Woody seedling community responses to deer herbivory, introduced shrubs, and ash mortality depend on canopy competition and site wetness

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ABSTRACT

Emerald ash borer (EAB) (*Agrilus planipennis*), non-native shrubs, and white-tailed deer (*Odocoileus virginianus*) have been independently shown to affect woody seedling communities. Our objective was to determine the relative importance as well as additive and interactive-effects of these stressors in the context of two environmental factors, canopy tree competition and site wetness. We sampled 24 sites, representing three natural non-congruent gradients in ash mortality, deer browse, and introduced shrub invasion. We explored the responses of seedling species abundance, diversity and richness to an array of deer herbivory, ash mortality, and introduced shrubs and varying levels of canopy tree competition, site wetness. The effects of each stressor on the differences in the relative abundance of seedling species was also evaluated. Our results indicate a persistent negative effect of non-native shrubs in drier forest plots on native seedling abundance, richness, and diversity. In wetter forests, non-native shrubs had no effect on native seedling richness or abundance and were positively related to diversity. Deer browse had a negative effect on seedling diversity in wetter forests and no effect in drier forests. Canopy tree competition had a positive effect on seedling diversity in drier forest plots, but negatively affected diversity in wetter forest plots. Ordination analysis revealed that site wetness, non-native shrubs and the total basal area of trees in the stand had the largest impacts on the species composition of seedlings found at each site. Our results suggest that site wetness and chronic stressors like deer and introduced shrubs are interacting to shift seedling communities towards fewer native species as well as to reduce seedling species richness and diversity.

1. Introduction

Disturbance plays an integral role in the successional trajectory of the eastern deciduous forest (Fischer et al. 2013). However, anthropogenic alterations to disturbance regimes have influenced species composition and diversity (Nuttle et al. 2013), thus altering the successional trajectory. Climate change, invasive shrubs, overabundant ungulate populations, and invasive pests and disease have been recognized as novel disturbances affecting the eastern deciduous forest (Webster et al. 2018). The effects of these novel disturbances on the seedling layer are of great interest to land managers because of the importance of this layer for forest regeneration (Webster et al. 2018). Managers of the eastern deciduous forest are particularly interested in the effect of introduced shrubs, white-tailed deer (*Odocoileus virginianus*) herbivory, and emerald ash borer (*Agrilus planipennis*) (EAB)-caused ash (*Fraxinus* spp.) mortality on future forest composition.

Previous studies have indicated that each of these disruptions can influence seedling communities. However, it is not clear which of these may have the greatest impact, or if interactive or additive-effects between perturbations could lead to greater effects. Introduced shrubs have been shown to inhibit native woody seedling regeneration (Webster et al. 2006) by hindering survival (Merriam and Feil 2002; Gorchov and Trisel 2003; Hartman and McCarthy 2004) and growth (Fagan and Peart 2004), resulting in lower abundance (Woods 1993; Hutchinson and Vankat 1997; Collier et al. 2002), species richness (Hutchinson and Vankat 1997; Collier et al. 2002), and diversity (Hejda et al. 2009).

Deer are considered a keystone herbivore, through their direct and

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indirect-effects on forest community composition and dynamics (McShea and Rappole 1992; Waller and Alverson 1997; Rooney 2001). Deer can skew seedling community composition based on palatability leading to long-term changes that greatly influence canopy species composition (Bradshaw and Waller 2016). Greater deer density has also been shown to lower absolute and relative native abundance (Waller and Alverson 1997) as well as species richness (Horsley et al. 2003) of tree seedlings. Deer also influence forest plant communities indirectly by avoiding less palatable species (Rooney 2009) and promoting browse-resistant invasive plants through competitive release (Eschtruth and Battles 2009). Moreover, deer may augment introduced shrub populations by increasing rates of colonization through seed dispersal (Vellend 2002, Myers et al. 2004, Castellano and Gorchov 2013, Guiden et al. 2015).

EAB-caused ash mortality can alter seedling community composition by depleting the ash seed bank (Klooster et al. 2014), decreasing ash seed production (Kashian 2016), decreasing green ash (*F. pennsylvanica*), black ash (*F. nigra*), and white ash (*F. americana*) seedling abundance (Klooster et al. 2014, Spei and Kashian 2017), and improving relative growth rates (RGR) in height for sugar maple (*Acer saccharum*) seedlings

(Hoven et al. 2020). Additionally, the abundance of seedlings of the invasive shrub, *Lonicera maackii* (Hoven et al. 2017), as well as those of introduced woody species overall (Hoven et al. 2020), are greater in sites affected by EAB-caused ash mortality. EAB may also cause far-reaching system-state shifts from forested wetlands into wetter systems dominated by herbaceous plants (Diamond et al. 2018).

Earlier studies have investigated the combined effects of deer and introduced shrubs (Ward et al. 2013; Loomis et al. 2015; Ward et al. 2018; Owings et al. 2017, Haffey and Gorchov 2019), and introduced shrubs and EAB (Hoven et al. 2017; Hoven et al. 2020) on woody seedlings. However, no previous studies have explored the additive and interactive-effects of EAB, deer, and introduced shrubs on woody seedlings.

We conducted a multi-year study on the effects of introduced shrubs and deer herbivory across a natural gradient of EAB–caused ash mortality to evaluate individual, additive, and interactive-effects on woody seedling communities. Additionally, we accounted for two environmental factors that could also affect seedling communities, specifically canopy competition and site wetness. The following five hypotheses were evaluated: (1) EAB-caused ash mortality releases native and
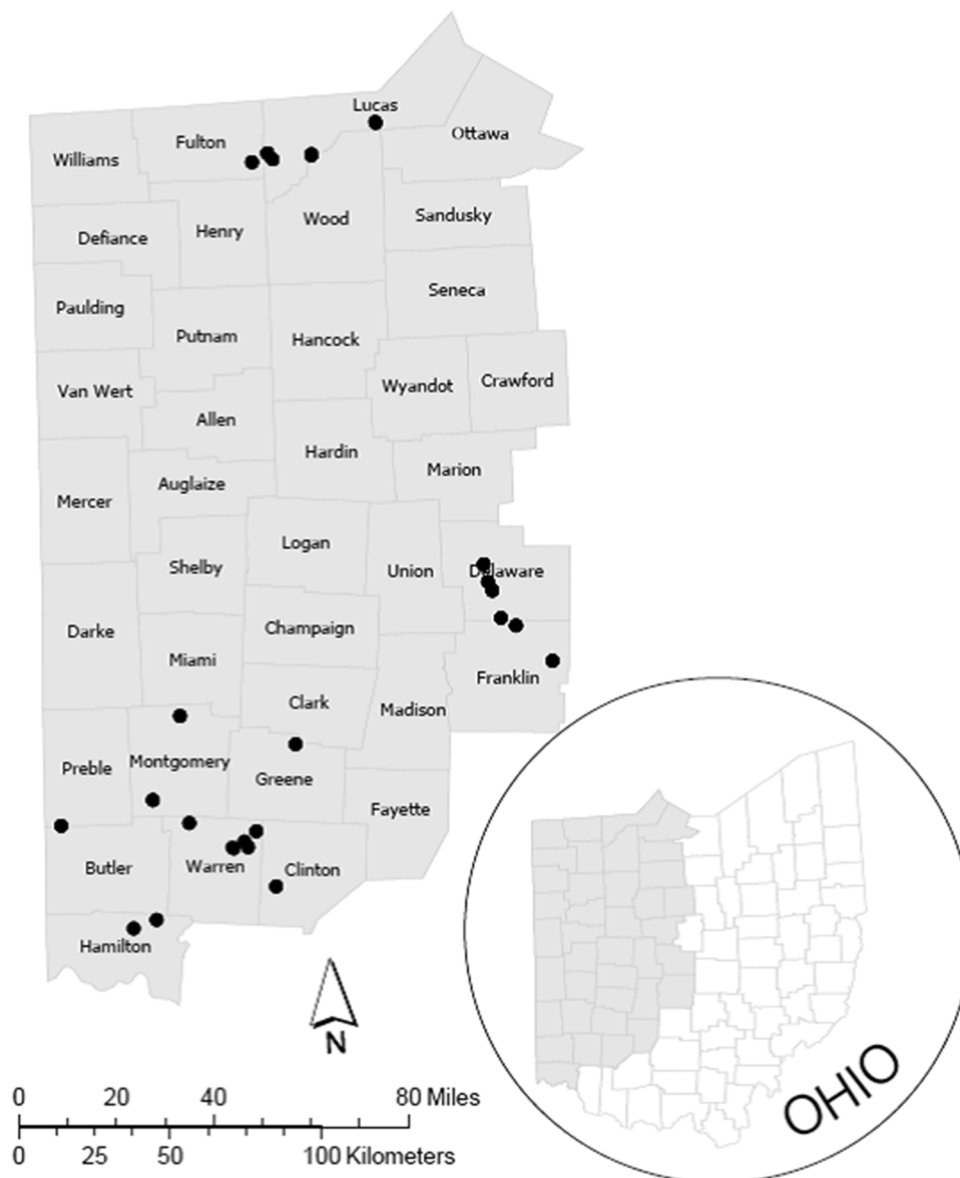

