



The invasive tree, *Ailanthus altissima*, impacts understory nativity, not seedbank nativity

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ABSTRACT

Ailanthus altissima, the invasive forest tree commonly known as the tree-of-heaven, has been associated with decreased levels of plant species richness and native species diversity. However, this relationship with resident plants has been inconsistently found and the tree's influence on the seedbank has yet to be studied. To further understand the long-term impact of this tree, ten paired invaded-uninvaded sites were identified in Virginia, USA in a variety of different-aged stands. The herbaceous and woody understories for each plot were inventoried and soil samples were collected and grown out for 34 weeks in a greenhouse. All plants were identified to the most detailed taxonomic level possible. In total, 35 woody understory species, 62 herbaceous understory taxa, and 77 seedbank taxa were identified. The relationship between *A. altissima* presence and i) the proportion of individual plants that are native, ii) the proportion of species that are native, iii) the native diversity, and iv) the nonnative diversity were analyzed. In addition, models including the invasion age were also considered. We show that *A. altissima* invasions were associated with a decrease in the proportion of native plants and species in the understory, but not in the seedbank. Nonnative woody diversity also increased with *A. altissima* presence. Additionally, the impact on the nativity of the woody understory became more extreme over time. We end by discussing the benefits of both managing *A. altissima* invasions early to limit its overall impact and including the management of other nonnative plants in *A. altissima* restoration plans.

1. Introduction

Invasive species are an ever-increasing global problem, with ecological and economic consequences that we are just starting to understand (Hanley and Roberts, 2019; Pyšek and Richardson, 2010). In the United States alone, it is estimated that 50,000 nonnative species are present and causing damages of at least 120 billion USD per year (Pimentel et al., 2005). Of these, 5,000 are plants, representing about one of every five plant species found in the country, with these numbers likely continuing to increase (Hanley and Roberts, 2019; Pimentel et al., 2005). With such a large incidence and impact comes the need for management (Epanchin-Niell, 2017; Pyšek and Richardson, 2010). However, to make matters more challenging, when an invasive plant is successfully removed from an area it often leaves behind a “weed shaped hole” ready to be filled by other nonnative plants (Buckley et al., 2007; Prior et al., 2017). This secondary invasion of other nonnative species is a global problem for any restoration effort (Pearson et al., 2016; Prior

et al., 2017). Therefore, understanding how major invasive species impact local flora can help land managers better predict post-removal restoration needs.

One such major invader is the invasive forest tree, *Ailanthus altissima* (Mill.) Swingle (Sapindales: Simaroubaceae), commonly known as the tree-of-heaven. This tree has spread from its native Chinese range to the temperate and subtropical zones of all continents except Antarctica (Kowarik and Sämel, 2007). Since its first introduction to the United States in 1784 as a prized ornamental tree (Hu, 1979; Kasson et al., 2013), it has spread to 44 of the 50 states and is the dominant tree in many localized areas (EDDmapS, 2019). With this expansive presence, many corresponding impacts have been documented. These impacts include overtaking agricultural fields (Hepting, 1971), causing infrastructure damage (Hu, 1979; Kowarik and Sämel, 2007), and supporting invasive insects (Hoebeke et al., 2017; Song et al., 2018; Wallner et al., 2014). However, this tree's impact on the surrounding vegetation, including wildlife habitat and timber resources, may be the most

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concerning for land managers focused on long-term site restoration.

A variety of work comparing invaded areas to adjacent uninvaded areas has established that *A. altissima* can impact the resident vegetation. In the Mediterranean, areas invaded with *A. altissima* have decreased levels of native plant species diversity (Vilà et al., 2006), but do not differ in overall plant species richness (Traveset et al., 2008). In a Paris forest, it was found that understory vegetation was less diverse and made up of more common species under *A. altissima* trees, and that *A. altissima* sprout densities correlated negatively with floristic richness (Motard et al., 2011). In contrast in Greece, the overall floristic diversity was higher in *A. altissima* stands (Fotiadis et al., 2011). However, Fotiadis et al. (2011) did not consider the nativity of the vegetation, and this higher plant diversity could have been driven by secondary invasions and an increase in nonnatives. Lack of nonnative species consideration may help explain some inconsistent impacts observed, especially since the majority of ecosystems include invasions by multiple nonnative plant species (Kuebbing et al., 2013). For example, a meta-analysis in Mediterranean-type ecosystems found invasive tree species contributed to a decline in native plant richness, but did not look at their impacts to nonnative species (Gaertner et al., 2009).

Studies looking at vegetation after *A. altissima* control considered nativity in their assessments. For example, when *A. altissima* was removed in Virginia using chemical herbicides, the number of native dominant herbaceous species increased (Burch and Zedaker, 2003). Similarly, when *A. altissima* was removed in Pennsylvania using the proposed biopesticide *Verticillium nonalfalfae*, stands became dominated by native tree species (O'Neal and Davis, 2015). However, they also noted that in some areas nonnative herbaceous plants became dominant (O'Neal and Davis, 2015). Two other studies in Pennsylvania found that *A. altissima* removal caused very little impact on nonnative or native understory plants (Harris et al., 2013), and that there was no change in the mean number of native woody plants (Kasson et al., 2014). Therefore, to fully understand *A. altissima*'s impacts and to account for these inconsistent findings, additional research studying how *A. altissima* impacts the woody and herbaceous understory is still needed.

One potential difference between invaded-uninvaded and managed-unmanaged studies, is the importance of the seedbank (Brown, 1992). It is reasonable to consider that post-management findings may be exacerbated or minimized by the inputs from a seedbank. No previous studies have investigated how *A. altissima* impacts the seedbank. In a meta-analysis of a variety of nonnative species, Gioria et al. (2014) showed that the seedbank in invaded areas had lower native species richness and density and higher nonnative species richness and abundances. This shift in proportions of native and nonnative on the seedbank could help explain and predict the impact *A. altissima* has on the surrounding plant composition.

Ailanthus altissima's impact on the understory and the seedbank may become more severe as the invasion increases in age (Strayer et al., 2006). Though this trend has been seen with other nonnative plants, *A. altissima*'s impact over time has yet to be studied. For example, an Australian study comparing the time since invasion (ranging between 8 and 25 years) of the woody shrub *Cytisus scoparius* (scotch broom) found that native species richness and cover declined over the length of the invasion (Wearne and Morgan, 2004). Knowledge of how, if any, of *A. altissima*'s impact on the understory and the seedbank changes over time may help shape our understanding of this highly impactful invasive tree and its post-management restoration needs.

The objective of this research was to study the relationship between *A. altissima* invasion and the nativity of the woody understory, herbaceous understory, and the seedbank by looking at paired invaded-uninvaded plots in Virginia, USA. The age of the invasion was also studied to determine if it accounted for any differences in impact observed. We hypothesized that *A. altissima*'s invasion will decrease the native vegetation in both the understory and the seedbank, and that this decrease will become more severe over time.

