effects of tree fall gaps.

Throughout the Midwestern and Eastern U.S. Amur honeysuckle, *Lonicera maackii*, is an invasive shrub that dominates many anthropogenically altered forest stands (Hutchinson and Vankat 1997). Introduced from East Asia to North America in 1896 for ornamental and wildlife purposes, it escaped by the mid-1920s and naturalized by the 1950s (Luken and Thieret 1996). Currently it is established in 27 states and the province of Ontario (www.plants.usda.gov 2016), and is one of 85 plant species ranked as 'high impact' invasives by NatureServe (2015). Like many invasive shrubs, *L. maackii* is most common along forest edges where its seedlings readily establish (Luken and Thieret 1996). Shade tolerance coupled with an ability to readily utilize ephemeral light increases (e.g. tree-fall gaps) (Luken and Thieret 1996) positions *L. maackii* to potentially benefit greatly from EAB-caused ash mortality. Luken et al. (1997) found that *L. maackii* has higher growth rates under high light environments than the native spicebush *Lindera benzoin*; while Hutchinson and Vankat (1997) found an inverse relationship between tree canopy cover and *L. maackii* cover. Canopy disturbance could also benefit *L. maackii* shrubs through improved fecundity, as has been observed in other native (Hicks and Hustin 1989) and non-native (Burnham and Lee 2010; Gorchov et al. 2011; Driscoll et al. 2016) understory shrubs.

Once established, *L. maackii* has been shown to have numerous negative effects on forest plant communities including reduced survival of native tree seedlings, likely due to shading (Gorchov and Trisel 2003; Hartman and McCarthy 2004) as well as reduced growth of canopy trees, attributed to nutrient competition and perhaps allelopathy (Hartman and McCarthy 2007).

Interactions between co-occurring invasive species can be facilitative, competitive, or neutral in nature (Kuebbing et al. 2013). Facilitative interactions result in one species benefiting while the other species is not affected (commensalism) or enhanced (mutualism, i.e. 'invasional meltdown') (Simberloff and Von Holle 1999; Simberloff 2006). Simberloff and Von Holle (1999) review a few examples where non-native animals alter environments in a manner that aids plant invasion. Specifically, large non-native ungulate grazing and trampling facilitates the spread of invasive herbaceous plants in numerous ecosystems (Mack 1989). Additionally, feral pig (*Sus scrofa*)-induced soil disturbance in the Hawaiian Islands has a strong association with alien plant community composition (Aplet et al. 1991).

There has been interest and some research addressing the effects of ash mortality on understory tree species (Looney et al. 2015) and invasive plants (Klooster 2012), however, our research is novel in that it addresses the combined effects of invasive shrubs and ash mortality on understory woody plants. The aim of our research was to evaluate the effects of EAB on *L. maackii*, and the individual and combined effects of these two invasive species on woody seedling populations. This study is applicable to extensive areas of Eastern North American woodlands where *L. maackii* (USDA and NRCS 2016) and EAB (USDA APHIS 2016) occur and continue to spread. We investigated the direct effects of EAB-caused ash decline on *L. maackii*, as well as the direct effects of EAB, *L. maackii*, and stand basal area, and their potential additive effects, on woody seedling populations. We tested the following hypotheses: (1) EAB-caused ash decline benefits *L. maackii*; (2) EAB-caused ash decline positively affects native and invasive seedlings; and (3) greater *L. maackii* BA and/or cover impairs native and invasive seedlings. From these hypotheses we made the following predictions: (1) relative growth and reproduction of *L. maackii* shrubs, as well as abundance, survival, recruitment, and relative growth of *L. maackii* seedlings, are positively associated with ash decline; (2) species richness, abundance, recruitment, and survival of native and invasive seedlings are positively associated with ash decline; and (3) greater BA and/or cover of *L. maackii* is associated with lower native and invasive seedling species richness, abundance, survival, and recruitment.

Materials and methods

Study area

We conducted our study in Ohio, USA on public and private forest stands in a matrix of suburban and agricultural lands. Sites were located in closed canopy, mostly secondary forests where both EAB and *L. maackii* are well established and their ecological impacts could be assessed. In Ohio, EAB was first discovered in 2003 in the northwest part of the state (www.aphis.usda.gov 2016). The five native species of ash in Ohio (Hausman et al. 2010) number approximately 279 million individuals, constituting approximately 6% of all trees in the state (Wildman 2008). In contrast, *L. maackii* was first reported as escaping cultivation near Chicago, Illinois, USA by the mid-1920s (Luken and Thieret 1996), and naturalized populations were reported in Hamilton County, Ohio, USA by 1961 (Braun 1961). Currently it has become a common component of many second-growth forests in the Midwestern and Eastern US (Luken and Thieret 1996; Hutchinson and Vankat 1997).

Sixteen sites located throughout southwestern and central Ohio (Fig. 1) were selected to represent a chronosequence since EAB infestation, based on first appearance of D-shaped exit holes (2007–2015, Knight, unpublished data). The sites also varied in their percent cover of *L. maackii* (0–91%) and its basal area (Appendix 1). The variation of both invasive species among sites in Ohio provided us with ideal locations to explore the relative roles of *L. maackii* and EAB on seedlings. Our 16 sites are a subset of sites established by the U.S. Forest Service to study impacts of EAB across a range of habitat types and ash densities (Knight et al. 2013). All except one site were upland forests; for the five central Ohio stands and seven of the 11 southwest Ohio stands, the principal *Fraxinus* species (based on BA in plots, Appendix 1) was *F. americana*, for three stands it was *F. quadrangulata*. The single wetter site contained *F. pennsylvanica*, *F. profunda,* and *F.nigra*. Although the year of initial infestation by EAB is unknown due to the difficulty of early detection, the presence of EAB was confirmed through yearly documentation of characteristic D-shaped exit holes on dying ash trees in all except two sites (Caesar Creek State Park 4 and Clifton Gorge) and yearly trapping of EAB adult beetles in a subset of sites. EAB was likely present at a

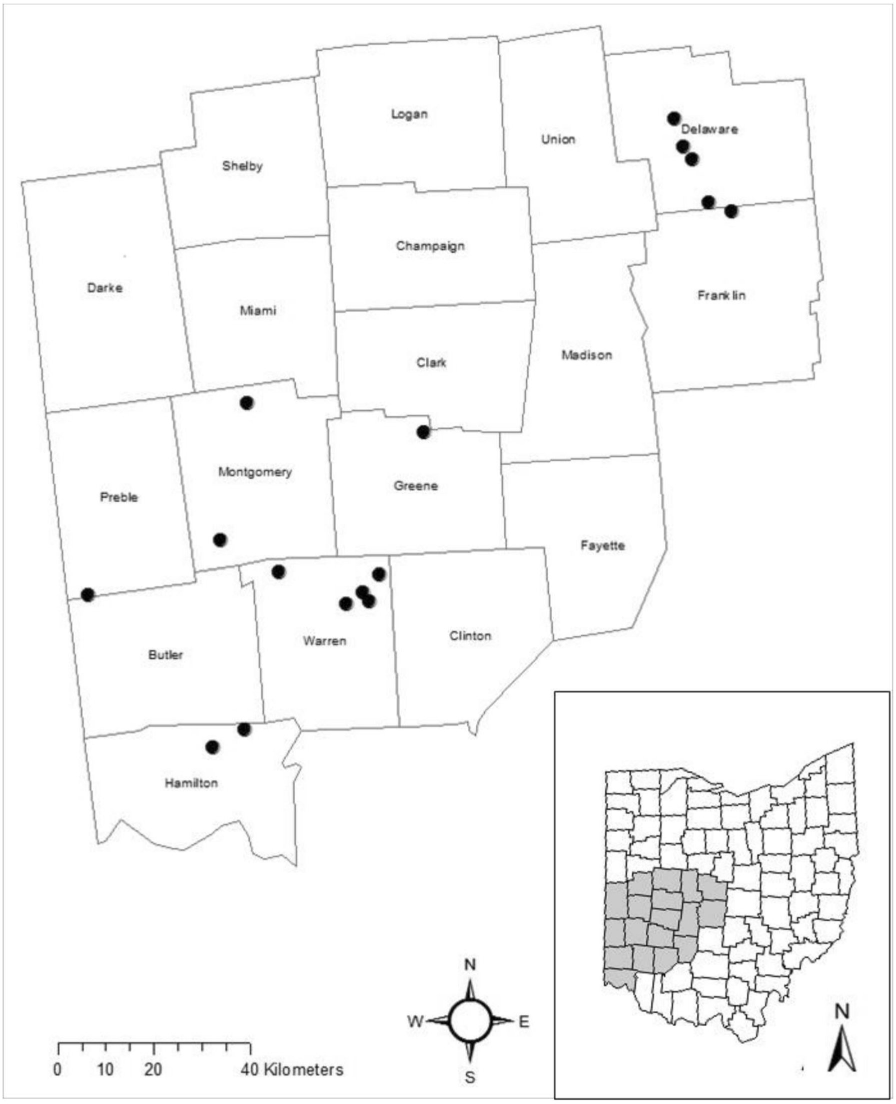

Fig. 1 Map of 16 sites where data was collected (2012–2014) in Ohio, USA. *Each dot* denotes a site, nested within each site were three 400 m^2 plots. Sites and plots were established by the United States Forest Service for monitoring long-term EAB ecological impacts

site at low densities before these methods confirmed its presence. Using these methods, the gradient of known duration of EAB presence in the other 14 sites was 1–7 years at the time of last plant measurements (2014). Tree diameters, ash health, seedling measurements, as well as *L. maackii* basal diameters and percent cover, were recorded annually in June–August, 2012–2014. *Lonicera maackii* fecundity was measured in a subset of 11 sites annually in September–October, 2012–2014.