Fig. 1. Map of 24 study sites in Ohio, USA. Each dot denotes a site; nested within each site were three 400 m^2 plots. Sites and plots were established by the United States Forest Service for monitoring long-term EAB ecological impacts.

introduced seedlings; (2) Deer herbivory depresses native species while promoting invasive species; (3) Introduced shrubs suppress native seedlings and encourage introduced seedlings; (4) Soil wetness suppresses both native and introduced seedlings; and (5) Canopy competition depresses both introduced and native seedlings. Based on Hypotheses 1–5, we predict: (i) EAB-caused ash mortality shows positive relationships with seedling abundance, richness, and diversity; (ii) deer herbivory is negatively related to seedling abundance, richness, and diversity, while positively related to introduced seedling abundance; (iii) introduced shrub BA is negatively associated with native seedling abundance, species richness, and diversity, while positively associated with abundance of introduced seedlings; (iv) wetter plots are associated with fewer seedlings and (v) plots with greater canopy competition are associated with fewer seedlings. Our results will contribute relevant information to land managers and conservation practitioners across all eastern deciduous forests as they make decisions concerning the management of EAB, deer herds, and introduced shrubs.

2. Materials and methods

2.1. Study area

We conducted our study in 24 sites (Fig. 1), selected from those established by the U.S. Forest Service to study impacts of EAB (Knight et al. 2013), throughout Northwest, Central and Southwest Ohio. Northwest Ohio region experiences annual average temperatures of 11.9 °C and annual precipitation levels of 85.2 cm (https://www.usclimatedata.com), soils are loamy and clayey, level to gently sloping, very to somewhat poorly drained (websoilsurvey.nrcs.usda.gov). Central Ohio region is characterized by 142.5 cm of annual precipitation and annual average temperatures of 11.6 °C (https://www.usclimatedata.com), with soils that are silt loam, level to complex slopes, moderate to poorly drained (websoilsurvey.nrcs.usda.gov). Southwest Ohio region experiences annual temperatures are 11.6 °C, and annual precipitation levels are 105.6 cm (https://www.usclimatedata.com), soils are a silt loam, mainly level to moderately steep, moderate to well drained (websoilsurvey.nrcs.usda.gov).

EAB was first confirmed in Ohio in 2003 (http://www.emeraldashborer.info/). The north to south EAB-infestation in western Ohio represents a natural gradient in EAB-caused ash mortality effects, where the oldest infestations are in the north, and further south includes more recent invasions (see Hoven et al. 2020 Appendix 1). Sites also represent variation in level of deer browse intensity in a state with an estimated deer population of ~ 700,000 (https://wildlife.ohiodnr.gov). Introduced shrubs also pose a serious threat to the forests of Ohio, and the eastern deciduous forest at large, through the inhibition of native tree seedlings and forest herbs (Webster et al. 2006). Due to the extended simultaneous occurrence of these three stressors, Ohio presented an ideal location to conduct this investigation. Sites were public or private, mostly secondary forests with minimal management located within a matrix of suburban and agricultural lands.

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 (CCSP4 and CLF) and yearly trapping of EAB adult beetles in a subset of sites (Hoven et al. 2020). EAB was likely present at a site at low densities before these methods confirmed its presence. Using these methods, the gradient of known duration of EAB presence in the other 22 sites was one to nine years at the time of last plant measurements (2014).

2.2. Environmental factors

Three circular plots of 400 m² were nested within each of the 24 sites (Appendix: Fig. A.1). 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 plot during June-August 2012, we identified and measured the DBH of all trees ≥ 10 cm DBH (hereafter 'canopy trees'). Basal area for all canopy trees, including dead and dying ash, was calculated using DBH, and is hereafter referred to as 'Stand BA.' We considered Stand BA as a surrogate for canopy competition since it is typically used to assess stand density and competition (Stancioiu and O'Hara 2006). Stand BA is better for assessing competition since it signifies previous competition for both above- and below-ground resources, whereas light measurements only represent a single resource (Stancioiu and O'Hara 2006).

To characterize site wetness of each plot, we calculated an index based on the waterlogging tolerance values (Niinemets and Valladares 2006) of the canopy tree species in the plot. Niinemets and Valladares (2006) scored each species on a scale from 1 (*very intolerant- it does not tolerate water-saturated soils for more than a few days during the growing season*) to 5 (*very tolerant-it survives deep, prolonged waterlogging for more than one year*) (Appendix: Table B.1). We considered mean waterlogging ranking (MWR) to be a proxy for an integrated long-term measure of soil wetness, as the conditions over time that allowed canopy tree species to establish and survive should be more ecologically relevant to seedling communities than short-term direct measurements of soil wetness. MWR was used in models as a continuous variable, however, it was treated as a two-level category in figures to facilitate viewing and discussion of differences between the wettest sites, where seasonal inundation may harm trees, and the rest of the sites. Using the Niinemets and Valladares (2006) scores and canopy tree plot data, two rankings of waterlogging tolerance were devised (Appendix: Table C.1). Weighted Waterlogging Ranking (hereafter, WWR) was calculated by multiplying the 2012 basal area for each canopy tree by its waterlogging ranking and then dividing the sum for each plot by the 2012 stand BA (Appendix: Table C.1). Mean Waterlogging Ranking (hereafter, MWR) was calculated by averaging the waterlogging ranking for each canopy tree present per plot (Appendix: Table C.1). We considered mean waterlogging ranking (MWR) to be a proxy for soil wetness, as the tolerance of the canopy trees should be a better long-term ecologically relevant measurement of soil wetness than short-term direct measurements.