2. Materials and methods

2.1. Site selection

Ten paired *A. altissima* invaded-uninvaded field plots were identified in Montgomery, Giles, and Pulaski Counties in Virginia, USA during the winter of 2017 to 2018 (Fig. 1). This paired invaded-uninvaded experimental design, commonly used to assess the impact of an invader, is based on the assumption that the uninvaded area is reflective of what the invaded area would have been like if never invaded (Barney et al., 2015; Gioria et al., 2014; Levine et al., 2003; Walker and Smith, 1997). Therefore, paired plots were selected to minimize any differences besides the invasion status of *A. altissima* (Gioria and Osborne, 2010; Hejda et al., 2009). Accordingly, these plots were chosen based on the presence of a discrete *A. altissima*-dominated area within a stand that contained no other *A. altissima* and whether the stand appeared homogeneous with respect to disturbance history. To achieve the same disturbance history, sites were only selected that were adjacent to a public roadway with similar aspects and slopes that were highly likely disturbed at the same time during past construction. To minimize any direct influences of *A. altissima* to uninvaded plots, paired plots were separated by a distance of at least 2x the height of the tallest *A. altissima* tree present but by no more than 100 m. These paired plots help account for differences between sites, such as the variations in salt additions from winter maintenance, residential density, and roadway speed and usage. All sites were located in rural areas, not adjacent to any actively managed lawns, and along public and active roadways.

All plot centers were identified, mapped (Fig. 1), and marked with metal tree tags. At invaded plots, the plot center was placed at the estimated invasion origin (the area containing the densest and largest *A. altissima* stems), while at uninvaded plots, the plot center was chosen in a location an appropriate distance away with similar terrain. To estimate the age of the invasion, the *A. altissima* with the largest diameter at breast height (DBH) was cored and the growth rings were counted (Kasson et al., 2013).

2.2. Established vegetation measurements

To quantify the stand composition, a 10-degree (basal area factor) prism (Cruise-Master Prisms Inc., Sublimity, OR) was used to estimate the basal area (BA, m²) of the dominant tree species while standing at all plot centers. In total, 24 different species had measurable basal area (Fig. 2). Of these, 13 species were measured at invaded sites and 21 species at uninvaded sites. The only nonnative species present were *A. altissima* and *Lonicera maackii*. *Ailanthus altissima* was only identified at invaded plots, making up 80% of their measurable basal area, while, *L. maackii* represented <2% of all measurable basal area at of both

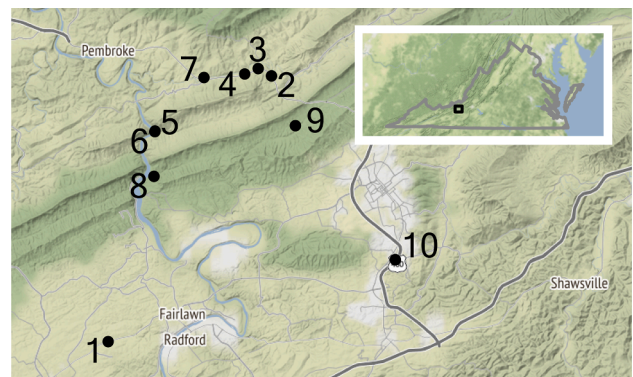


Fig. 1. Site location of all invaded-uninvaded paired plots used in this study located in southwestern Virginia (map produced using ggmap and ggplot2, Kahle and Wickham, 2013; R Core Team, 2018).

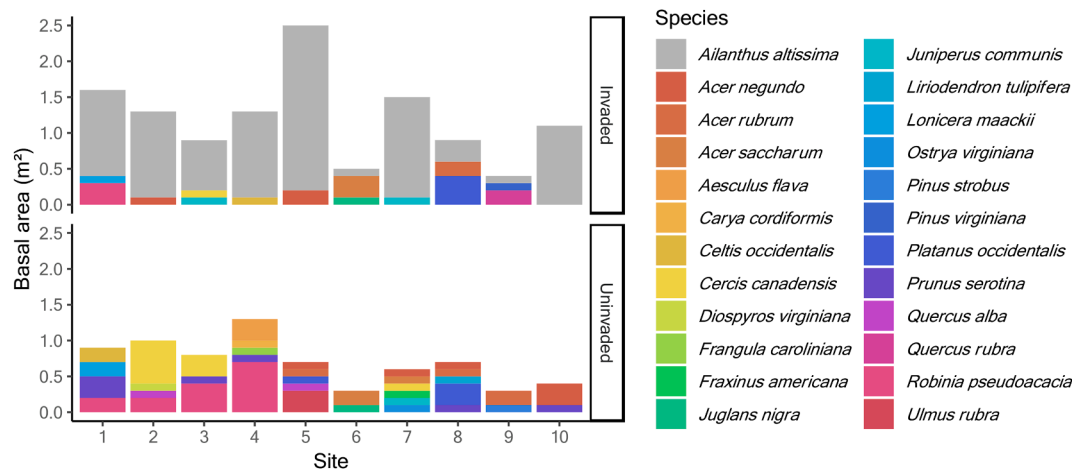


Fig. 2. Basal area (m^2) of all canopy level plants estimated using a wedge 10-degree prism. Data are separated by plot and invasion status (invaded or uninvaded) and species are distinguished by color.

invaded and uninvaded plots.

The established understory species composition of all plots was measured on 23 – 25 July 2018 during peak growing season. Site 3 was excluded due to destruction by roadside construction during the time-frame of this study. To quantify the understory plants present, three locations in each plot were selected by running a meter tape from the plot center to its edge at 0, 120, and 240 degrees away from the roadway. Then, at the location one-third of the way from the plot center to the stand edge a 1×1 m quadrat was placed. If the stand edge was not obvious in uninvaded plots, the samples were taken at the distance comparable to that of the paired invaded plot samples. A visual estimation of percent cover of all herbaceous plants and a count of any woody plants (excluding canopy trees) was recorded in each quadrat. All understory species present in this area were either identified in the field or sampled and taken back to the lab for later identification. All plant identifications, scientific and common names, and nativity (native, nonnative, unknown) were confirmed using the Flora of Virginia App (Weakley et al., 2017). All taxa were identified to the highest possible taxonomic resolution. If this identification was not to species, the plant's nativity was determined based on all possible species it might be. Individuals with unclear or unknown nativity were designated as such.

2.3. Seedbank collection, germination, and identification

To determine what germinable propagules were in the soils, a seedbank emergence method was used (Brown, 1992). This method focuses on what seedlings germinate and ignores any propagules that are not viable or remain dormant. To sample the seedbank, three soil samples at each plot were collected between 19 February and 6 March 2018 and placed into separate Ziplock bags. Each soil sample, 2 L in volume, was excavated just inside of where the understory measurements were taken. These samples were excavated from a 20 cm diam and 5 cm deep area using a 70% EtOH cleaned spade. All organic materials besides large sticks (greater than 20 cm) were included in the samples. This collection time allowed seeds from the previous growing season to go through a natural cold dormancy while limiting any germination caused by the next growing season. Samples were stored at 4 degrees C until planted.