Study design

Three circular plots of 400 m^2 were nested within each of the 16 sites (Appendix 2). All plots were located away from forest edges or trails, and spaced >50 m apart. All plots included at least two ash trees >10 cm diameter at breast height (DBH). In each 400 m^2 plot we identified and annually measured DBH for all trees $\geq$10 cm DBH, and also assessed the health of each ash on a scale of 1–5 (Smith et al. 2015) (Appendix 3). Basal area (BA) for all stand trees, including dead and dying ash, was calculated using DBH (basal area of all trees $\geq$10 cm DBH is hereafter 'stand BA').

We calculated three metrics of ash decline for each plot. The first, Ash Decline Index (ADI), was calculated as the total BA of ash trees that received a rating between 3 and 5 (Appendix 3) divided by stand BA. ADI allowed us to capture declining ash in our indices, and thus account for the possible effect that thinning ash canopies have on understory resource availability. The second, Ash Mortality Index (AMI), was the BA of dead ash (rated 5) divided by stand BA. Basal area measurements and ash condition ratings from 2012 were used in calculating both variables. ADI and AMI are reported as percentages. The third was 'Year25% Dead' (the first year 25% of ash within a site received a 5 rating); five of the sites had only 4–24% dead by 2014, and these were assigned a year of 2015.

Located at the center of each plot was a circular 200 m^2 subplot (Appendix 2) where we measured *L. maackii* fecundity (within a subset of the sites $N = 11$) and basal area (BA) and cover. In each subplot we tagged the two largest *L. maackii* shrubs in each of the four quadrants, for a total of up to eight in each subplot. Annually we measured the basal diameter of each stem for each tagged *L. maackii*. Using these basal diameters we calculated basal area for each stem and summed these for each shrub, following the methods of Elliott and Swank (1994). For *L. maackii*, BA is a significant predictor of total above ground biomass (Lieurance and Landsbergen 2016). We then averaged these to obtain a mean *L. maackii* basal area for each plot, and used these to calculate relative BA growth of *L. maackii* shrubs by dividing the growth increment ($BA_{2014} - BA_{2012}$) by BA_{2012}.

During the autumn of 2012 and 2013 we conducted fruit counts for each of the tagged *L. maackii* (within a subset of the sites $N = 11$) to determine fecundity. Fruit counts were conducted in September–October, prior to fruit ripening and removal by birds (Bartuszevige et al. 2006), by individually counting each fruit on shrubs with <300 fruits and, for plants with >300, by counting fruits on a representative portion of the shrub and then extrapolating to the entire shrub (e.g. counting the fruit on 1/3 of the shrub and then multiplying by 3). For each year we averaged the fruit counts for all tagged *L. maackii* within each plot.

Percent cover of *L. maackii* was quantified using the line-point intercept method (Godinez-Alvarez et al. 2009). Seven parallel transects were checked annually in each subplot. Transects were 2 m apart and points were sampled every 2 m. Five center transects had seven sample points each and the two transects which flanked the center transects had five sample points each, for a total of 45 sample points per plot. At each sample point ($N = 45$/plot) the presence or absence of *L. maackii* was recorded. The number of points where *L. maackii* was present was divided by 45 to determine *L. maackii* percent cover.

Woody seedlings were sampled in each plot within four permanent circular 4 m^2 micro-plots, located 6 m from plot center, one in each of the four cardinal directions (Appendix 2). In 2012, we identified, measured the height, and tagged all tree and shrub seedlings (no vines) that were 20-100 cm tall in each of the micro-plots. The 2012 seedling counts served as the abundance values in our analyses. In 2013 and 2014 all tagged seedlings were re-measured. Seedlings which entered the 20–100 cm threshold in 2013 or 2014 were identified, tagged, and measured. All seedlings that were added in 2013 or 2014 were pooled and serve as the seedling recruits in the analyses. Seedling species richness was calculated by pooling all species present within a plot (2012–2014). Survival was calculated as the proportion of 2012 seedlings still alive in 2014. Heights for *L. maackii* seedlings that survived from 2012 to 2014 were averaged by plot and used to calculate relative height growth. For each plot, relative *L. maackii* seedling height growth was calculated by dividing the growth increment ($height_{2014} - height_{2012}$) by $height_{2012}$. Seedlings were divided into four categories: *L. maackii*, invasive (excluding *L. maackii*), shade intolerant natives, and shade tolerant natives. Seedling categories were created to differentiate between native and invasive species. We further categorized the 41 native species (some of which were rare) into categories reflecting shade tolerance (Appendix 4), since light limitation is often cited as the most limiting resource in closed canopy forests (Pacala et al. 1994).

To assign native species to shade intolerant or tolerant, we constructed a frequency distribution of shade tolerance values for the ($N = 2145$) seedlings, using the value for each species reported in Niinemets and Valladares (2006), who used a scale from 1 (shade intolerant) to 5 (shade tolerant) (Appendix 5). This distribution was bimodal, so we used the break between the peaks to identify two groups (Appendix 5). Species with values of 1–2.99 were classified as shade intolerant, while those ranked 3–5 were classified as shade tolerant (Appendix 4).

Statistical analysis

We conducted statistical analyses using generalized linear mixed and linear mixed models (Bolker et al. 2009) in the R packages lme4 and nlme in R version 3.0.2 (Bates et al. 2015) of the R programming language (R Development Core Team 2016). Linear mixed models were used when the response variable could be transformed to normality and generalized linear mixed models were used when the response variable followed a Poisson error distribution or binomial distribution. Because analyses used observations from three plots at each site, all models used site as a random variable. Using site as a random variable also allowed us to account for potential differences between sites.

When conducting hypothesis testing we used a Likelihood ratio test to evaluate a specific predictor variable for its statistical significance. Hypothesis testing was only used to determine if ash mortality led to an increase in the relative growth of *L. maackii* BA. To do this we individually tested all three variables of ash decline as predictors: ADI, AMI, Year25% Dead.

However, for all other response variables there were multiple predictor variables and multiple combinations of predictors that we were interested in testing. To identify the best predictive models for each response, we conducted model selection. Predictor variables for these models included: ADI, AMI, *L. maackii* percent cover, *L. maackii* BA, and stand BA (all trees $\geq$10 cm DBH); each calculated from measurements made in 2012. We also evaluated six two-variable additive models where one of the predictor variables was an ash decline variable (ADI or AMI) and the other predictor variable was *L. maackii* percent cover, *L. maackii* BA, or stand BA. Additive models were not included in *L. maackii* fecundity analyses, since data only existed for 11 sites, we did not have sufficient replication to evaluate all models used in other assessments. We did not include the predictor Year25% Dead in model selection, as this variable was not significant in the previous analysis. All predictor variables listed above were used for evaluating responses (abundance, recruitment, and survival) of total woody seedlings (all species pooled) as well as responses of the four subsets of woody seedlings (*L. maackii*, invasive species (excluding *L. maackii*), native shade-tolerant, and native shade-intolerant).

Best-fitting models included predictor variables that provided the lowest value of the Akaike Information Criteria corrected for small sample size (AICc), based on model comparisons using the R package AICcmodavg (Mazerolle 2015). Models with ΔAICc < 2 were considered competing models (Burnham and Anderson 2002).

The relative strength of evidence for alternative models (best vs competing models) was assessed using Akaike weights (reported as w). Employing AICc allowed us to evaluate and rank models to assess which best approximate reality (Burnham and Anderson 2002). Best-fitting and competing models are reported in Table 1, and discussed in the Results. For those instances where the null model was found to be a competing model (ΔAICc < 2), all predictor variables were considered to have no effect on the response variable. Additional assessment of best-fitting and competing models were conducted for statistical significance and goodness-of-fit. To determine the proportion of the variance explained by the predictor(s) variable itself (marginal R^2) (fixed effects) and by the full model that included the predictor and random variables (conditional R^2) (fixed plus random effects) (Nakagawa and Schielzeth 2013), we calculated goodness-of-fit, marginal and conditional R^2 using the R packages MUMIn (Barton 2016) and lmmR2 W (Maj 2011). We also conducted a likelihood ratio test comparing each best model to the null model. Our null model was a model that did not include any fixed effects but did include site as a random effect.

