Spatial patterns of native Robinia pseudoacacia and invasive Ailanthus altissima and their influence on regeneration, abundance, and diversity of neighboring trees at local and regional scales

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Research Article

Keywords: Basal area, contagion, forest inventory and analysis program, mapping, species distribution.

Posted Date: March 17th, 2023

DOI: https://doi.org/10.21203/rs.3.rs-2688023/v1

Version of Record: A version of this preprint was published at Landscape Ecology on August 30th, 2023.
See the published version at https://doi.org/10.1007/s10980-023-01760-5.

Abstract

Context. Native early-successional plants and invasive exotic plants often colonize the same disturbed space and have similar functions, making interactions likely. Knowing whether these interactions are facilitative or competitive across different scales will help determine the influence of such species across a forested landscape.

Objective. We evaluated the impacts of an early-successional, nitrogen-fixing native (facilitator), *Robinia pseudoacacia,* and an allelopathic invasive (inhibitor), *Ailanthus altissima,* on regeneration, basal area, and diversity of forests at local and regional scales.

Methods. Locally, all woody stems were mapped in three post-disturbance, mid-successional plots at two sites in Virginia, US. Plots contained *A. altissima* or *R. pseudoacacia* or both. Target species were evaluated regionally and spatially using USDA Forest Inventory and Analysis data across 31 eastern states, US.

Results. Spatial contagion was found between *A. altissima*and *R. pseudoacacia* at both scales. Regeneration of *A. altissima* was much greater than that of *R. pseudoacacia* but native tree regeneration was negatively associated with both target species. Regionally, *R. pseudoacacia* was more common than *A. altissima*. At both scales, *A. altissima* was more likely to form dense stands than *R. pseudoacacia*. Locally, plot types did not differ in tree diversity. Regionally, *R. pseudoacacia* plots had higher tree diversity than plots without either target species.

Conclusions. *Robinia pseudoacacia* and *A. altissima*'s positive association is maintained into mid- and late-successional forests and *A. altissima* inhibits regeneration locally and regionally. *Robinia pseudoacacia* shows a positive effect on diversity but only when compared with mature forests at the regional scale.

Introduction

Invasive species are nonnative species that successfully become established and spread within an ecosystem, causing harm to the environment, the economy or human health (Federal Executive Order 13112 1999). Previous research has shown that invasive plants can displace native plant species (D'Antonio and Vitousek 1992; Fritts and Rodda 1998; Gurevitch and Padilla 2004; Stinson et al. 2006; Fahey et al. 2018), deteriorate the quality of native forests (Alvarez and Cushman 2002), threaten the integrity of native forest ecosystems (Vitousek 1990; Klooster et al. 2018; Davis 2003), change soil chemical properties (Musil 1993; Parker et al. 1999; Lavoie 2017), and change soil microbiomes (Rodrigues et al. 2015). Invasive plants may also manifest substantial long-term impacts on plant community composition because they alter existing plant-plant, plant-insect, plant-fungus, or plant-microbe interactions (Mack et al. 2000; Simberloff 2006; Weidenhamer and Callaway 2010; Richardson and Rejmánek 2011). Invasive species that restructure and transform ecosystem processes by altering

feedback mechanisms, including changes in seed bank composition, fire, litter decomposition, and soil biota, are the most impactful (MacDougall and Turkington. 2005; Gaertner et al. 2014).

Invasive plant impacts on plant community composition and diversity in forests depend on the forest conditions (dominant vegetation, age, disturbance, and physiography) at the time of introduction, the functional traits of the invasive plants, and their interactions with other species after establishment (Mack et al. 2000; Richardson et al. 2000; Pyšek et al. 2009). Nonnative invasive and native plants that share similar growth habits and utilize resources at similar levels and rates are functionally similar and are likely to interact the most during forest succession (Case et al. 2016; Nilsen et al 2018). Many invasive species colonize disturbed sites in which they also interact with early successional native species. The outcomes of interactions (i.e., competition and/or facilitation) among native and nonnative species may impact successional trajectories of the invaded communities, potentially leading to alternative stable states (Suding et al. 2014; Ghazoul et al. 2015).

Our study focused on a common invasive tree, *Ailanthus altissima* (Mill.) Swingle (tree of heaven), and an important nitrogen-fixing tree, *Robinia pseudoacacia* L. (black locust), in the Appalachian region of the U.S. (Integrated Taxonomic Information System (https://www.itis.gov)). In the U.S. these two species are fast-growing (Roach 1965; Kowarik 1995), preferentially colonize disturbed, open sites (Hu 1979; Huntley 1990), and reproduce both sexually and vegetatively by producing abundant seed and extensive root systems and root suckers (Huntley 1990; Kowarik 1995; Wickert et al. 2017). Because of their similar functional traits and habitat preferences, these two species are often found together in post-disturbance forests (Call and Nilsen 2003).