On 18 May 2018, each soil sample was moved to a greenhouse and mixed with 4 L of potting soil (Miracle-Gro® Potting Mix 0.21–0.11–0.16) to ensure drainage and nutrient needs of all seeds were met, and with 120 ml of powdered activated charcoal (Biogize-SD™ Soil Detox, Dovecreek, CO) to limit the influence of any allelochemicals present (Callaway, 2003; Lawrence et al., 1991). Activated charcoal was added to allow a comparison of invaded and uninvaded seedbanks

regardless of allelochemical influences and because *A. altissima* allelochemicals disappear quickly in the soil once *A. altissima* has been removed (Heisey, 1990). Each soil-seedbank mixture was spread in a tray (47×33 cm) and watered as needed. Corresponding invaded-uninvaded germination trays were placed adjacent to each other and switched twice a month to limit the uneven influence of any environmental gradients within the greenhouse.

Seedling germination was monitored weekly. Once seedlings were identified to species, they were removed from the tray to minimize competition. If numerous identical seedlings germinated at the same time, they were counted and thinned to three representative seedlings until identification could be confirmed. If seedling identification did not occur within a reasonable amount of time, the plant was repotted to minimize its influence on the rest of the seedbank until identification could occur. Seedling identification and related information was based on the information provided in the Flora of Virginia App (Weakley et al., 2017). Seedling germination was allowed to occur for 34 weeks (until 1 November 2018).

2.4. Analysis

2.4.1. Invasion's influence on nativity

To determine the influence of *A. altissima* invasion on the herbaceous understory, the woody understory, and the seedbank, all taxa (excluding *A. altissima*) in each category were analyzed. The understory vegetation was analyzed in two data subsets due to the differences in field quantification (individual counts vs. percent cover) and *A. altissima* was excluded to ensure the response variables were independent of *A. altissima* presence (Vilà et al., 2006; Wearne and Morgan, 2006). These three vegetation categories were quantified using four different response variables: i) proportion native plants, ii) proportion native species, iii) native diversity, and iv) non-native diversity.

The “proportion native plants” measured the proportion of native individuals out of the total individuals counted (or in the case of the herbaceous understory, native percent cover out of the total percent cover). Similarly, the “proportion native species” calculated the number of native taxa present out of the total number of taxa identified.

The “native diversity” and “nonnative diversity” were measured by calculating a diversity index for either the native or the nonnative subset of the data. The chosen diversity index, the probability of an interspecific encounter (PIE), measures the probability that two individuals randomly drawn from a population represent different taxa (Hurlbert, 1971). This diversity index ranges from zero to one, with larger numbers indicating a higher diversity. PIE is calculated with the following equation,

$$PIE = \left(\frac{N}{N-1} \right) \left[1 - \sum_{i=1}^S (p_i)^2 \right]$$

where p_i is the fraction of the total number of individuals that consists of taxon i , N is the total number of individuals, and S is the total number of taxa. This diversity index was chosen because it can be meaningfully interpreted, it is insensitive to small sample sizes, and it can be modified to include non-count data (Gotelli, 2008). For example, when used for percent cover, PIE calculates the probability that two randomly chosen points in an area land on different taxa.

Within each of these vegetation categories, these four response variables were fit to linear mixed models containing two additive effects. The first being invasion status (invaded or uninvaded) as a fixed effect and the second being site as a random effect. These were fit using the lmer function from the “lme4” package in R (Bates et al., 2015; R Core Team, 2018). Chi² and p-values were then calculated using the likelihood ratio test comparing each model to a null model containing only the random effect and considered significant if $p < 0.05$ (Bates et al., 2015). Data were transformed as needed to meet parametric assumptions. Values that could not be calculated due to the lack of any vegetation present in a plot were excluded. To minimize excluded data, this analysis was completed on response variables pooled to the plot level for all calculations.

2.4.2. Age of the invasion's influence on nativity

The proportion of native individuals and proportion of native species were compared over time to determine if stand age helps account for the variation observed in any of the above analyses. These response variables for each of the three vegetation categories were analyzed using a linear mixed model. This model contained two interactive fixed effects (invasion status and age of the invasion) and an additive random site variable. These were again fit using the lmer function from the lme4 package in R (Bates et al., 2015; R Core Team, 2018). Chi² and p-values were then calculated using the likelihood ratio test comparing each model to a null additive model containing invasion status as a fixed effect and site as a random effect, with $p < 0.05$ indicating significance. If the model was determined to be significant, it was also compared to a second null model which contained three additive effects: age of the invasion and invasion status as fixed effects and site as a random effect. This additional comparison was completed to determine which effect or interaction was driving the significance observed.

2.4.3. Seedbank and resident vegetation similarity

The taxa found in the seedbank and the resident vegetation (including the herbaceous understory, woody understory, and canopy taxa) were compared at each plot using the Sørensen–Dice similarity index (Sørensen, 1948). This index calculates the similarity between the compared communities using the following equation:

$$\text{Sørensen - Dice similarity index} = \frac{2(c)}{a + b}$$

where a represents the total number of taxa found in one group, b represents the total number of taxa found in the other group, and c represents the number of taxa that are shared between the two groups. *Ailanthus altissima* was excluded from this calculation.

To determine if the age of the invasion or the invasion status influenced this similarity index, their relationship was analyzed using a linear regression containing two interactive predictor variables: invasion status and age of the invasion. The significance ($p < 0.05$) of the model, the two predictor variables, and their interaction was used to make conclusions about this relationship.

2.4.4. *Ailanthus altissima* seedbank presence

The prevalence of *A. altissima* seeds in the seedbank were analyzed separately to help predict long-term species-specific management needs.

The proportion of *A. altissima* in the seedbank at invaded plots was analyzed using a linear regression which contained only invasion age as a predictor effect (R Core Team, 2018). Uninvaded plots were excluded from this analysis since their *A. altissima* seedbank numbers were minimal. The significance of the regression and its adjusted R² value was used to validate this relationship.

3. Results

3.1. Invasion's influence on nativity

All herbaceous understory plants were identified to species excluding those in the *Carex*, *Hackelia*, *Solidago*, and *Triosteum* genera. These plants were not identified to species due to the quality of available samples (i.e. no production of flowers or seeds) needed for confident species identification. Of these, the nativity of the genus could be confirmed for everything but *Carex* spp. In total, 62 taxa were identified, of which 38.7% were nonnative (Table 1, Supplemental Table A.1).

The likelihood ratio tests used to determine if the invasion of *A. altissima* influenced the herbaceous understory's proportion native plants and the proportion native species were both significant. In both cases, these proportions were negatively influenced by *A. altissima* invasion, with the proportion of native individuals or species ranging from 0 – 1.0 at invaded sites compared to always being over 0.5 at uninvaded sites. The overall mean of the proportion of native plants was reduced from 0.82 to 0.49 while the proportion native species was similarly reduced from 0.71 to 0.43. In contrast, there was no indication that the invasion of *A. altissima* influenced the native diversity or the nonnative diversity of these plots (Fig. 3).