Results

Mean stand BA per plot was 35.7 ± 1.8 m^2/ha S.E. The chronosequence of the 16 sites is reflected in the range of dates when they reached 25% ash mortality: 2007-2015 (Appendix 1). The mean ADI was 21 ± 3% SE in 2012; whereas the mean AMI was 13 ± 2% SE for the same year (Appendix 1). *Lonicera maackii* percent cover in 2012 averaged 26 ± 4% SE; while mean *L. maackii* shrub BA averaged 9.1 ± 2.2 cm^2 SE (Appendix 1).

Table 1 Best-fitting and competing models for response variables. For each response variable, plot data were analyzed using linear mixed models with ‘site’ as the random factor

Response	Predictor models	AICc	ΔAICc	W	X^2	*p*	R^2 marginal	R^2 conditional
L. maackii Fecundity (2012)	*L. maackii* cover	141.87	0.00	0.91	17.94	<0.0001	0.53	0.74
L. maackii Fecundity (2013)	*L. maackii* cover	133.54	0.00	0.74			0.38	0.80
Species richness	*L. maackii* BA	237.26	0.00	0.46	13.10	0.0003	0.40	0.47
	AMI + *L. maackii* BA	238.19	0.93	0.29				
Abundance: All seedlings (Excluding *L. maackii*)	*L. maackii* cover	130.49	0.11	0.29	8.83	0.003	0.31	0.44
	L. maackii BA	130.38	0.00	0.31				
Abundance: *L. maackii* Seedlings	AMI + *L. maackii* cover	222.73	0.00	0.74			0.31	0.74
Abundance: invasive seedlings (excluding *L. maackii*)	Stand BA	147.54	0.00	0.31			0.13	0.48
	ADI + stand BA	148.17	0.63	0.22				
	AMI + stand BA	148.65	1.10	0.18				
Abundance: shade tolerant native seedlings	*L. maackii* cover	137.30	0.00	0.41			0.14	0.70
Recruitment: all seedlings (excluding *L. maackii*)	*L. maackii* BA	112.45	0.00	0.50	23.09	<0.0001	0.51	0.51
	ADI + *L. maackii* BA	114.36	1.91	0.19				
	AMI + *L. maackii* BA	113.54	1.09	0.29				
Recruitment: shade tolerant native seedlings	*L. maackii* BA	130.45	0.00	0.45			0.38	0.57
Recruitment: shade intolerant native seedlings	*L. maackii* BA	135.86	0.00	0.26			0.26	0.54
	ADI + *L. maackii* cover	137.37	1.51	0.12				
	AMI + *L. maackii* cover	137.10	1.24	0.14				
	ADI + *L. maackii* BA	137.04	1.17	0.14				
	AMI + *L. maackii* BA	136.63	0.77	0.18				

Predictor variables tested were the measures of EAB-caused ash decline (ADI, AMI), *Lonicera maackii* BA and cover, and Stand BA. Response variables evaluated were *L. maackii* fecundity, woody seedling species richness (2012–2014), abundance (2012), recruitment (2013 and 2014), and survival (2012–2014) for both all seedlings and subsets of seedlings. Only best-fitting models ($\Delta AIC = 0$) as well as competing models with $\Delta AIC \leq 2$ indicating substantial support (Burnham and Anderson 2002) are reported in this table. Where a competing model for a response was the null model, no entry is made in this table. The complete set of results is reported in “Appendices 6, 7, 8, and 9”. AICc is the small sample Akaike’s information criterion; ΔAIC is the difference between the AICc of a model and the AICc of the best model, and w is Akaike’s weight. ADI represents Ash Decline Index and AMI represents Ash Mortality Index. Statistics reported are based on likelihood ratio and goodness-of-fit tests with

Lonicera maackii growth, fecundity, and seedling responses

We found that mean relative BA growth in *L. maackii* from 2012 to 2014 was 51 ± 9% SE relative *L. maackii* growth was significantly greater in sites with higher values of ADI (i.e. where ash condition was poorer) ($\chi^2 = 5.28$, $p = 0.02$) (Fig. 2). In 2012 and 2013 *L. maackii* fruit production per plot averaged 191 ± 59 SE and 133 ± 37 SE berries, respectively.

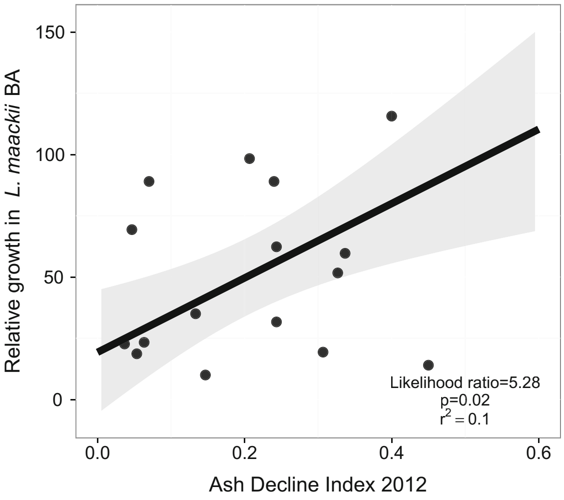

Fig. 2 Regression of *Lonicera maackii* relative basal area (BA) growth from 2012 to 2014 on Ash Decline Index. *Each point* represents one study site (the mean of 3 plots per site). The *solid black line* illustrates the line of the best fit to these site means and the *gray shaded* region represents the standard error around that line. However, the statistics reported are based on hypothesis testing of plot data using linear mixed models ($\chi^2 = 5.28$, $p = 0.02$) with 'site' as the random factor

In each year, the best model for *L. maackii* fruit production included only a single predictor variable; *L. maackii* percent cover (Table 1; Appendix 6). Each year fruit production was greater in sites where *L. maackii* percent cover was greater. One site with very high *L. maackii* fruit production and cover appeared to be an outlier. When this site was dropped from the analysis, the best model included only the single predictor variable of *L. maackii* BA, another measure of the amount of *L. maackii* in the plot. None of the models with a predictor variable associated with ash decline or mortality was a competing model for *L. maackii* fecundity.

The mean number of *L. maackii* seedlings per plot was 4.5 ± 0.7 SE (all seedling counts are based on the total sampled area of the micro-plots, i.e. 16 m^2 per plot). The best model for the number of *L. maackii* seedlings per plot included effects of both *L. maackii* cover and AMI (Table 1; Appendix 7). More *L. maackii* seedlings were found in sites with more dead ash and greater *L. maackii* cover. The mean number of *L. maackii* seedlings recruited during the study period was 2.2 ± 0.3 SE The null model was a competing model for the number of *L. maackii* recruits (Appendix 8). Mean *L. maackii* seedling survival was 96 ± 2% SE, with the best model being the null model (Appendix 9). *Lonicera maackii* seedlings had a mean relative growth in height of 20 ± 4% SE from 2012 to 2014. The null model was a competing model for *L. maackii* seedling growth (Appendix 6).

Seedling species richness and abundance

Seedling species were divided into four ecological groups for analysis based on shade tolerance and whether they were native to North America. Shade tolerance values ranged from 1.35 to 4.87 (Appendices 4, 5). There were a total of 51 species encountered in the seedling layer: *L. maackii,* 9 other invasives, 24 shade tolerant natives, and 17 shade intolerant natives (Appendix 4). The average number of seedling species per plot was 9.2 ± 0.5 SE. The best model for species richness consisted of the single predictor variable, *L. maackii* BA (Table 1; Fig. 3; Appendix 7). One site with very high *L. maackii* BA appeared to be an outlier. When this site was dropped from the analysis, the best model remained the same. There was one competing model for seedling species richness; this model included both the effect of *L. maackii* BA and the effect of AMI (Table 1). Sites with larger *L. maackii* had fewer seedling species, while sites with poorer ash condition had more seedling species.