2.3. Stressors

We quantified the stressor of EAB-caused ash mortality in each plot by calculating two metrics, following Hoven et al. (2017) and Hoven et al. (2020) (Appendix: Table C.1). First, we assessed the health of each ash canopy tree on a scale of 1–5, where 1 is a healthy tree, 5 is a dead tree, and 2–4 are in progressive stages of decline (Knight et al. 2013). All ash mortality observed in our sites was due to EAB attack (Charles E. Flower, *personal communication*) rather than from 'Ash Decline', which is suggested to be caused by environmental conditions (e.g., spring drought) (Palik et al., 2011) or viral infection (Sinclair and Griffiths, 1994). After assessing ash health, we calculated the total BA of canopy ash trees that received a rating between 3 and 5 and then divided this value by the total stand BA, as calculated above. This value will be referred hereafter as the Ash Decline Index or ADI. The second metric, referred to hereafter as Ash Mortality Index or AMI, was calculated as the BA of canopy ash trees rated 5 (dead individuals) divided by the total stand BA. These two indices were calculated to differentiate between the effects of thinning ash canopies (ADI) and the effects of ash mortality (AMI) on understory resource availability. Basal area measurements and ash condition ratings from data collected in June-August 2012 were used in calculating both variables.

We quantified the stressor of introduced shrubs within a circular 200 m² subplot that was located at the center of each 400 m² plot (Appendix: Fig. A.1). Identification and classification of shrub species as native or introduced was completed using (http://plants.usda.gov) (Appendix: Table D.1). We quantified introduced shrubs per subplot using two different variables: BA and percent cover. For BA, we first tagged the two largest shrubs of each introduced species in each of the four quadrants of

each subplot, for a total of up to eight individuals per species in each subplot. In June-August 2012, we measured the basal diameter of each stem of the tagged shrubs. Basal diameters were used to calculate BA for each stem and then summed these within individuals and then for each species. For percent cover of non-native shrubs, we used the line-point intercept method, following Hoven et al. (2017) and Hoven et al. (2020). Seven parallel transects per subplot were delineated in June-August 2012. At each sample point (N = 45/plot) the presence or absence of an introduced shrub was recorded. The number of sample points where an introduced shrub was present was divided by 45 to determine introduced shrub percent cover.

We quantified the stressor of deer herbivory within each plot using a browse index previously developed in the literature that focuses on sugar maples (Frelich and Lorimer 1985; Rooney and Waller 2003; hereafter the sugar maple browse index or SMBI). Sugar maple is a favored phytometer for deer herbivory intensity in eastern North America due to being ubiquitous and a moderately-preferred browse species. At seven sites sugar maple was absent, so we substituted silver maple, *A. saccharinum* (1 site), red maple, *A. rubrum* (3 sites) or ash, *Fraxinus* spp. (3 sites), whichever was most common, because they had the same browse preference rankings based on Latham et al. (2005). During June-July 2015, one survey was conducted within each 400 m² plot, and each survey consisted of three ≥ 20 m transects (Appendix: Fig. E.1). This resulted in a total of 72 surveys conducted across the 24 study sites. For each survey, 21 *Acer* or *Fraxinus* saplings between 30 and 200 cm tall within a meter of the transect line were assessed for the presence of deer feeding damage on the terminal stem (Rooney and Waller 2003). To obtain a fair representation of browse damage within a plot we inspected seven seedlings per transect. If the initial three 20 m transects did not contain 21 seedlings for assessment, then we extended the length of each transect line by 5 m and continued with additional 5 m extensions until the 21-seedling quota was reached. On a few occasions transects contained more than seven seedlings that met the sampling requirements. In those cases, seven saplings per transect approximately equidistant apart on each transect were sampled. A browse index for each plot was calculated by dividing the number of browsed terminal twigs by 21 (total twigs sampled per plot) (Rooney and Waller 2003).

2.4. Seedlings

The diversity, abundance, richness and community composition of seedlings (20–100 cm) were quantified in June-August 2014. All woody tree and shrub seedlings were sampled within four permanent circular 4 m² micro-plots that were located 6 m from each 400 m² plot center and positioned in each of the four cardinal directions (Appendix: Fig. A1), following Hoven et al. (2017) and Hoven et al. (2020). Seedlings were identified to the level of genus or species depending on the identifying characteristics present and classified as native or introduced (Appendix: Table F.1). Data from the four micro-plots were pooled (Appendix: Table G.1) for all measures of seedlings.

2.5. Statistical analysis

Our analyses were conducted using generalized linear mixed and linear mixed-effects models with maximum likelihood estimation for fixed-effects (Bolker et al., 2009) in the R packages lme4 and nlme in R version 3.0.2 (Bates et al., 2017) of the R programming language (http://www.r-project.org/). Linear mixed models were used when the response variable could be transformed to achieve normality of the residuals and generalized linear mixed models were used when the response variable followed a Poisson or binomial error distribution. Goodness of fit tests were used to determine appropriate model structure. Because analyses used observations from three replicate plots at each site, all models used 'site' as a random variable, allowing us to account for the variation across plots nested within sites.

Four woody-seedling response variables were tested in models: (1) abundance of native seedlings, (2) abundance of introduced seedlings, (3) Shannon diversity index (effective number of equally abundant tree seedlings), and (4) number of woody seedling species (richness). Seedling species richness was modeled using a Poisson error distribution. Abundance of native and introduced seedlings were log transformed to meet the assumptions of normality, while the Shannon diversity index of seedlings was transformed using exp(H). This was done to convert the values to an effective number of species so that one community value could be compared with other community values.

To identify the most parsimonious models for each response variable, we conducted model selection using a candidate set of models. Different combinations of the three stressors and two environmental factors were included as predictors in models. Prior to including potential predictor variables in our analyses, we tested for collinearity. The following predictor variables were correlated: Ash decline index (ADI) and ash mortality index (AMI), introduced shrub basal area (BA) and percent cover, and mean waterlogging ranking (MWR) and weighted waterlogging ranking (WWR). After careful consideration, we decided to retain ADI, introduced shrub BA, and MWR. We kept ADI because it encompasses a broader set of EAB impacts than AMI. We retained introduced shrub BA because the effects of shrub size were a better indicator of time since invasion than shrub cover. We chose MWR because the calculation was less ambiguous than the WWR calculation. Predictor variables for the candidate set of models included: ADI, introduced shrub BA, SMBI, stand BA, and MWR.

For each response variable, we evaluated 26 models: 5 single predictor models, all 10 two-predictor variable additive models, all 10 two-predictor variable interaction models, and the null model (no fixed-effects, site included as a random effect). Evaluating additive models allowed us to determine if multiple predictor variables were influencing our response variables. Additionally, testing interaction models allowed us to determine if the effect of each predictor variable was dependent on the value of the other predictor variables in the model. Stand BA and introduced shrub BA variables were both log-transformed to standardize difference in magnitude among predictors.

For each response variable, the most parsimonious model was the one 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 approximating vs competing models) was assessed using Akaike weights (reported as *w*). Employing AICc allowed us to evaluate and rank models to assess which most closely approximated reality based on the data that was collected during the study (Burnham and Anderson, 2002).