In total 1,437 woody understory plants were counted, comprised of 35 species, of which only five species were nonnative (*A. altissima*, *Celastrus orbiculatus*, *Ligustrum obtusifolium*, *Lonicera japonica*, and *Lonicera maackii*) (Table 1, Supplemental Table A.1).

The likelihood ratio test that analyzed how the woody understory (excluding *A. altissima*) was influenced by *A. altissima* invasion was significant for three of the four response variables. This output indicated that the proportion native individuals, the proportion native species, and the nonnative diversity are all influenced by the invasion of *A. altissima*. Both proportions decreased with invasion while nonnative diversity increased. The proportion of native individuals was very variable, ranging from almost 0 to 1, while the proportion of native species was always at or above 0.5. The overall mean of the proportion of native plants was reduced from 0.66 to 0.40, with the mean proportion of native species reduced similarly from 0.87 to 0.74. The woody understory's nonnative diversity index hovered roughly around 60% at both sites (increasing just slightly with *A. altissima* invasion), compared to the native diversity index which tended to be closer to 90%. The overall mean of the nonnative diversity index was increased from 0.55 to 0.66 (Fig. 3).

In total, 1,771 seedlings germinated and were all identified to species, excluding those in the *Carex* and *Solidago* genera. Of the two genera, the nativity could only be determined for species in the *Solidago* genus. These seedlings included 77 different taxa, of which almost half (48%) were nonnative (Table 1, Supplemental Table A.1).

The likelihood ratio test, which analyzed how the seedbank (excluding *A. altissima*) was influenced by the presence of *A. altissima*, showed that none of the four response variables were significantly changed (Fig. 3). In all cases, seedbank samples from plots were never exclusively native or nonnative, with the diversity indexes always higher than 50%.

3.2. Age of the invasion's influence on nativity

When considering the age of the invasion, the linear regressions were significant for both the woody understory's proportion native plants and its proportion native species (Fig. 4). Comparing both of these models to

Table 1

The 20 most abundant taxa as determined by the total percent cover (PC) or total count (count) of the herbaceous understory, woody understory, and the seedbank split by invasion status (invaded or uninvaded) is shown. The nativity (nonnative or native) of each taxa is also recorded. Identification and nativity was determined using the Flora of Virginia App (Weakley et al., 2017).

	Herbaceous understory			Woody understory			Seedbank		
	Taxa	PC	Nativity	Taxa	Count	Nativity	Taxa	Count	Nativity
Invaded	<i>Eupatorium godfreyanum</i>	29.0	native	<i>Lonicera japonica</i>	341	nonnative	<i>Microstegium vimineum</i>	225	nonnative
	<i>Microstegium vimineum</i>	23.5	nonnative	<i>Ailanthus altissima</i>	53	nonnative	<i>Muhlenbergia frondosa</i>	178	native
	<i>Rubus phoenicolasius</i>	23.0	nonnative	<i>Acer negundo</i>	37	native	<i>Ailanthus altissima</i>	153	nonnative
	<i>Polystichum acrostichoides</i>	16.5	native	<i>Lonicera maackii</i>	30	nonnative	<i>Oxalis stricta</i>	97	native
	<i>Amphicarpaea bracteata</i>	16.0	native	<i>Toxicodendron radicans</i>	21	native	<i>Glechoma hederacea</i>	64	nonnative
	<i>Geum canadense</i>	15.0	native	<i>Parthenocissus quinquefolia</i>	16	native	<i>Veronica hederifolia</i>	33	nonnative
	<i>Rubus allegheniensis</i>	10.5	native	<i>Celastrus orbiculatus</i>	15	nonnative	<i>Galinsoga quadriradiata</i>	25	nonnative
	<i>Alliaria petiolata</i>	7.8	nonnative	<i>Prunus serotina</i>	8	native	<i>Ranunculus abortivus</i>	25	native
	<i>Leersia virginica</i>	7.5	native	<i>Liriodendron tulipifera</i>	7	native	<i>Cardamine flexuosa</i>	24	nonnative
	<i>Hylodesmum nudiflorum</i>	7.0	native	<i>Hypericum prolificum</i>	3	native	<i>Erechtites hieracifolius</i>	15	native
	<i>Centaurea stoebe</i>	6.1	nonnative	<i>Smilax rotundifolia</i>	3	native	<i>Securigera varia</i>	15	nonnative
	<i>Ipomoea pandurata</i>	6.0	native	<i>Betula alleghaniensis</i>	2	native	<i>Galium tinctorium</i>	14	native
	<i>Persicaria maculosa</i>	6.0	nonnative	<i>Ligustrum obtusifolium</i>	2	nonnative	<i>Verbascum thapsus</i>	14	nonnative
	<i>Galium mollugo</i>	5.0	nonnative	<i>Lindera benzoin</i>	2	native	<i>Bidens bipinnata</i>	13	native
	<i>Solidago</i> spp.	5.0	native	<i>Acer rubrum</i>	1	native	<i>Acalypha virginica</i>	12	native
	<i>Verbesina occidentalis</i>	5.0	native	<i>Acer saccharum</i>	1	native	<i>Acer negundo</i>	12	native
	<i>Persicaria virginiana</i>	4.0	native	<i>Carya ovata</i>	1	native	<i>Geum virginianum</i>	11	native
	<i>Dactylis glomerata</i>	3.0	nonnative	<i>Cornus florida</i>	1	native	<i>Pueraria montana</i>	11	nonnative
	<i>Carex</i> spp.	3.0	unknown	<i>Fraxinus nigra</i>	1	native	<i>Solanum ptychanthum</i>	11	native
	<i>Cryptotaenia canadensis</i>	3.0	native	<i>Ulmus rubra</i>	1	native	<i>Ageratina altissima</i>	9	native
Uninvaded	<i>Amphicarpaea bracteata</i>	92.1	native	<i>Lonicera japonica</i>	120	nonnative	<i>Ranunculus abortivus</i>	99	native
	<i>Phryma leptostachya</i>	32.0	native	<i>Acer negundo</i>	49	native	<i>Muhlenbergia frondosa</i>	77	native
	<i>Sporobolus compositus</i>	31.5	native	<i>Toxicodendron radicans</i>	45	native	<i>Oxalis stricta</i>	72	native
	<i>Leersia virginica</i>	26.0	native	<i>Lonicera maackii</i>	44	nonnative	<i>Verbascum thapsus</i>	35	nonnative
	<i>Ipomoea pandurata</i>	16.0	native	<i>Staphylea trifolia</i>	21	native	<i>Cardamine hirsuta</i>	31	nonnative
	<i>Rubus allegheniensis</i>	15.5	native	<i>Parthenocissus quinquefolia</i>	20	native	<i>Ailanthus altissima</i>	26	nonnative
	<i>Alliaria petiolata</i>	14.9	nonnative	<i>Celastrus orbiculatus</i>	18	nonnative	<i>Acalypha virginica</i>	25	native
	<i>Solidago</i> spp.	14.2	native	<i>Ulmus rubra</i>	8	native	<i>Microstegium vimineum</i>	23	nonnative
	<i>Polystichum acrostichoides</i>	13.0	native	<i>Viburnum prunifolium</i>	7	native	<i>Veronica hederifolia</i>	22	nonnative
	<i>Hylodesmum nudiflorum</i>	12.0	native	<i>Celtis occidentalis</i>	6	native	<i>Glechoma hederacea</i>	21	nonnative
	<i>Collinsonia canadensis</i>	10.5	native	<i>Acer saccharum</i>	4	native	<i>Solanum ptychanthum</i>	19	native
	<i>Microstegium vimineum</i>	10.3	nonnative	<i>Celastrus scandens</i>	4	native	<i>Barbarea vulgaris</i>	15	nonnative
	<i>Geum canadense</i>	10.0	native	<i>Juglans cinerea</i>	4	native	<i>Erechtites hieracifolius</i>	15	native
	<i>Symphytotrichum cordifolium</i>	9.0	native	<i>Prunus serotina</i>	4	native	<i>Rubus phoenicolasius</i>	14	nonnative
	<i>Galium mollugo</i>	6.0	nonnative	<i>Diospyros virginiana</i>	3	native	<i>Carex</i> spp.	11	unknown
	<i>Securigera varia</i>	5.4	nonnative	<i>Cercis canadensis</i>	2	native	<i>Geum virginianum</i>	10	native
	<i>Verbesina occidentalis</i>	5.0	native	<i>Fraxinus americana</i>	2	native	<i>Nepeta cataria</i>	10	nonnative
	<i>Tussilago farfara</i>	4.5	nonnative	<i>Liriodendron tulipifera</i>	2	native	<i>Acer negundo</i>	9	native
	<i>Cirsium arvense</i>	3.5	nonnative	<i>Pinus strobus</i>	2	native	<i>Ageratina altissima</i>	9	native