Total seedling abundance, excluding *L. maackii*, averaged 28 ± 3 SE per plot in 2012. The best model for total seedling abundance was *L. maackii* BA; sites with larger *L. maackii* had fewer seedlings (Table 1; Appendix 7), while *L. maackii* cover was a competing model (Table 1). Again the same site appeared to be an outlier because it also had very high *L. maackii* BA. When this site was dropped from the analysis, the best model remained consistent. Mean abundance of invasive (excluding *L. maackii*) seedlings was 2.2 ± 0.9 SE per plot. The best model for invasive seedling abundance included only stand BA (Table 1; Appendix 7). There were also two competing models for invasive seedling abundance, one included both stand BA and ADI, while the other included stand BA and AMI (Table 1). More invasive seedlings were present in sites with lower stand BA and sites with poorer ash condition. Shade tolerant native seedlings averaged 19.7 ± 2.9 SE per plot. The best model for shade tolerant native seedling abundance contained *L. maackii* cover (Table 1; Appendix 7). Sites with more *L. maackii* cover had fewer shade tolerant native

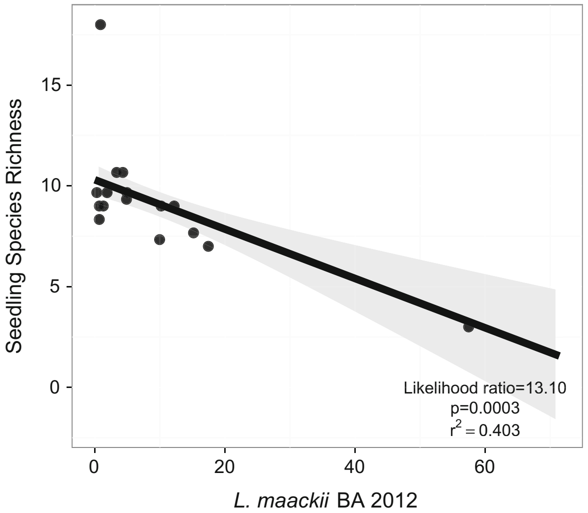

Fig. 3 Regression of woody seedling species richness (all years pooled) on *L. maackii* basal area (BA) 2012. *Each point* represents one study site (the mean of 3 plots per site). The *solid black line* illustrates the line of the best fit to these site means and the *gray shaded* region represents the standard error around that line. Statistics reported are based on likelihood ratio and goodness-of-fit tests with plot data using linear mixed models with 'site' as the random factor. One site appears to be an outlier; when it was dropped, *L. maackii* BA, remains the best predictor

seedlings. Mean shade intolerant native seedling abundance was 6.2 ± 0.9 SE per plot. The null model was a competing model for the abundance of shade intolerant native seedlings (Appendix 7).

Seedling recruitment

An average of 18.6 ± 2.5 SE seedlings, excluding *L. maackii*, were recruited per plot in 2013 and 2014 combined. The best model had the single predictor variable *L. maackii* BA (Table 1; Fig. 4; Appendix 8). There were two additional competing additive models for seedling recruitment; both included the effect of *L. maackii* BA, one had the additive effect of AMI and the other ADI. Greater seedling recruitment was found in sites with smaller *L. maackii*, as well as in sites with poorer ash condition. Again analyses were also conducted omitting the site with the very high *L. maackii* BA and the same results were obtained. An average of only 1.2 ± 0.2 SE invasive seedlings other than *L. maackii* recruited per plot, and the null model was a competing model for recruitment of these invasives (Appendix 8). Mean recruitment of shade tolerant native seedlings was 11.9 ± 2.2 SE per plot. Once more the best model consisted of only *L. maackii* BA (Table 1; Appendix 8); sites with less *L. maackii* had more shade tolerant recruits. Recruitment of shade intolerant native seedlings averaged 5.5 ± 0.8 SE per plot. Yet again the best model contained only *L. maackii* BA as a predictor (Table 1; Appendix 8).

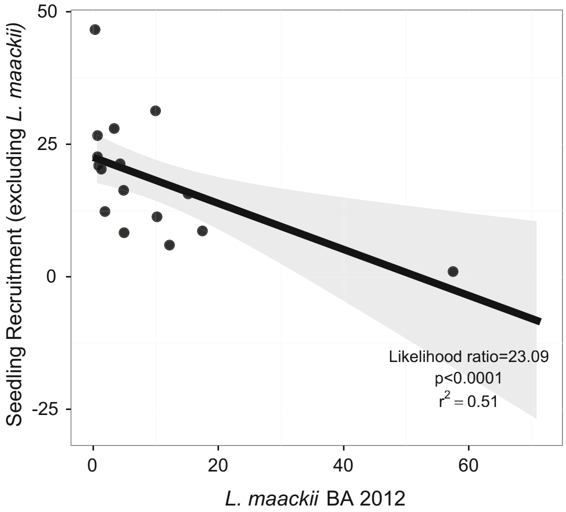

Fig. 4 Regression of woody seedling recruitment (Σ 2013 and 2014) on *L. maackii* basal area (BA) 2012. *Each point* represents one study site (the mean of 3 plots per site). The *solid black line* illustrates the line of the best fit to these site means and the *gray shaded region* represents the standard error around that line. Statistics reported are based on likelihood ratio and goodness-of-fit tests with plot data using linear mixed models with 'site' as the random factor. One site appears to be an outlier; when it was dropped, *L. maackii* BA, remains the best predictor

There were four competing models for intolerant native seedling recruitment; two of these included the additive effect of *L. maackii* BA and a measure of ash decline (ADI in one and AMI in the other). The two remaining competing models both contained additive effects of *L. maackii* cover and a measure of ash decline (ADI or AMI). Greater shade intolerant native seedling recruitment was associated with sites with less *L. maackii* (BA or cover) and sites with poorer ash condition.

Seedling survival

Among plots, mean survival for seedlings, excluding *L. maackii,* from 2012 to 2014 was 77 ± 2% SE. The null model was a competing model for seedling survival, excluding *L. maackii* (Appendix 9). Mean seedling survival was 96 ± 2% SE for invasive seedlings (excluding *L. maackii*); the null model was a competing model (Appendix 9). Shade tolerant native seedling mean survival was 75 ± 3% SE; the null model was a competing model (Appendix 9). For shade intolerant native seedlings mean survival was 82 ± 3% SE; the null model was a competing model (Appendix 9).

Discussion

Our findings were consistent with our first prediction: EAB-caused ash decline was associated with greater *L. maackii* radial growth. In turn, greater *L. maackii* BA and cover was associated with lower woody seedling species richness, abundance, and recruitment, consistent with our third prediction. However, few seedling parameters were associated with EAB-caused ash decline directly, as we expected in our second prediction. Our findings therefore support a hypothesis that EAB-caused ash decline is indirectly affecting forest structure and diversity through enhancement of *L. maackii* growth, which in turn results in greater *L. maackii* BA and cover.

Lonicera maackii growth responses

One of the most dramatic findings in our study was the positive effect that EAB-caused ash mortality had on relative radial growth of *L. maackii*. Previous studies exploring the effect of canopy gaps on native and invasive understory woody plant growth have produced mixed results. This could be due in part to differences in plant growth responses. In understory trees, gaps typically promote terminal growth (Collins 1961) but not radial growth (Eschtruth et al. 2006; Knapp and Canham 2000), which could be due to their adaptive response of stem elongation in response to higher light. However, in shrubs, increased radial growth (Hicks and Hustin 1989; this study) or increased stem density (Burnham and Lee 2010) appears to be a more common response to canopy decline. While Klooster (2012) did not find greater invasive or native shrub growth where ash succumbed to EAB, this may because she used crown dimensions, rather than basal area, to quantify growth. Radial growth (secondary growth) is a well-established and well-accepted way to measure shrub growth (Elliott and Swank 1994), is a significant predictor of *L. maackii* above-ground biomass (Lieurance and Landsbergen 2016), and is more dependable than crown dimensions (primary growth) which can vary widely from year to year due to both growth and death of individual stems. Our finding of enhanced *L. maackii* growth with ash decline is similar to shrub responses to the widespread decline of American elm (*Ulmus americana*) due to Dutch Elm Disease (*Ophiostoma* spp.) (DED) (Huenneke 1983; Dunn 1986). Elm was once a dominant component of riparian communities (Lovett et al. 2006) but now no longer attains the historical age and size structure it once did; large, long-lived trees have been replaced by smaller and younger individuals that eventually succumb to DED (Loo 2009). Dunn (1986) found a positive relationship between shrub density and dead elm density caused by DED; while Huenneke (1983) found that large canopy gaps were more often colonized by shade intolerant shrub species. Both investigators also predicted that shifts to a dense understory of shrubs following canopy dieback may inhibit tree seedling regeneration.

The absence of a relationship between *L. maackii* seedling growth and ash-decline was surprising since *L. maackii* adult growth exhibited a positive response. Perhaps the short duration (3 years) of the study or else interception of resources by upper strata (e.g. canopy, sub-canopy, and shrubs) explains this discrepancy.