To determine how the three stressors and two environmental factors influenced the relative abundance of woody seedlings among sites, we carried out ordination using distance-based redundancy analysis (dbRDA) with Bray-Curtis dissimilarity (McArdle and Anderson, 2001). We standardized seedling data using relative abundances. This constrained ordination technique (dbRDA) allowed us to test hypotheses concerning the effects of both environmental stressors and site characteristics on seedling community composition (McArdle and Anderson, 2001; Anderson et al. 2011). We included the following variables to quantify site stressors: ADI and AMI, introduced shrub BA, introduced shrub percent cover, and SMBI. MWR, WWR, and stand BA were included to assess site characteristics. We decided to retain AMI, introduced shrub BA, SMBI, stand BA, and MWR as predictor variables for the candidate set of models. We kept AMI because it performed better in the ordination analyses than ADI. The best approximating model rendered the lowest ΔAICc and p-values produced with an ANOVA with random permutations (999 permutations). We conducted a dissimilarity analysis using the capscale function in the Vegan package of R (Oksanen et al. 2022).

3. Results

3.1. Environmental factors and stressors

Two environmental factors, canopy competition and site wetness, modulated the effects of stressors on the seedling community. The average Stand BA, a proxy for canopy competition, was 39.1 ± 1.8 (SE) m^2 ha^{-1}. MWR, a proxy for site wetness, averaged 2.2 ± 0.1 and WWR averaged 2.3 ± 0.1 (Appendix: Table C.1), with most plots on the drier end of the distribution and a smaller number of wetter plots. While MWR was used in models as a continuous variable, it was treated as a two-level category in figures to facilitate viewing and discussion of differences between the drier sites and the wettest sites, where seasonal flood waters or anoxic conditions in saturated soils were likely to reduce survival of less tolerant tree species.

Stressors measured included ash mortality, invasive shrubs, and deer browse, which all had substantial variation among plots and encompassed a wide range of stressor levels. On average, ash (including dead and dying) made up 40 ± 2 % of stand BA; ash species differed most strongly among regions, and to a lesser extent, among sites (see Hoven et al. 2020, Appendix 1). ADI ranged from 0 % to 81 % with a mean of 25 ± 2 % and mean AMI (ash mortality) was 19 ± 2 % in 2012 (Appendix: Table C.1). Surprisingly, ash mortality did not have strong effects on tree seedling communities. SMBI (deer herbivory) ranged from 0 to 100 % with a mean of 38.3 ± 3 % (Appendix: Table C.1). Percent cover of introduced shrubs ranged from 0 to 98 % cover with a mean of 21 ± 3.3 %; mean introduced shrub BA was 0.32 ± 0.07 m^2/ha (Appendix: Table C.1).

3.2. Introduced and native seedling abundance

Seedling communities were strongly affected by deer herbivory and invasive shrubs, but those effects depended on site wetness and canopy competition. Surprisingly, ash mortality did not have a significant effect on seedling communities. All model results are reported in Table 1; best approximating and competing models for response variables are presented in bold and discussed. When the null model was included in the set of competing models ($\Delta AICc < 2$), the effects of predictor variables also included in the set were not considered further.

The mean abundance of introduced seedlings per plot (16 m^2 sample area) was 6 ± 1 individuals (Appendix: Table G.1). The null model was a competing model for introduced seedling abundance (Table 1). The mean abundance of native seedlings was 30 ± 3 individuals (Appendix: Table G.1). The most parsimonious model for native seedling abundance included an interactive effect between introduced shrub BA and MWR (soil wetness) (Table 1). To visualize interaction models, plots were divided into two groups based upon the median MWR value (2.055) (MWR is a continuous variable which ranged from 1.3 to 3.6): drier plots (N = 60) (MWR ≤ 2.055) and wetter plots (N = 12) (MWR ≥ 2.056). Sites containing wetter plots consist of one site that is classified as a riparian floodplain, one that is classified as a swamp forest, and four that are described as low-lying and seasonally inundated (see Hoven et al. 2020, Appendix 1). In addition to being dominated by waterlogging tolerant plants, wetter forest plots also had watermarks on trees (Berkowitz and Pietroski 2021) indicating seasonal inundation. Mean cover and BA of introduced shrubs for drier plots was 26 ± 5 % and 0.37 ± 0.11 m^2/ha, respectively, and for wetter plots 15 ± 5 % and 0.21 ± 0.08 m^2/ha, respectively. In drier plots there was a negative relationship between native seedling abundance and introduced shrub BA, whereas for wetter forest plots, there was no relationship (Fig. 2).

3.3. Species richness and effective number of species

The mean number of woody seedling species per plot was 6 ± 0.4 species (Appendix: Table G.1). The most parsimonious model for seedling species richness included an interactive effect between MWR (soil

Table 1

Model comparison results for models testing the additive-effects of introduced shrubs, EAB-caused ash decline, and white-tailed deer abundance, and Stand BA. Best approximating ($\Delta AIC = 0$) and competing models [$\Delta AIC \leq 2$, indicating substantial support (Burnham and Anderson 2002)] for response variables are presented in bold. For each response variable, plot data were analyzed using linear mixed models with 'site' as the random factor. Predictor variables tested included: introduced shrub basal area (BA) (Shrub basal area (BA)), mean waterlogging ranking (MWR), EAB-caused ash decline (ADI), sugar maple browse index (SMBI) (an estimate of white-tailed deer abundance) and Stand BA. 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. Statistics reported are based on likelihood ratio and goodness-of-fit tests.