Ailanthus altissima, from China, has been an invasive tree in U.S. forests for more than 200 years (Feret 1973). Several studies have suggested that *A. altissima* can have a negative influence on forest diversity because of its putative allelopathic nature (Small et al. 2010; Novak et al. 2018). *Robinia pseudoacacia* is native to the Mid- Appalachian Mountain region of the eastern U.S., but also is viewed as an invasive species in areas west of VA and worldwide (Castro-Díez et al. 2008). The nitrogen fixation activity of *R. pseudoacacia* has been documented to enhance forest diversity (Boring et al. 1984 a,b) and facilitate *A. ailanthus* early growth. However, this facilitory relationship changes to one where *A. altissima* appears to inhibit *R. pseudoacacia's* growth after the first year of association, possibly in response to *A. alttissima's* allelopathic properties (Nilsen et al. 2018). Both species have relatively rapid leaf decomposition rates (Lee et al. 2010; Medina-Villar et al. 2015) and an ability to use the increase in available N rapidly, though the relative decreasing growth of *R. pseudoacacia* over time implies *A. altissima* may use available N faster than *R. pseudoacacia* (Nilsen et al. 2018).

The Call and Nilsen (2003) study, which revealed a pattern of *A. altissima* and *R. pseudoacacia* being found together more than would be expected at random, focused on distribution patterns in a newly harvested forest (6–7 year post-harvest). We question if this contagion pattern would also be found in mid- to late-successional forests at the local scale and occur at a regional scale. Secondly, we question if *A. altissima* and *R. pseudoacacia* will have opposite impacts on advance tree regeneration and diversity

at both local and regional scales because *R. pseudoacacia* as a nitrogen fixing tree would exhibit positive impacts (Boring and Swank 1984a), whereas *A. altissima* with allelopathic effects would exhibit negative impacts (Gómez-Aparicio and Canham 2008a) and can better take advantage of increases in nitrogen associated with its rapidly decomposing leaves (Nilsen et al. 2018).

Answering these questions will address if *A. altissima* has a larger impact on community structure than a native tree with a similar growth form and similar aggressive tendencies. Moreover, knowing whether *A. altissima*'s negative impact on community structure as predicted also counteracts any positive impact of *R. pseudoacacia* when they grow together would predict a net negative impact. More specifically, we hypothesize that (1) each target species has a clumped distribution and both species are clumped together when they are both part of a forest stand, (2) advance tree regeneration is positively associated with *R. pseudoacacia* and negatively associated with *A. altissima*, (3) diversity and basal area of other tree species decreases as the total basal area of *A. altissima* trees increases, but diversity and basal area of other native tree species increases as the basal area of *R. pseudoacacia* increases, and (4) the faciliatory effects of *R. pseudoacacia* on diversity and native tree basal area is negated by *A. altissima*'s allepathic effects when *R. pseudoacacia* and *A. altissima* occur simultaneously in the same community.

We used both a local and regional approach to address these four hypotheses. In the local approach we mapped the spatial distribution of all adults, saplings and seedlings in forest stands containing either *R, pseudoacacia*, *A. altissima*, or both species, using the mapped stands to test hypotheses 1 and 2. In the regional approach, we used USDA Forest Service Forest Inventory and Analysis (FIA) species abundance tree data to evaluate the relationship between our two target species' distribution and native tree species basal area and diversity or hypotheses 1, 3 and 4. Regeneration (seedling) FIA data were not available for our study area.

Material And Methods

Local approach: site descriptions and experimental design

The Blandy Experimental Farm (BL) in Boyce, VA (39°3'41"N, 78°4'29"W) and a nearby privately owned forest (AL), in Berryville, VA (39°7'39"N, 78°5'41"W) were the two general locations used for the local-scale portion of this study. Both sites were approximately 350 km north of the early succession sites used by Call and Nilsen (2003). The BL mid-successional site is a woodlot that has been kept as unmanaged research forest since 1937 with infrequent disturbances (40 years since the last disturbance at the time of this study). The soils are Nicholson-Duffield silt loam and Poplimento silt loam (Soil Survey Staff 2022) with an elevation of about 176 m and less than 15% slope inclination. The AL late-successional site is16 km distant from BL and contains forested land that has gone through natural old-field succession without management for about 100 years, except for the construction of several 1.5-2 m wide trails. The soils are Berks-Berks channery silt loam and Weikert-Berks channery loam (Soil Survey Staff 2022) with an elevation of about 200 m and less than 10% slope inclination. Dominant native trees in both sites include *Juglans nigra* L., *Celtis occidentalis* L., *Acer rubrum* L., and *Nyssa sylvatica* Marshall.