We found no effect of EAB-caused ash decline on *L. maackii* fruit production, unlike Schulz and Wright (2015) who found a positive association between reduced canopy cover and *L. maackii* fruit production. Additionally, Goodell et al. (2010) found that pollinator visitation to forest edge *L. maackii* flowers was higher than to those in the forest interior in one of two sites; resulting in double the pollen deposition and almost twice as many seeds per flower. There are two potential reasons we may have been unable to find a relationship between *L. maackii* fruit production and ash decline. First, ash decline may not have resulted in a great enough resource increase to have a measurable effect on fruit production. Alternatively, since *L. maackii* cover was the best predictor of fruit production, perhaps additional resources were invested into vegetative growth leading to an indirect increase in fecundity rather than a directly increasing fruit production.

Sites with poorer ash condition and greater *L. maackii* cover had a greater abundance of *L. maackii* seedlings in 2012. There are two potential hypotheses that could explain how poorer ash condition increases the number of *L. maackii* seedlings: greater seed production in these sites or greater survival of seedlings. Although we did not find a direct relationship between ash condition and fruit production, the first hypothesis (sites with dying ash produce more *L. maackii* seedlings via more seeds) is supported by our finding that *L. maackii* shrubs grow faster where ash has declined, combined with our finding of a positive relationship between *L. maackii* BA and *L. maackii* fruit production. Alternatively, reduced shade or other competition from ash may improve demographic rates of *L. maackii* seedlings (recruitment, survival, and/or growth). However, we found that *L. maackii* seedling recruitment, survival, and growth were not affected by either ash decline or *L. maackii* BA or cover. Therefore, we think the correlation of *L. maackii* seedling abundance with ash decline is due to increased seed production by mature plants.

Tree and shrub seedling responses

We found minimal support for our second prediction, that EAB-caused ash decline has a direct effect on tree and shrub seedlings. Only for *L. maackii* seedling abundance was a measure of ash decline included in the best model; although ash decline was included in competing models for abundance of other invasive seedlings and for seedling species richness, in both cases this was a positive association. Similarly, girdling of *Fraxinus nigra* to simulate mortality of EAB did not affect survival of tree seedlings in Minnesota (Looney et al. 2015).

It is possible that seedling dynamics of some individual tree and shrub species do respond directly to ash decline, but that our grouping of species into invasives, shade-tolerant natives, and shade-intolerant natives obscured these responses. In Michigan, recruitment of *Fraxinus pennsylvanica* seedlings was high following EAB attack, but this correlated with a mast year rather than differences among stands in time-since-EAB attack (Kashian 2016). Klooster et al. (2014) found that over a 3 year period there was a significant interaction between year and hydrological soil class for ash seedling establishment, where seedling establishment was greatest in 2010 on xeric transects. *Fraxinus* spp. were included with shade intolerant native seedlings in our analyses, and while we found that recruitment in this group was positively correlated with ash decline, this was in 'competing' models that also included *L. maackii* BA and cover as a predictor. This result is in contrast to what Klooster et al. (2014) found, where for 2 years there was a positive correlation between sites with healthier ash canopies and ash seedling establishment. Differences in methodology may be one reason for the dissimilar results, in their study any seedling lacking cotyledons was considered established whereas we only included seedlings taller than 20 cm. Furthermore, the positive correlation that we found between ash decline and higher recruitment of shade intolerant native seedlings could be due to improved seed germination, seedling survival, or seedling height growth; all of which likely correlate with increased resource availability and thus ash decline. We recognize that many factors, including nutrients and moisture, influence woody seedling demography, but our purpose was to determine if ash decline and *L. maackii* shape these responses despite this underlying variation.

Ash decline is indirectly affecting forest structure and diversity through improving *L. maackii* growth, which negatively affects seedling populations, as several findings aligned with our third prediction. First, sites with greater *L. maackii* BA and cover had lower seedling species richness overall, fewer total seedlings (excluding *L. maackii*), and fewer shade tolerant native seedlings. Furthermore, recruitment for all seedlings (excluding *L. maackii*), as well as shade tolerant and intolerant native seedlings, was also depressed by greater *L. maackii* BA. Our findings are consistent with previous findings that show that *L. maackii* and the closely related *L. tatarica* have deleterious effects on woody seedlings including lower species richness (Hutchinson and Vankat 1997; Collier et al. 2002), diminished tree seedling abundance (Woods 1993; Hutchinson and Vankat 1997; Collier et al. 2002), recruitment (Cameron et al. 2016) and survival (Gorchov and Trisel 2003). Hypothesized mechanisms for these effects include shading (exacerbated by extended leaf phenology) (Woods 1993; Gorchov and Trisel 2003; McEwan et al. 2009), water uptake (Pfeiffer and Gorchov 2015), and allelopathy (Dorning and Cipollini 2006).

Invasive seedlings, excluding *L. maackii*, were not influenced by either of our measures of *L. maackii*. Instead the abundance of invasive seedlings was greater in sites with less stand basal area. This finding could be due to greater light availability in less mature forests leading to either higher fruit production (Burnham and Lee 2010; Gorchov et al. 2011; Driscoll et al. 2016) and/or greater invasive seedling success (Gurevitch et al. 2008).

Chronic and acute effects

The effects of EAB and *L. maackii* on forest regeneration can be interpreted within the framework of long-term ecological effects. Strayer et al. (2006) suggested that temporal influences must be considered when evaluating the ecological effects of invasive species; particularly the difference between chronic and acute ecological effects. Based on its longevity, *L. maackii* is expected to have a chronic effect on forest regeneration. Indeed we found that *L. maackii* does profoundly alter woody seedling composition. On the other hand; rapid ash mortality caused by EAB is expected to have an acute effect on woody plant growth. Surprisingly, EAB-caused ash decline had a relatively small direct effect on tree and shrub seedling measures.

Concluding remarks

We revealed that there is a facilitative relationship between EAB and *L. maackii*. EAB-caused ash decline was correlated with increased radial growth of *L. maackii*. Additionally, we discovered that the greatest number of *L. maackii* seedlings occurred in sites with both poor ash health and greater *L. maackii* cover. Furthermore, we found that *L. maackii* BA and cover has a negative association with tree and shrub seedling populations, which will have negative repercussions for future forest composition. Our system does not demonstrate a classic case of 'invasional meltdown' (Simberloff and Von Holle 1999), whereby both invasive species mutually benefit from the presence of one another and thus exacerbate their negative effects. Instead, our system is an example of a new invasive species (EAB) facilitating the negative effect of an invasive species that was already present (*L. maackii*).We did not explore facilitation of EAB by *L. maackii* as we were not aware of any mechanism for such a relationship.

Determining if other shrubs, both invasive and native, in both human-impacted and more pristine forests, respond in similar ways to ash decline will be important for determining how other North American forests respond to EAB-caused ash decline. Furthermore, investigations focusing on invasive shrub responses to invasive insect-caused tree mortality (e.g. Asian longhorned beetle, *Anoplophora glabripennis* and hemlock wooly adelgid, *Adelges tsugae*) will be important for North American forests as these co-occurring invasive pests become an ever increasing threat.

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Appendix 1

See Table 2.

Table 2 Location and summary data for 48 plots (16 sites) for data collection on EAB-caused ash decline and woody plant growth responses in central and southwestern Ohio, USA (2012–2014)

Plot	Latitude	Longitude	Year25%	ADI (%)	AMI (%)	Stand BA m^2/ha	Mean *L. maackii* BA cm^2/200 m^2	*L. maackii* % cover/ 200 m^2 (%)	Prevalent ash species
Caesar Creek Gorge SNP 1	39.4903	−84.0984	2015	3	0	29.8	71.4	91	*F. quadrangulata; F. americana*
Caesar Creek Gorge SNP 2	39.4873	−84.0925	2015	32	0	26.3	35.5	87	*F. americana*
Caesar Creek Gorge SNP 3	39.4870	−84.0922	2015	9	0	29.9	65.5	76	*F. americana*
Caesar Creek State Park 1_1	39.4893	−84.0370	2012	2	2	33.1	14.4	58	*F. americana*
Caesar Creek State Park 1_2	39.4899	−84.0371	2012	0	0	29.0	3.0	0	*F. americana*
Caesar Creek State Park 1_3	39.4899	−84.0378	2012	9	5	28.6	13.1	67	*F. americana*
Caesar Creek State Park 4_8	39.5066	−84.0503	2015	0	0	31.8	3.9	7	*F. americana*
Caesar Creek State Park 4_9	39.5071	−84.0510	2015	12	0	78.7	1.7	4	*F. americana*
Caesar Creek State Park 4_9B	39.5059	−84.0507	2015	9	9	36.5	4.5	11	*F. americana*
Caesar Creek State Park 5_10	39.5362	−84.0033	2015	0	0	40.1	17.3	56	*F. americana*
Caesar Creek State Park 5_11	39.5366	−84.0033	2015	3	3	28.8	12.7	53	*F. americana*
Caesar Creek State Park 5_12	39.5368	−84.0035	2015	13	0	59.1	6.5	51	*F. americana*
Clifton Gorge SNP 1	39.7916	−83.8412	2015	3	3	27.4	28.6	44	*F. quadrangulata*
Clifton Gorge SNP 2	39.7923	−83.8409	2015	2	0	31.8	16.2	20	*F. quadrangulata*
Clifton Gorge SNP 3	39.7937	−83.8400	2015	14	1	49.8	7.5	13	*F. quadrangulata; F. pennsylvanica/ profunda*
Dempsey Middle School 1	40.3081	−83.0848	2008	30	23	14.0	1.9	62	*F. americana*
Dempsey Middle School 2	40.3078	−83.0845	2008	18	18	41.6	37.2	89	*F. americana*