the second null model, the inclusion of the age variable ($p = 0.01$ and 0.0001 , respectively) appeared to be driving the significance over the interaction ($p = 0.051$ and $p = 0.21$, respectively). No other models were significant.

3.3. Seedbank and resident vegetation similarity

When combined, the seedbank and established vegetation (including the canopy trees) contained 144 different taxa. Of these, 67 taxa were found only in the resident vegetation, 47 taxa were found only in the seedbank, and 30 taxa were found in both. The Sørensen–Dice similarity index was calculated for all plots, excluding those at site 3, which were destroyed before established vegetation could be quantified. The overall similarity index was 0.30 in invaded plots and 0.29 in uninvaded plots, with individual plots ranging in value between 0.00 and 0.30 (Fig. 5).

The interactive linear model relating the similarity index to both the invasion age and invasion status was not significant ($F(3, 14) = 2.173$, $p = 0.1368$) (Fig. 5), nor were either predictor variables or their interaction.

3.4. *Ailanthus altissima* seedbank presence

In total, 179 *A. altissima* seedlings germinated from the collected soils. Not surprisingly, of these, 85.5% germinated from soil collected at invaded sites. *Ailanthus altissima* represented 10.1% of the total

seedbank, or 14.1% of the invaded seedbank and 3.8% of the uninvaded seedbank.

Regarding the relationship between the proportion of *A. altissima* in seedbank samples at invaded plots and the age of the invasion, the selected linear model was significant ($F(1,28) = 28.39$, $p = 0.00001$), and showed a positive relationship between the two variables (Fig. 6). The model's adjusted R^2 indicated that the age of the invasion explained over 49% of the variations seen. To meet parametric assumptions, the percentage of *A. altissima* in the seedbanks was natural log transformed prior to this analysis, with the addition 0.0465 to account for zeros (1 over the median denominator (21.5)). To estimate the percent increase per year, the model's slope parameter (0.04792) was used ($e^{\text{slope parameter}}$). Therefore, an estimated increase of 4.9% in the proportion of *A. altissima* seeds in the seedbank per year is predicted by the model. In addition, the model's marginal effect size was estimated at five representative points (10, 20, 30, 40, and 50 years) resulting in 0.0027, 0.0044, 0.0072, 0.012, and 0.019. This indicates that a marginal increase of one year increases *A. altissima* seed proportion in the seedbank by between 0.0027 and 0.019 every year, with older stands seeing a larger increase.