| Models	Introduced Abundance			Native Abundance			Shannon Diversity Index exp(H')			Species Richness		
	AICc	ΔAICc	w	AICc	ΔAICc	w	AICc	ΔAICc	w	AICc	ΔAICc	w
1 Shrub BA	**224.50**	**1.23**	**0.07**	226.95	7.32	0.02	278.38	6.76	0.01	155.98	13.13	0.00
2 MWR	**225.23**	**1.97**	**0.05**	227.61	7.98	0.01	**272.15**	**0.52**	**0.14**	149.70	6.85	0.02
3 ADI	**224.27**	**1.00**	**0.08**	230.22	10.59	0.00	279.37	7.75	0.00	156.66	13.81	0.00
4 SMBI	**224.75**	**1.48**	**0.06**	228.15	8.52	0.01	276.53	4.91	0.02	150.78	7.92	0.01
5 Stand BA	225.96	2.69	0.03	229.56	9.94	0.00	279.26	7.63	0.00	157.06	14.20	0.00
6 ADI + Shrub BA	**224.86**	**1.59**	**0.06**	226.90	7.27	0.02	280.68	9.06	0.00	157.18	14.32	0.00
7 ADI + SMBI	**225.02**	**1.76**	**0.05**	229.74	10.12	0.00	278.79	7.16	0.00	152.86	10.01	0.00
8 ADI + MWR	225.86	2.59	0.04	229.35	9.73	0.00	274.18	2.56	0.05	151.90	9.04	0.01
9 ADI + Stand BA	226.57	3.31	0.02	221.33	11.71	0.00	281.57	9.94	0.00	158.90	16.04	0.00
10 SMBI + Shrub BA	225.92	2.66	0.03	224.37	4.75	0.06	277.09	5.47	0.01	149.99	7.13	0.02
11 SMBI + MWR	226.47	3.20	0.03	227.37	7.74	0.01	**272.20**	**0.57**	**0.13**	146.34	3.49	0.10
12 SMBI + Stand BA	227.06	3.79	0.02	228.43	8.81	0.01	278.82	7.19	0.00	152.73	9.87	0.00
13 Shrub BA + MWR	225.90	2.63	0.03	223.26	3.63	0.10	**272.63**	**1.00**	**0.11**	148.15	5.29	0.04
14 Shrub BA + Stand BA	226.80	3.53	0.02	226.78	7.16	0.02	280.63	9.00	0.00	157.85	14.99	0.00
15 Stand BA + MWR	227.54	4.27	0.02	228.73	8.95	0.01	273.95	2.32	0.06	151.97	9.11	0.01
16 ADI * Shrub BA	227.15	3.89	0.02	227.49	7.87	0.01	283.06	11.44	0.00	157.82	14.97	0.00
17 ADI * SMBI	227.33	4.06	0.02	231.94	12.31	0.00	281.16	9.54	0.00	154.76	11.91	0.00
18 ADI * MWR	228.03	4.77	0.01	229.50	9.88	0.00	275.68	4.05	0.02	153.35	10.50	0.00
19 ADI * Stand BA	228.56	5.29	0.01	232.76	13.14	0.00	281.05	9.42	0.00	159.34	16.48	0.00
20 SMBI * Shrub BA	228.30	5.04	0.01	225.30	5.68	0.04	279.47	7.84	0.00	152.22	9.36	0.01
21 SMBI * MWR	227.26	3.99	0.02	229.16	9.54	0.01	**273.19**	**1.57**	**0.08**	145.49	2.63	0.16
22 SMBI * Stand BA	225.27	2.01	0.05	230.79	11.16	0.00	281.20	9.57	0.00	154.66	11.81	0.00
23 Shrub BA * MWR	**223.27**	**0.00**	**0.13**	**219.62**	**0.00**	**0.64**	**271.62**	**0.00**	**0.18**	**142.86**	**0.00**	**0.60**
24 Shrub BA * Stand BA	228.87	5.61	0.01	228.58	8.95	0.01	282.31	10.69	0.00	160.23	17.38	0.00
25 Stand BA * MWR	229.92	6.65	0.00	230.79	11.17	0.00	**271.98**	**0.35**	**0.15**	151.83	8.97	0.01
26 Null Model	**223.72**	**0.45**	**0.10**	229.08	9.45	0.01	277.13	5.51	0.01	155.03	12.18	0.00
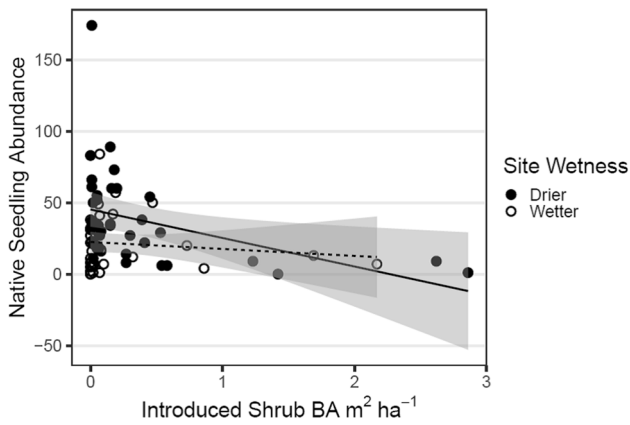
Fig. 2. Scatterplot of native seedling abundance (counts) (2014) on introduced shrub BA (basal area) for 72 plots. Plots are divided into two categories based on median (2.055) Mean Waterlogging Ranking (MWR): drier ($R^2 = 0.07$) (closed circle and solid line) and wetter ($R^2 = -0.10$) (open circle and dotted line). Lines illustrate the best fit to plot means and the gray shaded regions represent the standard errors around those lines.

wetness) and introduced shrub BA (Table 1). There was a negative relationship between seedling species richness (7 ± 0.4) and introduced shrub BA in drier forest plots, while there was no relationship between seedling richness (5 ± 0.5) and introduced shrub BA in wetter forests (Fig. 3).

The mean true diversity of woody seedlings per plot was 1.1 ± 0.1 (Appendix: Table G.1). The most parsimonious model for the effective number of woody seedling species included the interaction between introduced shrub BA and MWR (soil wetness) (Fig. 4A). There were five additional competing models: one contained the single predictor MWR, the other four were 2-term models: the additive and interaction models of MWR and SMBI (deer herbivory), the additive model of MWR and Shrub BA, and the interaction model of Stand BA and MWR (Table 1). There was a negative relationship between seedling diversity (1.72 ± 0.08) and introduced shrub BA for drier plots. In wetter forests, there was positive relationship between seedling diversity (0.95 ± 0.11) and introduced shrub BA (Fig. 4A). For the competing model of true seedling diversity that included the interaction between MWR and SMBI, there was a negative relationship between true diversity and SMBI in wetter forests and no relationship in drier forests (Fig. 4B). For the competing model that included the interaction between MWR and Stand BA, in
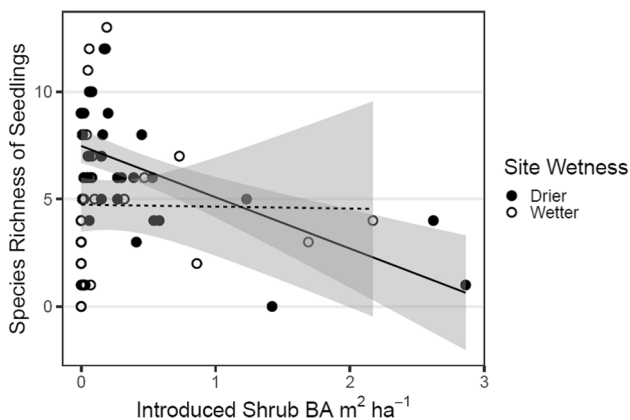