Table 2 continued

Plot	Latitude	Longitude	Year25%	ADI (%)	AMI (%)	Stand BA m^2/ha	Mean *L. maackii* BA cm^2/200 m^2	*L. maackii* % cover/ 200 m^2 (%)	Prevalent ash species
Dempsey Middle School 3	40.3080	−83.0852	2008	25	25	15.9	6.4	96	*F. americana*
Edwards Furniture 1	39.5668	−84.2603	2008	39	39	51.9	20.6	73	*F. americana; F. quadrangulata*
Edwards Furniture 2	39.5671	−84.2602	2008	40	40	39.2	4.3	36	*F. americana*
Edwards Furniture 3	39.5672	−84.2605	2008	19	16	20.3	5.0	20	*F. americana*
Englewood Metropark 1	39.8880	−84.2830	2014	22	4	29.0	1.6	0	*F. pennsylvanica/ profunda*
Englewood Metropark 2	39.8881	−84.2832	2014	35	30	34.0	2.7	4	*F. nigra; F. pennsylvanica/ profunda*
Englewood Metropark 3	39.8885	−84.2838	2014	15	3	33.7	1.3	7	*F. pennsylvanica/ profunda*
Germantown Metropark 1	39.6389	−84.3969	2014	0	0	41.0	2.8	4	*F. americana*
Germantown Metropark 2	39.6393	−84.3974	2014	10	5	27.0	2.3	9	*F. americana*
Germantown Metropark 3	39.6390	−84.3985	2014	4	0	42.0	9.7	29	*F. americana*
Glenwood Gardens 1	39.2566	−84.4857	2015	12	0	49.7	0.6	2	*F. quadrangulata; F. americana*
Glenwood Gardens 2	39.2568	−84.4858	2015	50	20	49.3	1.5	11	*F. quadrangulata; F. americana*
Glenwood Gardens 3	39.2568	−84.4851	2015	0	0	26.7	0.0	2	*F. quadrangulata*
Highbanks Metropark 1	40.1452	−83.0271	2007	46	41	30.0	1.1	4	*F. americana*
Highbanks Met opark 2	40.1453	−83.0274	2007	45	42	32.1	1.2	2	*F. americana*
Highbanks Metropark 3	40.1454	−83.0264	2007	44	36	26.6	0.3	0	*F. americana*
Hueston Woods SNP 1	39.5696	−84.7539	2011	8	0	43.2	1.1	0	*F. americana*
Hueston Woods SNP 2	39.5696	−84.7534	2011	60	25	60.7	0.2	0	*F. americana*
Hueston Woods SNP 3	39.5699	−84.7528	2011	52	0	41.8	0.8	0	*F. americana*
Seymour Woods SNP 1_1	40.2282	−83.0554	2009	39	32	35.6	1.7	2	*F. americana*

Table 2 continued

Plot	Latitude	Longitude	Year25%	ADI (%)	AMI (%)	Stand BA m^2/ha	Mean *L. maackii* BA cm^2/200 m^2	*L. maackii* % cover/ 200 m^2 (%)	Prevalent ash species
Seymour Woods SNP 1_2	40.2282	−83.0557	2009	37	28	27.4	1.1	0	*F. americana*
Seymour Woods SNP 1_3	40.2282	−83.0560	2009	16	8	37.9	1.1	4	*F. americana*
Sharon Woods Cincinnati 1	39.2808	−84.3972	2014	0	0	26.5	1.8	0	*F. americana; F. quadrangulata*
Sharon Woods Cincinnati 2	39.2808	−84.3966	2014	20	4	49.5	1.5	33	*F. americana*
Sharon Woods Cincinnati 3	39.2805	−84.3958	2014	20	0	41.6	11.3	62	*F. americana*
Sharon Woods Columbus 2_4	40.1205	−82.9713	2010	46	46	18.6	3.6	38	*F. americana; F. quadrangulata*
Sharon Woods Columbus 2_5	40.1201	−82.9705	2010	24	18	20.4	3.9	20	*F. americana; F. quadrangulata*
Sharon Woods Columbus 2_6	40.1205	−82.9690	2010	3	3	17.9	5.3	18	*F. quadrangulata*
Stratford ecological Center 1	40.2550	−83.0714	2009	27	27	49.6	0.0	0	*F. americana*
Stratford ecological Center 2	40.2552	−83.0722	2009	16	16	23.8	0.6	0	*F. americana*
Stratford ecological Center 3	40.2551	−83.0729	2009	58	58	52.3	0.3	0	*F. americana*
Plot mean	NA	NA	NA	21	13	35.7	9.1	26	NA

Prevalent ash species refers to the species that comprised >33% of *Fraxinus* BA in the plot; other abbreviations follow Table 1. Data collected in 2012 was used to calculate ADI, AMI, Stand BA, *L. maackii* cover, *L. maackii* BA and *Fraxinus* spp. composition. Data collected 2007–2014 was used to calculate Year25%

Appendix 2

See Fig. 5.

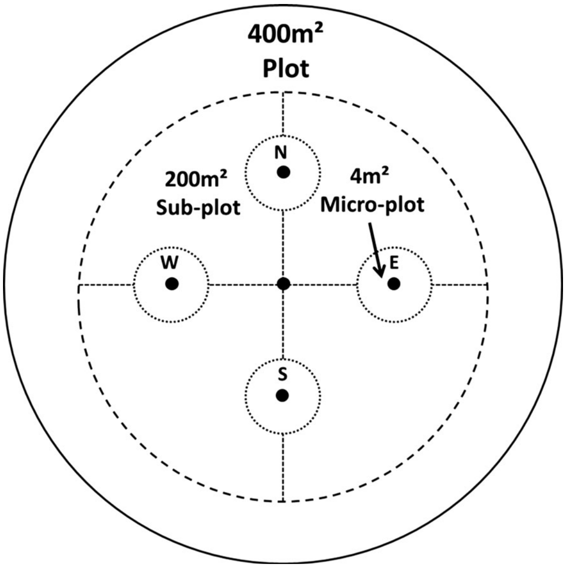

Fig. 5 Three circular 400 m^2 plots were nested within each of the 16 sites. Within the plot all canopy trees $\geq$10 cm diameter at breast height (DBH) were identified and DBH was annually measured, additionally the health of each ash was assessed (Appendix 3). Nested within each site was a 200 m^2 sub-plot (*circular dashed line*) where percent cover of *Lonicera maackii* was measured annually. Additionally, up to eight *L. maackii* shrubs (two per quadrant) were tagged, basal diameter and fecundity was measured. Within the four 4 m^2 micro-plots located in each cardinal direction 6 m from the center of each plot all tree and shrub seedlings (20–100 cm) were identified, tagged, and their height was measured. All measurements were conducted in 2012, 2013, and 2014

Appendix 3

See Fig. 6.

Fig. 6 Ash canopy (>10 cm DBH) health condition scale from Smith et al. (2015). Photo credit: Daniel A. Herms, The Ohio State University. Rating Scale Definitions: **1** a healthy full canopy; **2** thinning canopy, all topmost branches exposed to sunlight have leaves; **3** dieback is evident, thinning canopy, some topmost branches exposed to sunlight are dead (leafless); **4** dieback has occurred on more than 50% of the canopy; **5** canopy completely dead, entire canopy portion of the tree is dead (leafless), epicormics sprouts along the bole do not count

Appendix 4

See Table 3.