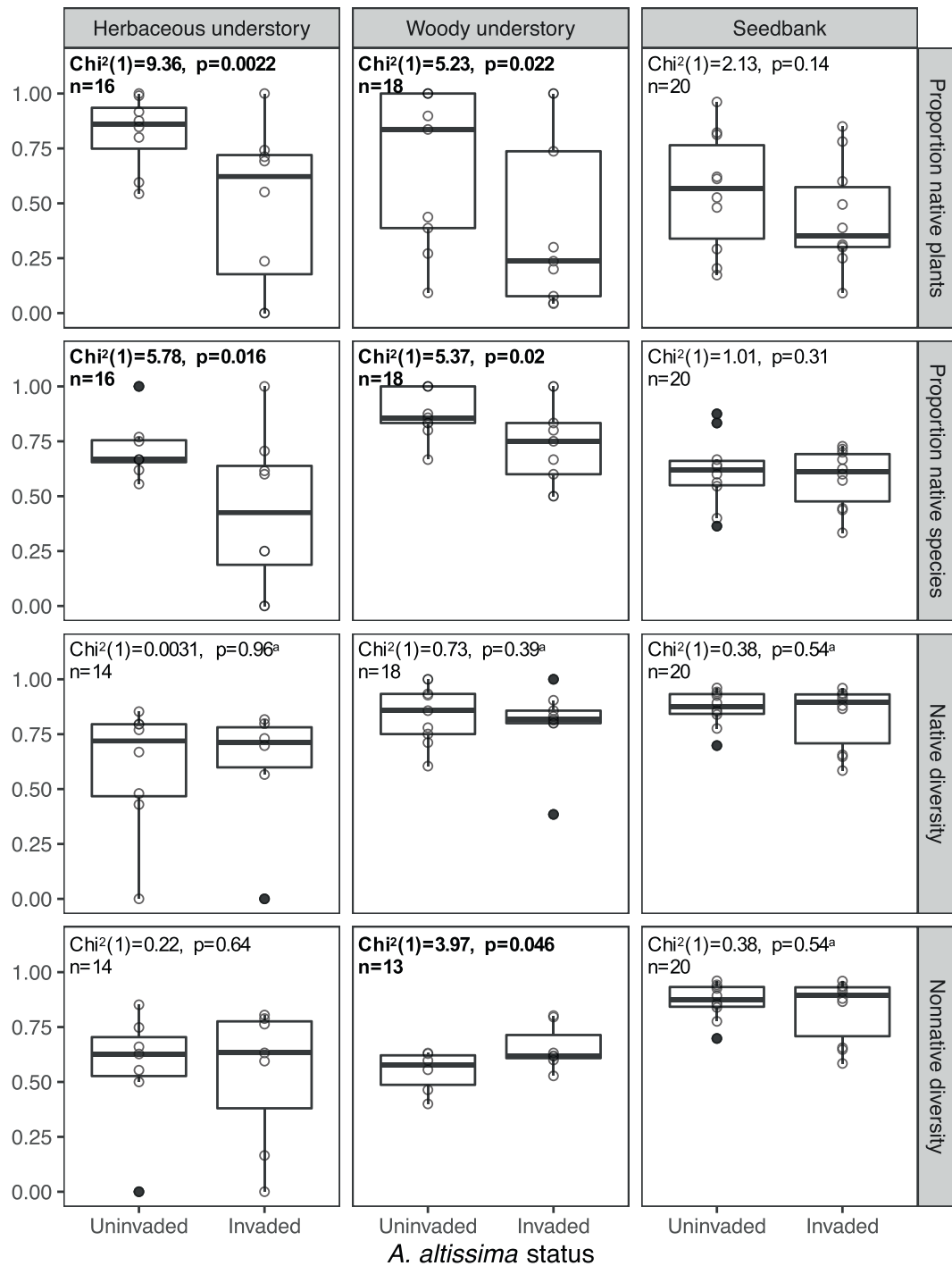


Fig. 3. For the herbaceous understory, the woody understory, and the seedbank, the proportion of total individuals that are native (“proportion native plants”), the proportion of species that are native (“proportion native species”), the diversity index for native plants (“native diversity”), and the diversity index for nonnative plants (“nonnative diversity”) are shown split by invasion status (uninvaded or invaded). All calculations are made on data pooled to the plot level with *A. altissima* excluded. The proportion native individuals and diversity indices for the herbaceous understory were calculated using percent cover, not counts. The diversity index chosen for this calculation is the “probability of interspecific encounters” or PIE, which measures the probability that two individuals randomly drawn from a population represent different taxa or, in the case of the herbaceous data, the probability that two randomly selected points land on two different taxa (Gotelli, 2008; Hurlbert, 1971). Center line on the boxplot represents the median of the data, not the mean. Each relationship was analyzed using a linear mixed model with invasion status (invaded or uninvaded) as a fixed effect and site as a random effect. P-values reported are from a likelihood ratio test comparing each model to a null model containing only the random effect, with bolded values indicating $p < 0.05$. Sample size (n) for each analysis is shown. Plots containing no data for a specific nonnative or native vegetation category have been excluded.

^a response variable arcsine square root transformed prior to analysis.

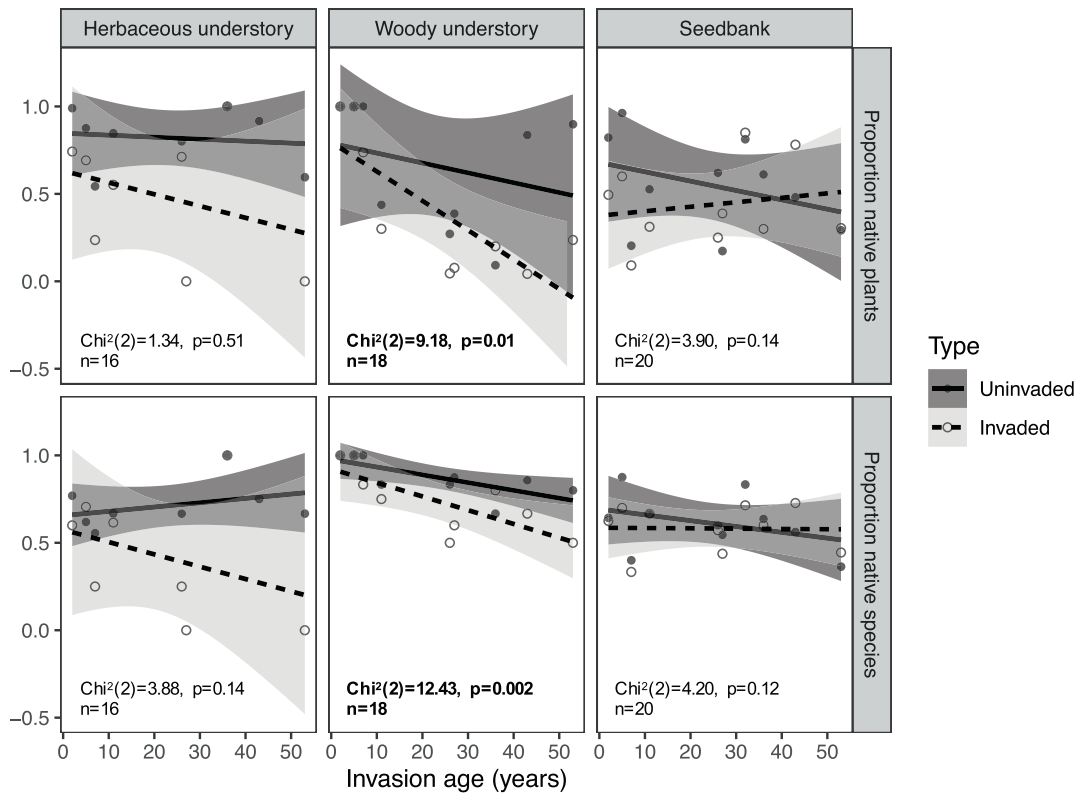


Fig. 4. The relationships between the invasion age, invasion status (uninvaded or invaded), and the proportion of total counts (individuals) or species that are native (“proportion native plants” and “proportion native species”) for the three vegetation categories (“herbaceous understory”, “woody understory”, and “seedbank”). All calculations are made on data pooled to the plot level with *A. altissima* excluded. Proportion native individuals for the herbaceous understory were calculated using percent cover, not counts. Significance was determined using a likelihood ratio test, in which the interactive model (age of invasion * invasion status + (1|site)) was compared to the null model (invasion status + (1|Site)) and shown bolded if significant ($p < 0.05$). Sample size (n) for each analysis is also displayed. Plots containing no data for a specific nonnative or native vegetation category have been excluded.

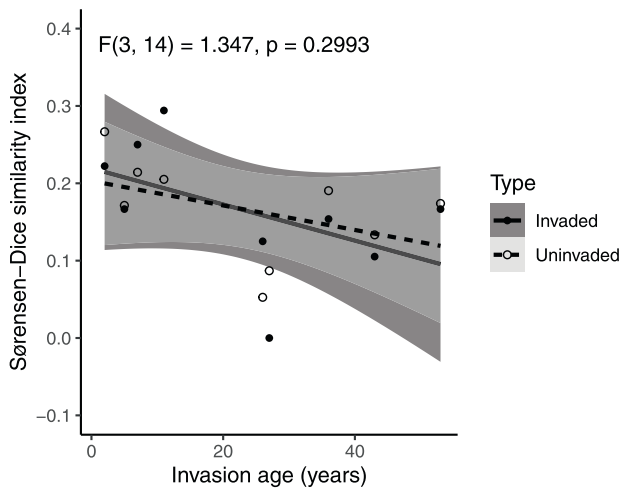


Fig. 5. The Sørensen–Dice similarity index comparing the below-ground (seedbank) and above-ground (understory and canopy) species for each plot compared to the age of the *A. altissima* invasion ($n = 18$). *Ailanthus altissima* was excluded from this analysis. The linear mixed models (lines) analyzing the interaction between the invasion status (invaded or uninvaded) and the age of the invasion with site as a random factor and their 95% confidence intervals (shaded areas) are shown. The regression, its predictors, and their interactions are all non-significant ($p > 0.05$). The regression details are displayed (R Core Team, 2018).