Fig. 3. Scatterplot of seedling species richness on introduced shrub BA (basal area) for 72 plots. Plots are divided into two categories based on median (2.055) Mean Waterlogging Ranking (MWR): drier ($R^2 = 0.11$) (closed circle and solid line) and wetter ($R^2 = 0.07$) (open circle and dotted line). Lines illustrate the best fit to plot means and the gray shaded regions represent the standard errors around those lines.
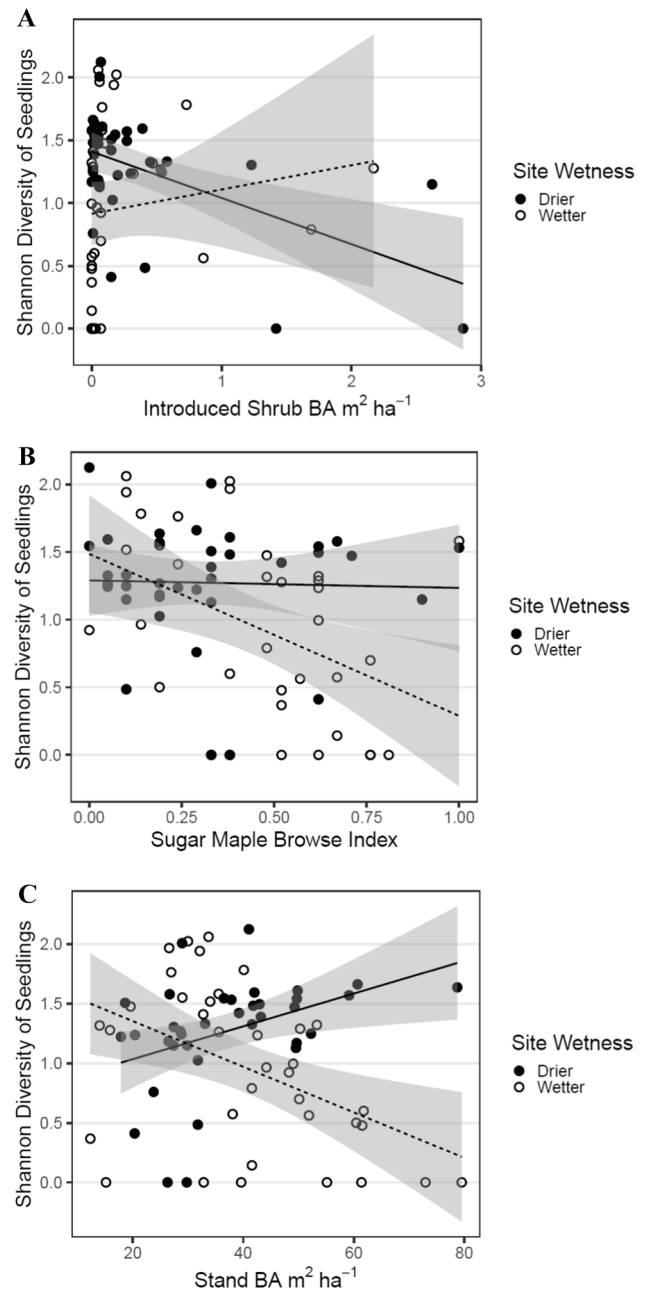

Fig. 4. Scatterplots of seedling Shannon Diversity [exp(H')] (2014) on (A) introduced shrub BA (basal area) For each figure, plots are divided into two categories based on median (2.055) Mean Waterlogging Ranking (MWR): drier ($R^2 = 0.05$) (closed circle and solid line) and wetter ($R^2 = 0.12$) (open circle and dotted line), (B) sugar maple browse index (SMBI) drier ($R^2 = 0.04$) (closed circle and solid line) and wetter ($R^2 = 0.28$) (open circle and dotted line), and (C) stand tree BA drier ($R^2 = -0.02$) (closed circle and solid line) and wetter ($R^2 = 0.19$) (open circle and dotted line). Lines illustrate the best fit to plot means and the gray shaded regions represent the standard errors around those lines.

drier forest plots effective number of seedling species was positively related to Stand BA, while in wetter forest plots there was a negative relationship (Fig. 4C).

3.4. Seedling community ordination

The species composition of seedlings was best explained by including the following factors in the constrained ordination model: SMBI, AMI, Stand BA, MWR, and introduced Shrub BA. Predictor variables that were

considered but were not included in the final model included ADI, WWR, and percent cover of introduced shrubs. The model explained 48 % of the variation in seedling community composition. AMI (ash mortality) and SMBI (deer herbivory) were both included in the final model, but neither was determined to have a significant effect on community composition, p = 0.064 and p = 0.071 respectively. Stand BA significantly affected seedling community composition (F = 3.7236, P = 0.001; Table 2); plots with greater basal area of trees were characterized by seedling communities containing more *Lindera benzoin* and *Acer saccharum* (Fig. 5). Soil wetness (MWR) also had a significant effect on seedling communities (F = 7.4319, P = 0.001; Table 2); the most common seedlings in wetter plots included *Acer rubrum*, *Quercus* spp., *Rhamnus cathartica*, *L. benzoin*, and *Fraxinus* spp. Greater basal area of introduced shrubs also affected seedling composition (F = 1.9874, P = 0.045; Table 2); plots with more introduced shrub BA not surprisingly had more seedlings of introduced species, including *Lonicera maackii*, *L. morrowii*, *Ligustrum* sp., and *Rosa multiflora*. Interestingly, the seedling communities of these plots were also characterized by more ash, *Fraxinus* spp., and hawthorn, *Crataegus* sp.

4. Discussion

Our findings indicate that the interactions between plot-level environmental factors, particularly site wetness (quantified by MWR), and broad-scale stressors (particularly introduced shrubs), are jointly responsible for influencing seedling communities. In most cases, the most parsimonious models for seedling parameters included the models with interaction terms, with many of the interactions involving site wetness. There was a consistent negative effect of introduced shrub BA in drier forest plots on native seedling abundance, richness, and diversity. The effects of introduced shrub BA on seedlings in wetter forest plots were less consistent; introduced shrub BA had no effect on native seedling abundance or richness but had a positive effect on diversity, providing partial support for Hypothesis 3 and Hypothesis 4. The impact of deer herbivory on seedling diversity was dependent on-site wetness; in wetter plots, it had a negative effect, whereas in drier plots it had no effect, providing support for Hypothesis 4 and limited support for Hypothesis 2. Finally, drier and wetter forest plots differed in how canopy competition affected seedling diversity, with canopy competition having a positive effect on seedling diversity in drier forest plots, and a negative effect in wetter plots, providing partial support for Hypothesis 5 and Hypothesis 4. Our results therefore highlight that canopy competition, deer browsing and introduced shrubs all affect native seedling communities, but these effects were all mediated by soil wetness. Surprisingly, ash mortality from emerald ash borer did not have large effects on the seedling community, indicating no support for Hypothesis 1.

4.1. Interaction-Effects

Variation in native seedling abundance, species richness, and diversity among plots were all best explained by the model including an

Table 2
Hypothesis test statistics for ordination of seedling-community composition. Environmental stressors and site characteristics were evaluated using distance-based redundancy analysis with Bray-Curtis dissimilarity. Ordination is illustrated in Fig. 5. The best approximating model was the one with the lowest AICc and p-values produced by an ANOVA with random permutations (999 permutations). The best model included Stand BA, MWR, AMI, introduced Shrub BA, and SMBI.

Predictor	Sum of Squares	F	P-value
MWR	**1.05684**	**7.4319**	**0.001 *****
Stand BA	**0.52951**	**3.7236**	**0.001 *****
Shrub BA	**0.28261**	**1.9874**	**0.045***
AMI	0.26952	1.8953	0.064
SMBI	0.24982	1.7568	0.071

interaction between MWR and introduced shrub BA. In drier plots, fewer native seedling species and fewer seedlings were observed in plots where there was greater introduced shrub BA. This was not surprising, because previous studies have also shown that the main effect of introduced shrubs suppress native tree seedling abundance (Woods 1993; Hutchinson and Vankat 1997; Collier et al. 2002; Hoven et al. 2017). Furthermore, previous research has shown a correlation between introduced shrubs and reduced seedling species richness (Hutchinson and Vankat 1997; Collier et al. 2002; Hoven et al. 2017); and species diversity (Hejda et al. 2009). In contrast, the relationship between seedling responses and interacting predictor variables in wetter forest plots was not as clear. Neither richness nor abundance of seedlings showed a relationship with introduced shrub BA, but seedling diversity showed a positive relationship, in these wetter plots.