Table 3 All seedling species encountered in micro-plots in 16 sites located in central and southwestern Ohio, USA (2012–2014)

Species	Shade tolerance ranking	Group
Acer negundo	3.47	Shade tolerant natives
Acer nigrum	3.00	Shade tolerant natives
Acer rubrum	3.44	Shade tolerant natives
Acer saccharum	4.76	Shade tolerant natives
Aesculus sp.	3.81	Shade tolerant natives
Asimina triloba	3.95	Shade tolerant natives
Berberis thunbergii	1.50	Invasives
Carpinus caroliniana	4.58	Shade tolerant natives
Carya cordiformis	2.07	Shade intolerant natives
Carya laciniosa	4.42	Shade tolerant natives
Carya ovata	3.40	Shade tolerant natives
Carya sp.	2.96	Shade intolerant natives
Celtis occidentalis	3.17	Shade tolerant natives
Cercis canadensis	3.00	Shade tolerant natives
Cornus amomum	3.00	Shade tolerant natives
Cornus florida	4.87	Shade tolerant natives
Cornus sp.	3.75	Shade tolerant natives
Crataegus sp.	2.13	Shade intolerant natives
Elaeagnus umbellata	1.35	Invasives
Euonymus alatus	4.33	Invasives
Euonymus atropurpureus	4.00	Shade tolerant natives
Fagus grandifolia	4.75	Shade tolerant natives
Fraxinus quadrangulata	1.84	Shade intolerant natives
Fraxinus spp.	2.67	Shade intolerant natives
Ligustrum vulgare	2.57	Invasives
Lindera benzoin	3.00	Shade tolerant natives
Liriodendron tulipifera	2.07	Shade intolerant natives
Lonicera maackii	3.57	*L. maackii*
Lonicera morrowii	3.57	Invasives
Morus alba	1.35	Invasives
Morus rubra	2.34	Shade intolerant natives
Ostrya virginiana	4.58	Shade tolerant natives
Prunus serotina	2.46	Shade intolerant natives
Pyrus calleryana	1.35	Invasives
Quercus alba	2.85	Shade intolerant natives
Quercus bicolor	2.98	Shade intolerant natives
Quercus muehlenbergii	2.22	Shade intolerant natives
Quercus rubra	2.75	Shade intolerant natives
Quercus sp.	2.52	Shade intolerant natives
Rhamnus sp.	1.93	Invasives
Ribes sp.	3.36	Shade tolerant natives

Table 3 continued

Species	Shade tolerance ranking	Group
Rosa multiflora	1.73	Invasives
Sambucus sp.	1.35	Shade intolerant natives
Sassafras albidum	1.68	Shade intolerant natives
Staphylea trifolia	1.93	Shade Intolerant Natives
Tilia americana	3.98	Shade tolerant natives
Ulmus sp.	3.22	Shade tolerant natives
Viburnum acerifolium	4.00	Shade tolerant natives
Viburnum dentatum	4.00	Shade tolerant natives
Viburnum prunifolium	4.00	Shade tolerant natives
Zanthoxylum americanum	2.50	Shade intolerant natives

Species identity, shade tolerance score (Niinemets and Valladares 2006), and analysis group are included for each species. Invasives refers to species not native to North America

Appendix 5

See Fig. 7

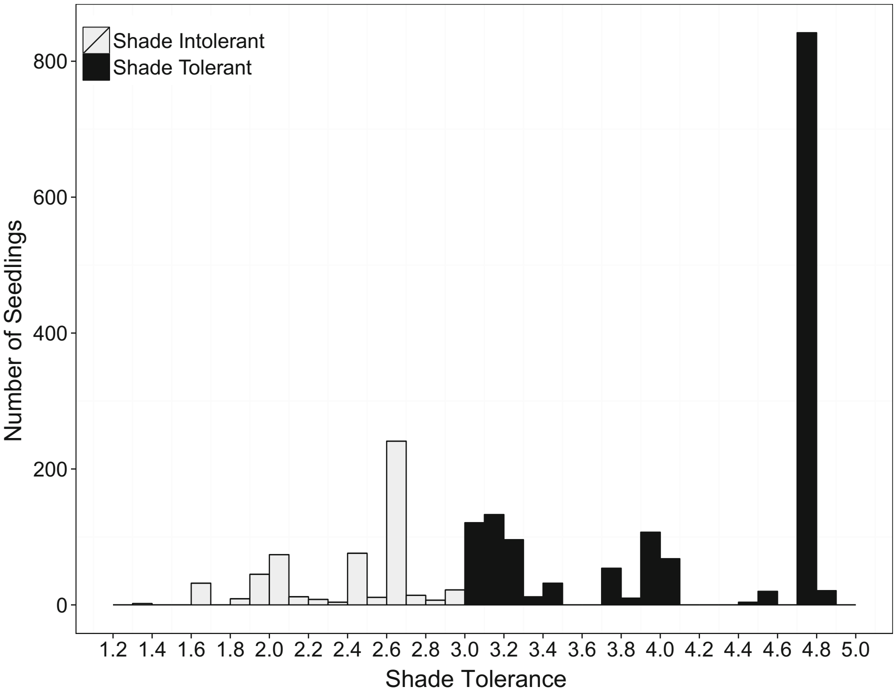

Fig. 7 Frequency distribution of shade tolerance scores (Niinemets and Valladares 2006) for native tree and shrub seedlings 20–100 cm tall censused in 16 deciduous forest sites in Ohio invaded by EAB and *Lonicera maackii*. We classified those ranked 1–2.99 as *shade intolerant* and those ranked (3–5) as *shade tolerant*

Appendix 6

See Table 4.

Table 4 Model comparison results for models testing the effect of EAB-caused ash decline and *Lonicera maackii* BA and cover on the response of *L. maackii* fecundity, and for models testing these predictor variables in conjunction with stand density on the response of relative *L. maackii* seedling growth

	ADI	AMI	Stand BA	*L. maackii* cover	*L. maackii* BA	ADI + Stand BA	AMI + stand BA	ADI + *L. maackii* cover	AMI + *L. maackii* cover	ADI + *L. maackii* BA	AMI + *L. maackii* BA	Null model
L. maackii Fecundity (2012)												
AICc	159.57	159.33	159.35	**141.87**	146.61	NA	NA	NA	NA	NA	NA	157.22
ΔAICc	17.69	17.45	17.47	**0.00**	4.74	NA	NA	NA	NA	NA	NA	15.34
w	0.00	0.00	0.00	**0.91**	0.09	NA	NA	NA	NA	NA	NA	0.00
L. maackii Fecundity (2013)												
AICc	148.95	149.19	148.83	**133.54**	135.66	NA	NA	NA	NA	NA	NA	147.37
ΔAICc	15.41	15.65	15.29	**0.00**	2.12	NA	NA	NA	NA	NA	NA	13.83
w	0.00	0.00	0.00	**0.74**	0.26	NA	NA	NA	NA	NA	NA	0.00
L. maackii seedling relative growth (2012–2014)												
AICc	28.13	28.37	27.70	**25.61**	**27.48**	30.09	30.17	28.00	28.11	29.91	29.98	**26.03**
ΔAICc	2.52	2.75	2.09	**0.00**	**1.87**	4.48	4.56	2.39	2.50	4.30	4.37	**0.42**
w	0.07	0.06	0.09	**0.24**	**0.10**	0.03	0.02	0.07	0.07	0.03	0.03	**0.20**

Models in bold are the best-fitting models (ΔAIC = 0) and any competing models with ΔAIC ≤ 2 indicating substantial support (Burnham and Anderson 2002). AICc is the small sample Akaike's information criterion; ΔAIC is the difference between the best model and every other evaluated model; and w is Akaike's weight. NA indicates that those models were not evaluated for the specified response variable. ADI represents Ash Decline Index and AMI represents Ash Mortality Index

Appendix 7

See Table 5.

Table 5 Model comparison results for models testing the effect of EAB-caused ash decline, stand BA, and *Lonicera maackii* BA and cover on woody seedling species richness (2012–2014) and abundance (2012) of all seedlings and four subsets of seedlings

	ADI	AMI	Stand BA	*L. maackii* cover	*L. maackii* BA	ADI + stand BA	AMI + Stand BA	ADI + *L. maackii* cover	AMI + *L. maackii* cover	ADI + *L. maackii* BA	AMI + *L. maackii* BA	Null model
Species richness												
AICc	249.48	248.65	250.36	242.46	**237.26**	251.79	251.01	243.93	242.26	239.42	**238.19**	248.08
ΔAICc	12.22	11.39	13.10	5.21	**0.00**	14.53	13.75	6.67	5.01	2.16	**0.93**	10.82
w	0.00	0.00	0.00	0.03	**0.46**	0.00	0.00	0.02	0.04	0.16	**0.29**	0.00
Abundance: all seedlings (excluding L. maackii)												
AICc	139.20	139.15	138.16	**130.49**	**130.38**	140.60	140.55	132.98	132.70	132.76	132.75	136.82
ΔAICc	8.82	8.77	7.78	**0.11**	**0.00**	10.23	10.17	2.60	2.32	2.39	2.37	6.44
w	0.00	0.00	0.01	**0.29**	**0.31**	0.00	0.00	0.08	0.10	0.09	0.09	0.01
Abundance: L. maackii seedlings												
AICc	240.30	236.39	245.50	227.33	244.70	240.15	235.13	225.61	**222.73**	232.49	231.68	247.19
ΔAICc	17.57	13.66	22.77	4.60	21.97	17.42	12.40	2.88	**0.00**	9.76	8.95	24.46
w	0.00	0.00	0.000	0.07	0.00	0.00	0.00	0.17	**0.74**	0.01	0.01	0.00