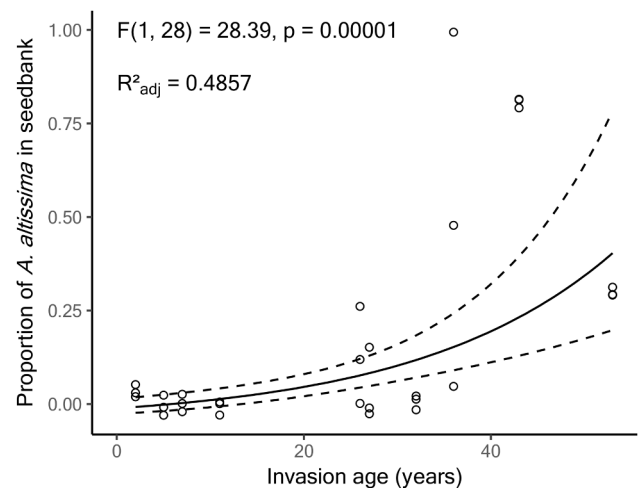


Fig. 6. Proportion of *A. altissima* in the seedbank sample as related to the age in years of the *A. altissima* invasion (estimated by determining the age of the oldest *A. altissima*) is shown ($n = 27$). The linear regression’s median (solid line) analyzing the natural log of the *A. altissima* proportion (with the addition of 0.0465 to account for zeros) given invasion age and its 95% confidence interval (dashed line) is shown back transformed to the response space. Points have been jittered vertically by 0.03 so overlapping points can be observed. The regression significance and adjusted R^2 values are displayed (R Core Team, 2018).

4. Discussion

4.1. *Ailanthus altissima* impacts understory nativity, not seedbank nativity

We found that *A. altissima* has a negative impact on the proportion of native plants (individuals and species) in the established understory, but not the seedbank (Fig. 3). This impact on the understory was expected, as it had been previously shown that invasive trees cause high levels of decline in resident native plant richness (Gaertner et al., 2009). Our results also showed that the nonnative diversity of the woody understory significantly increased with *A. altissima* invasion (Fig. 3), meaning that the decrease observed in the proportion of native woody plants in the understory was driven by an increase in nonnative plants, not a decrease in native plants. This potential facilitation between an invasive species and other nonnative species, referred to as an invasion meltdown, has been found in other systems, and is not unique to *A. altissima* (Simberloff, 2006; Simberloff and Von Holle, 1999).

The proportional change of the nativity we observed indicates that it is possible that the previous *A. altissima* impact studies that did not consider nativity of the resident species may have found similar impacts if nativity was included in their analysis (Fotiadis et al., 2011; Motard et al., 2011; Traveset et al., 2008). For example, Fotiadis et al. (2011) did not determine nativity, but found an increase in plant diversity in areas invaded by *A. altissima*. Though they suggested that the increase could have been caused by the presence of synanthropic species likely composed of many nonnatives, it was never analyzed.

We also found that the invasion of *A. altissima* had no impact on the seedbank's nativity or diversity. We are not the first to find that invasive plants impact the resident vegetation more than the seedbank. For example, Wearne and Morgan (2006) who looked at an invasive shrub, *C. scoparius* (Scotch broom), found few changes in seedbank composition or richness, while the above-ground species richness was reduced in older stands. Similarly, Vilà and Gimeno (2007) noted that the similarity between areas uninvaded and invaded by the invasive *Oxalis pes-caprae* (Bermuda buttercup) was higher in the seedbank samples than the vegetation samples, indicating seedbanks were not as influenced by invasion. Therefore, our results support the theory that seedbanks change more slowly than above ground vegetation in response to an invasive plant (Wearne and Morgan, 2006). Since numerous other invasive plants have been associated with seedbank changes (Gioria et al., 2014), it remains to be seen if this is lack of impact to the seedbank by *A. altissima* is consistently found.

Though we did not design this study to determine the mechanisms causing *A. altissima* influence, previous studies indicate that invasive species' impacts to co-occurring vegetation are usually caused by competitive effects (Levine et al., 2003). This might be especially true for *A. altissima*, as its competitive ability includes outgrowing native species (Martin et al., 2010), producing allelopathic chemicals that influence the growth of other species (Heisey, 1996; Mergen, 1959; Nilsen et al., 2018), directly influencing soil properties (Gaertner et al., 2009; Vilà et al., 2006), and interfering with ectomycorrhizal fungal colonization (Bauman et al., 2012). All of these competitive mechanisms were excluded from our seedbank emergence sampling by removing seedlings after germination, adding activated charcoal, and including nutrient-rich potting soil. This was done in order to quantify the entire germinable seedbank. However, these mechanisms would have all influenced the understory vegetation, and therefore competitive effects could account for the difference in *A. altissima* impact between the understory and the seedbank observed in this study. If this is the case, seedbank composition may actually be irrelevant to future stand composition, unless *A. altissima* with its competitive ability is eradicated from the site.

4.2. As *A. altissima* invasions age, their influence on the woody understory increases

We found that as the age of *A. altissima* invasions increases, the proportion of native plants in woody understory decreases (Fig. 4). This change was observed over an invasion age range of 2–53 years. This positive relationship of impact and invasion age matches the now popularized “invasion curve,” which shows that the area infested, impacts, and management costs all increase with time (Blackwood et al., 2010; Pyšek and Prach, 1993; Strayer et al., 2006; Yokomizo et al., 2009). Though not tested in this experimental design, invasion age may not be the only variable driving this change, as invasion age is also likely correlated with other variables such as invasion size, abundance, and successional changes.

This finding demonstrates how important invasion age can be when considering impacts, despite rarely being considered in most studies. Again, matching our results, the Australian study comparing the time since invasion (ranging between 8 and 25 years) of the woody shrub *C. scoparius*, showed that native species richness and cover declined over the length of the invasion (Wearne and Morgan, 2004). Similarly, Ortega et al. (2019) found that as the time since invasion increased for the woody exotic *Rhamnus cathartica* (common buckthorn), overstory cover of native woody species decreased. However, invasion age can often be hard to determine. The meta-analysis by Vilà et al. (2011) was unable to determine how impacts might change in regard to plant abundance, let alone invasion age, due to lack of data. Even previous studies looking at *A. altissima* impacts, which have the potential to characterize invasions with respect to age, have not accounted for it in their analyses (Fotiadis et al., 2011; Motard et al., 2011; Traveset et al., 2008; Vilà et al., 2006).