We did find some evidence of the effect of deer herbivory on seedling diversity. In wetter forests, mean SMBI (deer herbivory) was 12 % greater (44 ± 4 %) compared to drier plots (32 ± 4 %). In wetter plots, seedling diversity was lower with greater deer herbivory, while there was no relationship between diversity and deer herbivory (SMBI) in drier forests. Previous studies have shown that intensified deer herbivory depresses woody seedling species richness (Harlow and Downing 1970; Tilghman 1989; Ward et al. 2018) and seedling diversity (Harlow and Downing 1970; Tilghman 1989). The long-term, chronic effects of deer herbivory on forest communities have been well documented (Rooney 2001; Bradshaw and Waller 2016). Excessive deer herbivory has been shown to overwhelm other disturbances, such as fire and canopy gaps that typically promote seedling diversity (Nuttle et al. 2013). Our results suggest that the interaction between introduced shrubs and soil wetness (MWR) overshadowed the impact of deer herbivory on seedling species richness and abundance. Furthermore, deer herbivory (SMBI) was not included in the final ordination model, indicating it did not have a significant effect on community composition. Previous studies have investigated the interaction effects of non-native shrubs and deer herbivory on native seedling communities (reviewed by Gorchov et al. (2021). Ward et al. (2018) suggests actively managing both deer and non-native shrubs to improve diversity of large tree seedlings. (Aronson and Handel, 2011) found that natural tree seedling regeneration improved after the removal of both introduced Japanese stiltgrass (*Microstegium vimineum*) and deer herbivory; however, it was not an interactive relationship.

One explanation for more herbivory in wetter plots is that they host a seedling community more palatable to deer. Alternatively, they serve as deer wintering grounds, which are often characterized by more unpalatable species and less favored species (Van Deelen et al. 1996). Based on our seedling ordination analysis and their browse preference based on season we were able to assess these explanations. If a site was a wintering ground, we would expect species associated with the MWR vector (wetter plots) and opposed (drier plots) to be those that have low preference rank in winter. Wetter sites were dominated by *Acer rubrum*, *Cornus florida*, *Fraxinus* spp., all are high preference in winter (Latham et al. 2005) and *Rhamnus cathartica* which is low preference year-round (Heneghan, 2005), suggesting these sites are not wintering grounds. Common species in drier plots included *Acer saccharum* and *Ulmus* spp. which are moderately and highly preferred in winter, respectively (Wright et al. 2019). *Asimina triloba*, *Celtis occidentalis*, *Carya cordiformis*, and *Prunus serotina*, were all associated with drier plots and are not preferred browse for deer year-round (Latham et al. 2005). Greater prevalence of favored genera, particularly *Acer* and *Fraxinus*, in wetter sites compared to lower favored species in drier sites suggest more deer browse in wetter sites is a product of availability rather than seasonality.

The other competing interaction model predicting seeding diversity was the interaction of soil wetness (MWR) and Stand BA. Since light is typically the most limiting resource in closed canopy forests (Pacala et al. 1994), it seems likely that more canopy BA reduces light availability and seedlings. Furthermore, ordination analysis also indicated that canopy competition had a significant effect on woody seedling
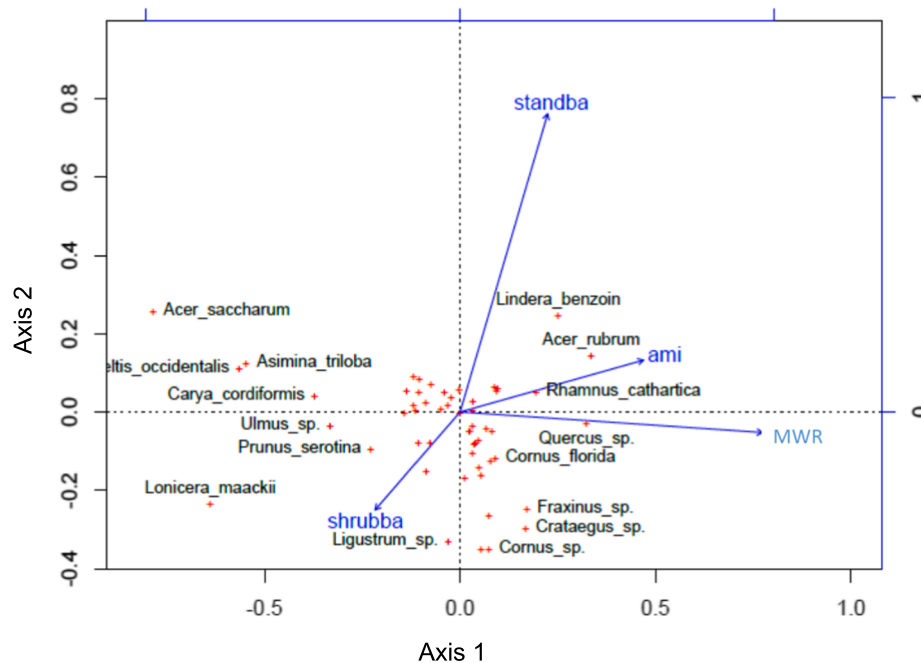
Fig. 5. Ordination of seedling species composition using distance-based redundancy analysis with Bray-Curtis dissimilarity. Constraining variables that were of importance included introduced shrubs basal area (BA) (shrubba), mean waterlogging ranking (MWR), canopy tree BA (standba), and ash mortality index (AMI).

composition. Specifically, plots with larger trees (greater Stand BA) were characterized by more seedlings of the native shrub *Lindera benzoin*, a moderately shade-tolerant species (Niinemets and Valladares 2006). Mean Stand BA in drier plots was 37.3 ± 2.2 m^2/ha, where it had a positive effect on seedling diversity (1.27 ± 0.08). In wetter plots, mean Stand BA (40.8 ± 2.7 m^2/ha) had a negative relationship with seedling diversity (0.95 ± 0.11). Lower seedling diversity in wetter plots is likely a response to more site wetness, which both limits seedling root respiration and augments canopy tree growth and thus increases competition. The positive relationship between Stand BA and seedling diversity in drier plots could potentially be explained by differences in introduced shrub BA or productivity. Based on Fig. 5, vectors Stand BA and introduced shrub BA are nearly opposing one another, suggesting that there is an inverse relationship. Since there was a negative relationship between seedling diversity and introduced shrub BA (Fig. 4A), more Stand BA is potentially limiting introduced shrubs and thus promoting seedling diversity. On the other hand, drier forests with greater Stand BA may be more productive either due to a difference in species present, differences in past management history, or perhaps greater productivity due to no seasonal inundation. Although introduced shrubs were associated with fewer native seedlings, they are not important in explaining abundance of introduced seedlings, as the null model was a competing model. This was surprising as we have previously noted a positive relationship between *Lonicera maackii* cover and *L. maackii* fecundity and recruitment (Hoven et al. 2017) as well as between introduced shrub cover and introduced seedling abundance in the same plots (Hoven et al. 2020). Perhaps the inclusion of soil wetness overshadowed the effect of introduced shrubs on the abundance of introduced seedlings. Even though introduced shrub BA did not affect introduced seedling abundance, it did have a significant effect on seedling composition based upon our ordination analysis. In particular, *L. maackii* and *Ligustrum* sp. Seedlings characterize plots with larger introduced shrubs. There are several reasons that may explain this positive relationship. Local introduced shrubs may be the source (propagule rain) of introduced seedlings. This was the most likely explanation for the positive association we found between larger *L. maackii* shrubs and more *L. maackii* seedlings (Hoven et al. 2017). Additionally, introduced seedlings could be best adapted to survive in

the presence of introduced shrub cover. There is evidence that some invasive shrubs such as *L. maackii* are allelopathic (Dorning and Cipollini, 2006) and their seedlings may be best adapted to tolerate that stressor. Additionally, similar biotic and abiotic factors that enabled larger introduced shrubs to become established, like disturbance (Davis et al., 2000), could have a strong effect in perpetuating the invasion process.