Table 5 continued

	ADI	AMI	Stand BA	*L. maackii* cover	*L. maackii* BA	ADI + stand BA	AMI + Stand BA	ADI + *L. maackii* cover	AMI + *L. maackii* cover	ADI + *L. maackii* BA	AMI + *L. maackii* BA	Null model
Abundance: invasive seedlings (excluding L. maackii)												
AICc	152.07	151.85	**147.54**	152.60	150.81	**148.17**	**148.65**	154.55	154.34	153.08	154.34	150.24
ΔAICc	4.53	4.30	**0.00**	5.06	3.27	**0.63**	**1.10**	7.01	6.80	5.54	6.80	2.70
w	0.03	0.04	**0.31**	0.02	0.06	**0.22**	**0.18**	0.01	0.01	0.02	0.01	0.08
Abundance: shade tolerant native seedlings												
AICc	142.76	142.73	142.31	**137.30**	140.16	144.73	144.72	139.77	139.67	142.61	142.65	140.38
ΔAICc	5.46	5.42	5.00	**0.00**	2.86	7.42	7.41	2.46	2.37	5.31	5.34	3.08
w	0.03	0.03	0.03	**0.41**	0.10	0.01	0.01	0.12	0.12	0.03	0.03	0.09
Abundance: shade intolerant native seedlings												
AICc	149.75	149.71	149.76	**146.99**	**146.28**	152.19	152.16	149.48	149.43	148.69	148.77	**147.40**
ΔAICc	3.47	3.43	3.48	**0.72**	**0.00**	5.91	5.89	3.20	3.15	2.42	2.49	**1.13**
w	0.05	0.05	0.04	**0.18**	**0.26**	0.01	0.01	0.05	0.05	0.08	0.07	**0.15**

Best-fitting and competing models are presented in bold as in Appendix 6. Analyses were conducted using AICc model selection; response variable rows and abbreviations are as per Appendix 6

Appendix 8

See Table 6.

Table 6 Model comparison results for models testing the effect of EAB-caused ash decline, stand BA, and *Lonicera maackii* BA and cover on woody seedling recruitment (2013 and 2014) of all seedlings and four subsets of seedlings

	ADI	AMI	Stand BA	*L. maackii* cover	*L. maackii* BA	ADI + stand BA	AMI + stand BA	ADI + *L. maackii* cover	AMI + *L. maackii* cover	ADI + *L. maackii* BA	AMI + *L. maackii* BA	Null model
Recruitment: all seedlings (excluding L. maackii)												
AICc	134.93	135.26	134.07	120.69	**112.45**	135.29	136.23	121.90	121.54	**114.36**	**113.54**	133.15
ΔAICc	22.48	22.82	21.62	8.25	**0.00**	22.84	23.78	9.45	9.09	**1.91**	**1.09**	20.70
w	0.00	0.00	0.00	0.01	**0.50**	0.00	0.00	0.00	0.01	**0.19**	**0.29**	0.00
Recruitment: L. maackii seedlings												
AICc	**190.96**	**190.30**	191.06	191.27	191.27	193.24	192.51	193.35	192.69	193.35	192.68	**189.00**
ΔAICc	**1.97**	**1.31**	2.06	2.27	2.27	4.24	3.51	4.35	3.69	4.35	3.68	**0.00**
w	**0.10**	**0.14**	0.10	0.09	0.09	0.03	0.05	0.03	0.04	0.03	0.04	**0.27**
Recruitment: invasive seedlings (excluding L. maackii)												
AICc	**146.45**	**145.18**	**146.37**	**147.11**	**146.80**	**146.75**	**145.74**	148.72	147.56	148.54	147.35	**145.18**
ΔAICc	**1.28**	**0.00**	**1.19**	**1.93**	**1.63**	**1.57**	**0.56**	3.54	2.38	3.37	2.17	**0.01**
w	**0.09**	**0.16**	**0.09**	**0.06**	**0.07**	**0.07**	**0.12**	0.03	0.05	0.03	0.06	**0.16**
Recruitment: shade tolerant native seedlings												
AICc	143.84	144.40	144.02	132.61	**130.45**	145.42	146.34	134.06	134.70	132.78	132.91	142.15
ΔAICc	13.39	13.95	13.56	2.16	**0.00**	14.96	15.89	3.60	4.25	2.32	2.45	11.70
w	0.00	0.00	0.00	0.15	**0.45**	0.00	0.00	0.07	0.05	0.14	0.13	0.00
Recruitment: shade intolerant native seedlings												
AICc	141.67	142.52	143.36	137.88	**135.86**	141.32	143.32	**137.37**	**137.10**	**137.04**	**136.63**	142.11
ΔAICc	5.80	6.66	7.49	2.01	**0.00**	5.46	7.46	**1.51**	**1.24**	**1.17**	**0.77**	6.24

Table 6 continued

	ADI	AMI	Stand BA	*L. maackii* cover	*L. maackii* BA	ADI + stand BA	AMI + stand BA	ADI + *L. maackii* cover	AMI + *L. maackii* cover	ADI + *L. maackii* BA	AMI + *L. maackii* BA	Null model
w	0.01	0.01	0.01	0.09	**0.26**	0.02	0.01	**0.12**	**0.14**	**0.14**	**0.18**	0.01

Best-fitting and competing models are presented in bold as in Appendix 6. Analyses were conducted using AICc model selection; response variable rows and abbreviations are as per Appendix 6

Appendix 9

See Table 7.

Table 7 Model comparison results for models testing the effect of EAB-caused ash decline, stand BA, and *Lonicera maackii* BA and cover on woody seedling survival (2012–2014) of all seedlings and four subsets of seedlings

	ADI	AMI	Stand BA	*L. maackii* cover	*L. maackii* BA	ADI + Stand BA	AMI + Stand BA	ADI + *L. maackii* cover	AMI + *L. maackii* cover	ADI + *L. maackii* BA	AMI + *L. maackii* BA	Null model
Survival: all seedlings (excluding L. maackii)												
AICc	209.24	209.28	209.06	**208.87**	209.13	211.44	211.45	211.16	211.24	211.41	211.50	**207.00**
ΔAICc	2.24	2.28	2.06	**1.87**	2.12	4.44	4.44	4.15	4.24	4.40	4.49	**0.00**
w	0.10	0.09	0.10	**0.11**	0.10	0.03	0.03	0.04	0.04	0.03	0.03	**0.29**
Survival: L. maackii s												
AICc	109.47	109.44	109.45	109.40	109.51	111.80	111.79	111.73	111.71	111.86	111.82	**107.23**
ΔAICc	2.24	2.21	2.22	2.17	2.28	4.57	4.56	4.50	4.48	4.63	4.59	**0.00**
w	0.10	0.10	0.10	0.10	0.10	0.03	0.03	0.03	0.03	0.03	0.03	**0.31**
Survival: invasive seedlings (excluding L. maackii)												
AICc	49.55	49.58	49.55	49.66	**49.42**	51.78	51.78	51.92	51.94	51.79	51.79	**47.52**
ΔAICc	2.03	2.06	2.03	2.15	**1.90**	4.26	4.26	4.40	4.42	4.27	4.27	**0.00**
w	0.10	0.10	0.10	0.10	**0.11**	0.03	0.03	0.03	0.03	0.03	0.03	**0.29**
Survival: shade tolerant native seedlings												
AICc	184.61	**184.26**	**184.78**	**184.07**	184.76	186.96	186.64	186.19	185.67	186.93	186.55	**182.50**
ΔAICc	2.11	**1.76**	**2.27**	**1.56**	2.25	4.45	4.13	3.69	3.17	4.43	4.04	**0.00**
w	0.09	**0.11**	**0.09**	**0.12**	0.09	0.03	0.03	0.04	0.06	0.03	0.04	**0.27**
Survival: shade intolerant native seedlings												
AICc	125.03	**124.60**	**123.43**	124.88	124.96	125.80	125.45	127.26	126.68	127.25	126.98	**122.77**
ΔAICc	2.26	**1.82**	**0.66**	2.11	2.19	3.03	2.68	4.49	3.91	4.48	4.21	**0.00**
w	0.08	**0.10**	**0.18**	0.09	0.08	0.05	0.06	0.03	0.03	0.03	0.03	**0.24**

Best-fitting and competing models are presented in bold as in Appendix 6. Analyses were conducted using AICc model selection; response variable rows and abbreviations are as per Appendix 6

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