It is possible that our study did not encompass the time frame needed to see impacts to the herbaceous understory or the seedbank increase over time, which might only become apparent over longer periods of time (Gaertner et al. 2009; Wearne and Morgan, 2004). Regardless, we found that at least part of *A. altissima*'s impact increased with the age of the invasion.

4.3. Site restoration recommendations

Land managers should be prepared to manage more nonnative plants in *A. altissima* invaded areas than in uninvaded areas. This is because with *A. altissima* invasion, the proportion of native understory plants decreased, both in terms of total plants and individual species (Fig. 3). Since small-scale eradication of *A. altissima* is now possible using chemical methods (Asaro et al., 2009; Gover et al., 2013) or a proposed biopesticide (Schall and Davis, 2009), restoration plans post-management are becoming a reality. This potential for a secondary invasion after management of the targeted invasive species has been shown to be a global problem (Pearson et al., 2016), and we therefore suggest monitoring all sites for other nonnative species both prior to and after management.

Given that *A. altissima*'s impact on the woody understory increased with invasion age (Fig. 4), management of *A. altissima* infestations should be completed early to help limit this impact. This is especially true since *A. altissima* impacts not just the woody understory's proportion of native plants and species, but also increases the nonnative woody diversity (Fig. 3). Therefore, any restoration plans focused on restoring the area's native woody canopy may face increasing difficulties as these invasions age. It is possible that in certain places *A. altissima* management can result in the re-establishment of native woody species, as seen by O'Neal and Davis (2015). However, in other areas it appears that *A. altissima* removal does not change the mean number of native woody plants (Kasson et al., 2014). It is possible that the difference in post-management woody composition observed may be due to the *A. altissima* invasion age at both of these sites. A study including pre-treatment data would better determine the outcome of the nonnative and native species post *A. altissima* restoration.

Though we found that *A. altissima* invasions did not impact the seedbank nativity or diversity (Fig. 3, Fig. 4), it is likely that additional nonnative species are present within the seedbank. This is because in all the seedbank soils collected, nonnative plants other than *A. altissima* were present. Additionally, like most forests, we found that these seedbanks and the resident vegetation had very low levels of similarity (Fig. 5) (Hopfensperger, 2007). Though we found that *A. altissima* invasions did not impact the seedbank, land managers should still be prepared for additional nonnative species not currently established to germinate during management activities.

Since we found the seedbanks uninfluenced by *A. altissima* invasion, we do not know if supplemental seeding post-management would be helpful. Seeding has been previously considered (Burch and Zedaker, 2003; Harris et al., 2013); however, to date, no experiments looking at supplemental seeding in this system have been reported. In fact, Burch and Zedaker (2003) found that when *A. altissima* was removed, reseeded with native herbaceous species was not necessary and therefore they did not include it in their study. Similar accounts of seedbanks being sufficient to recolonize with native vegetation after clearing have also been found in other systems, including with the invasive tree *Acacia longifolia* in South Africa (Fourie, 2008).

These management suggestions should be relevant to anyone wishing to control *A. altissima* along corridors in Virginia, one of the most highly infested areas in the country (EDDmapS, 2019; McAvoy et al., 2012). However, since *A. altissima* can invade many different habitat types (Traveset et al., 2008), and the impacts of invasive plants tend to vary by habitat (Burch and Zedaker, 2003), these findings might not be applicable everywhere. Nevertheless, with this knowledge of both the established vegetation and the seedbank, land managers should be able to better support the timely management of *A. altissima* and predict post-removal restoration needs.

4.4. The added risk of other invasive species

Since our work did not distinguish high-risk invasive species from naturalized nonnative species, we cannot be certain if *A. altissima*'s impact differs between the two. We did however find that other significant invasive species were both present and abundant within the understory and the seedbank (Table 1 & Supplemental Table A.1). Depending on management goals, these species likely deserve their own attention.

For example, the highly impactful invasive Japanese stilt grass, *Microstegium vimineum* (Adams and Engelhardt, 2009), was found in considerable quantities in both the understory and the seedbank samples, with highest numbers at *A. altissima*-invaded plots (with average understory cover increasing three-fold and average seedbank emergence counts increasing almost ten-fold in invaded plots compared to uninvaded plots) (Table 1 & Supplemental Table A.1). Additionally, *Pueraria montana*, the highly impactful invasive kudzu vine that can outcompete trees (Forseth and Innis, 2004), was found only in the seedbank, with highest numbers also in the invaded sites (with average emergence numbers increasing from 0.1 per uninvaded plot to 1.1 per invaded plot) (Table 1 & Supplemental Table A.1). Other highly impactful invasive species were also prevalent in the understory, including *Alliaria petiolata* (garlic mustard), *Lonicera maackii* (amur honeysuckle), and *Lonicera japonica* (Japanese honeysuckle; Table 1). The presence of these particular invasive species stresses the need for land managers to be able to identify and include numerous invasive species in the same management plan.

4.5. Manage *A. Altissima* early to limit its seedbank presence

Early intervention in *A. altissima* control is highly suggested to reduce the need for future *A. altissima* seedbank management. This is because *A. altissima*'s seedbank presence increased with *A. altissima* stand age (Fig. 6). In fact, this relationship is non-linear (multiplicative

not additive), meaning that this increase increases with time, with our model predicting a 4.9% increase in the proportion of the seedbank represented by *A. altissima* seeds yearly. With this increase in propagule pressure, the species' ability to invade an area after management activities will likely increase over time (Lockwood et al., 2005). Since *A. altissima* is an early-successional, gap-obligate tree, even if the established *A. altissima* were successfully removed, the seedbank could take advantage of any disturbance caused by the initial control (Carter and Fredericksen, 2007; Kasson et al., 2013; Knapp and Canham, 2000). With female *A. altissima* able to produce 10 million seeds over 40 years, it is not surprising that this increase of seed prevalence over time was found (Wickert et al., 2017).

We also found *A. altissima* seeds at low levels in the seedbanks of uninvaded plots (Supplemental Table A.1). This finding was not unexpected, since paired sites were located no more than 100 m from each other to minimize differences, and *A. altissima* seeds are well dispersed by wind (Kowarik and Von der Lippe, 2011). It is therefore important to remember that if *A. altissima* is present in your region, any disturbance may result in a release of *A. altissima* seedbank seeds. This concern is amplified by the recent work that found *A. altissima* seeds able to survive in the soil for much longer than initially expected (over five years) (Rebbeck and Jolliff, 2018).

4.6. Conclusions

We found that *A. altissima* invasion reduces the proportion of established native plants and species in the understory, but does not influence this proportion in the seedbank. This impact on the woody understory becomes more severe as the invasion ages. These findings can help direct *A. altissima* management programs and post-removal restoration needs. This is the first study to determine if *A. altissima* impacts the seedbank and to look at how its impact on established vegetation and the seedbank changes over time.

CRediT authorship contribution statement

Rachel K. Brooks: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing - original draft. **Jacob N. Barney:** Conceptualization, Methodology, Writing - review & editing. **Scott M. Salom:** Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing - review & editing.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119025>.

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