Following a complete tree survey of each site, an area of approximately 1.0 ha in size that contained both *A. altissima* and *R. pseudoacacia* was selected. Within each 1.0 ha area, three 20 m × 50 m rectangular plots (1,000 m^2 or 0.1 ha) were established. This 0.1 ha plot size was selected to maximize the ability to spatially map trees, saplings, and seedlings in a relatively homogeneous site. Larger plots would have contained differences in slope, aspect and possibly site history that would confound our attempt to spatially map species associations. This plot design is larger than that used in some vegetation studies (Von Holle et al. 2006) but smaller than that in other tree mapping studies (Chokkalingam and White 2001; Despeŕes et al. 2014). However, a 0.1 ha plot is a much larger plot than usually used for mapping advance regeneration (Yang et al. 2015). One of the three plots in each stand contained *A. altissima* but no *R. pseudoacacia* (AA), a second plot in each stand contained *R. pseudoacacia* but no *A. altissima* (RP), and a third plot in each stand had both *A. altissima* and *R. pseudoacacia* (BOTH). In AA and RP plots, the target trees accounted for approximately 20% of total trees present. In the BOTH plots the target species accounted for approximately 40% of trees present. All three plots were at least 40 m from each other in each site to ensure that each plot was independent.

Local approach: Measurements and data analysis

Every live tree, sapling, and seedling of all tree species was recorded in each plot. Trees were defined as those with a diameter at breast height (DBH, at the height of 1.3 m above ground) of 2.54 cm or greater, and saplings were defined as small trees with a height 1 m or taller, but a DBH less than 2.54 cm. Seedlings were tree species with a height less than 1 m. We did not differentiate if a seedling was the result of a germinated seed or a root sprout because it would not be possible to do so non-destructively, and this difference was not important for the goals of our study. The seedling class in this study is identified as advance regeneration (AR) hereafter.

Each of the six 0.1 ha plots was mapped on an X-Y coordinate grid. The start point was set as (0, 0), and the range of the X and Y axis were 50 m and 20 m, respectively. The X-Y coordinates and DBH of each tree, sapling, and seedling were recorded. A two-dimensional, virtual grid of the spatial location of each tree and sapling was built (Matlab 2020). Degree of clumping or contagion (hypothesis 1) was determined using a nearest neighbor analysis conducted in R (2020). This analysis determined the most frequent nearest neighboring tree species of all *A. altissima and R. pseudoacacia* individuals in each plot. The next four most frequent nearest neighbors in rank order within each plot type (AA, RP, and BOTH) were also determined.

The effect of site and plot type on tree, sapling and seedling counts, and overall species richness were evaluated using Chi square (x^2) tests; normality variance homogeneity assumptions were met. The effect of site and plot type on total basal area and diversity (Simpson's index) was evaluated using a two-way ANOVA; normality and variance homogeneity assumptions were met. Simpson's index of diversity was selected because it is most conservative when there are many species with 10 or fewer occurrences (Pielou 1969; Hill 1973).

Virtual circles were electronically drawn using three different radii around each mapped mature tree and sapling. The number of seedlings located within these virtual circles was determined. Because the impact of each tree and sapling is likely related to its size, the three radii we used were: 1) 10 × DBH of the center tree, 2) 20 × DBH, and 3) 50 × DBH. Seedlings counts within each virtual circle were summarized for each tree and sapling and averaged by species.

Because trees near the edge of the 1 ha site had partial virtual circles, we employed an edge correction to minimize any potential edge bias by generating 10,000 random points within the full circular area around each edge tree. A proportional correction was determined by dividing the number of points that fell within the 20 x 50 m plot area by the number of points that fell outside this area using the following equation where AR = advance regeneration:

$$TotalAR = ARinside + \left(ARinsidex \frac{randompointsoutside}{randompointsinside} \right)$$

The average percent of trees that needed this edge correction method increased with an increase in virtual circle diameter (10 x DBH = 16%, 20 x DBH = 27%, 50 x DBH = 57%).

The effect of each target tree on both advance regeneration and forest structure were evaluated by calculating community similarity among all plots and conducting a Bray Curtis ordination of the plots. Community similarity among all possible pairs of sampled plots was calculated using Sørensen's index (SI):

$$SI = 2C/(A + B)$$

where C is the number of common species in the two stands,

A is the total number of species in stand A

B is the total number of species in stand B

The SIs for trees, saplings, and seedlings were calculated separately. Students *t*-test was used to determine significant difference in Sørensen's index between site). A relative importance value was determined for each species by summing basal area and averaging this with the total count and dividing by the sum for all species. Importance values for trees and saplings were combined because separate ordinations were not stable. A Bray-Curtis ordination with a Sørensen distance measure was chosen because our hypothesis states that the AA plot type is negatively associated with species richness compared to the RP plot type, therefore, making the AA plot our point of reference. Endpoints were selected using variance-regression and a test for outliers was included (McCune and Grace 2002).