Individually, soil wetness (MWR) was a competing model for predicting seedling diversity. Wetter plots had less seedling diversity. Additionally, soil wetness (MWR) was included in the best model that explained 48 % of the variation in seedling community composition (Table 2), further indicating it is an important variable in shaping seedling communities. The key role of soil wetness in shaping seedling communities is not surprising due to the stress caused by saturated soils (Parent et al. 2008). Gaxiola et al. (2010) found that specific root length was reduced for seedlings growing in waterlogged soils compared to those grown in well-drained soils. Their findings also suggested that soil wetness could lead to retrogressive succession, whereby species-rich forests with taller trees shift to systems dominated by lower stature plants and a decrease in species richness (Gaxiola et al. 2010). Canopy ash trees, which are dead and dying, could lead to a decline in transpiration rates in lowland seasonally inundated ecosystems and may result in rising water tables (Slesak et al. 2014; Van Grinsven et al. 2017). Robertson et al. (2018) showed that EAB-caused ash mortality led to evapotranspiration declines and increases in shallow site wetness content. Additionally, at the plot level Slesak et al. (2014) and Telander et al. (2015) both concluded that a decline in transpiration rates resulted from EAB-caused ash mortality. The loss of these canopy trees may contribute to soil that is more frequently waterlogged and a decline in seedling species richness and diversity. In turn, this may severely limit recruitment of native seedlings and perhaps lead to greater cover by tolerant herbaceous species. In upland ecosystems, with relatively greater canopy tree diversity, transpiration decline due to ash loss will likely be offset by an increase in non-ash tree growth (Hoven et al. 2020), which would likely minimize community composition shifts. Interestingly, soil wetness (MWR) had a significant contribution to the woody seedling community composition based upon our ordination analysis; specifically, *Quercus* sp., *Cornus florida* and *Rhamnus cathartica*

were all associated with wetter soils in our study.

There was no support for Hypothesis 1; EAB-caused ash mortality did not affect seedling responses. This was surprising since previous studies including Klooster (2012), Hoven et al. (2017), Margulies et al. (2017), Dolan and Kilgore (2018), and Hoven et al. (2020), all found the seedling layer responded to EAB-caused ash mortality. Our inclusion of plot characteristics (e.g., site wetness as estimated by MWR) and chronic stressors like invasive shrubs and deer herbivory may have obscured the effects of ash mortality.

The best-fitting model for seedling composition included AMI (ash mortality), and two seedling species were associated with the AMI vector. One was the introduced *Rhamnus cathartica*, which further supports the Fluctuating Resource Hypothesis, where canopy ash tree mortality increases unused resource availability (Davis et al., 2000), improving the opportunities of non-native species to invade a community. Furthermore, it supports the hypotheses of Gandhi and Herms (2010) and Hausman et al. (2010) that an increase in canopy openness caused by ash mortality benefits introduced plants. The other seedling species associated with high AMI in the ordination was the native *Acer rubrum*, which could be in response to greater resource availability following ash mortality. Abrams (1998) reported that red maple seedling establishment and growth is best following disturbance.

4.2. Future forest composition

Based upon our results we can make a few predictions concerning future forest composition in these stands. Based upon seedling community data, both drier and wetter forest plots could move towards communities with greater shrub dominance. However, drier and wetter forest species could proceed along different trajectories depending on the influences of future broad scales stressors. The three most common seedling species encountered in drier forest plots were *Acer saccharum, Lonicera maackii*, and *Fraxinus* spp. We have previously shown that canopy *A. saccharum* benefited following the loss of ash to EAB (Hoven et al. 2020). We expect, therefore, the future canopy will have a greater percentage of maple. Maple-dominated stands would be susceptible to extensive canopy tree loss if invaded by a pest of maple, such as Asian longhorned beetle (ALB) (*Anoplophora glabripennis*). Increased light gaps are especially troubling if *L. maackii* is the species poised to fill the gaps. As previously noted, *L. maacki* can depress native seedling communities (see Hoven et al. 2017) and potentially shift these woodlands towards ones dominated more by introduced shrubs and reduced diversity in the future. Wetter forest seedling communities were dominated by *Fraxinus* spp., *Lindera benzoin, Lonicera maackii*, and *Celtis occidentalis. Fraxinus* seedlings might potentially recruit to larger size classes, but these would then be killed when EAB returned. The other common tree seedling, *Celtis occidentalis* (waterlogging ranking 2.65), is less tolerant of wetter soils, so massive ash loss could shift wetter forests to dominance by either herbaceous plants or shrubs. In forests where *Lindera benzoin* is established it seems to preclude *L. maackii*. We found that when percent cover of a site was ≥ 45 % *L. benzoin, L. maackii* cover was zero (*unpublished data*). This indicates that *L. benzoin* might prevent a shift towards a forest dominated by *L. maackii*.

4.3. Application to forest management

Introduced shrubs was the stressor shown to have the greatest negative effect on native seedling communities, with deer herbivory potentially important to seedling diversity. Separately considering seeding responses in drier and wetter forests illustrates how land managers could most effectively focus their efforts. Management of introduced shrubs can be used to promote native seedling richness and diversity. Introduced shrub control may be of greater importance in drier, upland forests where introduced shrubs predominate and their negative effects on native seedling communities are most pronounced. Deer limit seedling diversity predominantly in wetter forests where deer

management may be key for promoting regeneration. Finally, consideration of site-specific factors such as soil wetness and its potential interaction with other stressors may allow prioritization of forest management concerns. Understanding the severity with which stressors can negatively influence seedling communities in different forest types allows management to focus on locations where the work may have the greatest impact.

5. Conclusion

We investigated individual, additive, and interaction effects of acute and chronic stressors as well as site-level environmental characteristics on woody seedling communities in wetter and drier forests. We found evidence that site wetness interacts with other site-specific characteristics like canopy tree competition, as well as chronic stressors such as deer herbivory and introduced shrubs, to have a variety of effects on seedling diversity. Furthermore, the interaction of site wetness and introduced shrubs increases seedling diversity. By comparison, the acute effects of EAB were not important for shaping woody seedling communities. Our findings indicate that when mitigating for multiple stressors on seedling communities, chronic stressors such as introduced shrubs and deer herbivory may have the greatest impact. Consideration of how site-specific characteristics, such as soil wetness, interact with chronic stressors may allow more nuanced management decisions. Based on our findings, the most efficient way to promote native seedling abundance, richness, and diversity is to focus on removing introduced shrubs and managing deer herds. Introduced shrub removal in drier forests is likely to have the greatest positive affect. Seedling communities in wetter forests would benefit from lower deer densities.

Data availability

Data will be made available on request.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.

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