Regional approach: Forest Inventory and Analysis Database (FIADB)

We used FIA data from inventories (1999–2008) in 31 eastern states extracted by Kai Zhu (Duke University, personal communication), from FIADB version 4.0 published on 16 March 2010 (http://fia.fs.fed.us/), which resulted in a total of 43,396 inventory plots (Zhu et al. 2012; Zhu et al. 2014). We focused on trees (> 2.54 cm DBH) for our analyses. At each FIA plot there are four 200 m^2 subplots that are 24 m apart (subplot edge to edge). Only FIA plots within the native range of *R. pseudoacacia* in the Mid- Appalachian Mountain region were selected based on the distribution map of *R. pseudoacacia* (Little 1971) in Arc GIS FIADB were included at two levels: subplots and plots (summed subplots). All statistical analyses were done in R (2020).

Regional approach: Association between target species

To test the association between *A. altissima* and *R. pseudoacacia*, we created a rank-based *p*-value using the quantiles of the number of subplots in which the two target species co-occur. We first calculated the total number of subplots in which *A. altissima* or *R. pseudoacacia* were present with any other species but itself and *R. pseudoacacia* or *A. altissima*, respectively, in the data set and ranked the other nontarget species based on the number of subplots in which each of those species is present with *A. altissima* or *R. pseudoacacia*. Subsequently, we calculated a rank-based *p*-value by determining the quantile percentage of the number of subplots in which *A. altissima* co-exists with *R. pseudoacacia*.

A 2x2-contingency table was constructed with one variable being the presence of *A. altissima* in each subplot or plot and the other being the presence of *R. pseudoacacia* in each subplot or plot. Because subplots were far enough apart to include or exclude individual target trees, evaluating subplots separately vs as plots (summed subplots) could give different results. A Chi-square test was used to determine the dependency of the presence of the two species at either subplot or plot level. Another measure of association, Phi coefficient (Cramér 1999), was also calculated at subplot and plot levels. The Phi coefficient, which eliminates the effects of sample size has values between − 1 and 1 with 0 indicating no association, is a method for evaluating the indicator value (presence/absence) of a species with respect to a one-way grouping of sample units.

Regional approach: Association of target species with community metrics

Subplots and plots were separated into four types: 1) *A. altissima* present but *R. pseudoacacia* not present (“AA”), 2) *R. pseudoacacia* present but *A. altissima* not present (“RP”), 3) *A. altissima* and *R. pseudoacacia* both present (“BOTH”); 4) Neither *A. altissima* nor *R. pseudoacacia* present (“REF”). The total number and total basal area of the other species besides the two target species were also calculated for each subplot and plot. A Student’s t-test was used to compare if there were differences in the total number of tree stems (trees + saplings together) or total basal area of other tree species (trees + saplings together) among the RP, AA, Both and Ref plots and subplots.

At the plot level only, we evaluated how the relative richness of all nontarget tree species (calculated as nontarget species richness divided by the total of target and nontarget species richness) and relative

basal area of all nontarget species (nontarget species basal area divided by the total of nontarget and target species basal area) varied as total proportional basal area of each target species increased. To do so, we divided the richness and basal area the nontarget species totals along a gradient of *A. altissima* or *R. pseudoacacia* total basal area stratified in 5% intervals from 5% to a maximum of 50% for each target species within each plot. Significant differences in nontarget species (includes *A. altissima* when *R. pseudocacia* is the target species and *R. pseudoacacia* when *A. altissima* is the target species) richness and basal area were evaluated for each target species using Student's t-tests. In addition, whether or not each target species differed significantly from the null relationship (defined as only having a proportional effect) was determined for *A. altissima* and *R. pseudoacacia* species. Finally, regression analyses were conducted with total basal area of other species as the response variable and the percentage of basal area of *A. altissima* or *R. pseudoacacia* as the independent variable; we then tested if these two target species' regression slopes differed significantly in their response using ANCOVA. Finally, a one-way ANOVA was used to compare the difference in diversity values among the four plot types (AA, RP, BOTH, REF).

Results

Local approach: Site effects

The AL site generally had more saplings, greater tree and sapling basal area, more advance regeneration, and greater combined tree, saplings, and seedling species richness compared to the BL site (Table 1). Chi-square tests for site differences showed no significant difference in the mean tree density ($P = 0.628$), but mean sapling and seedling density were significantly greater in the AL site than in the BL site ($P < 0.0001$). Species richness was significantly higher at the AL site than in the BL site ($P = 0.0007$). Also, total basal area of trees was significantly larger in the AL site than the BL site ($P < 0.0001$), as was the basal area of saplings ($P < 0.0001$). Diversity averaged 0.85 ± 0.31 and 0.64 ± 0.34 for trees and saplings, respectively, at BL and was significantly higher for trees (1.795 ± 0.24) and saplings (1.787 ± 0.11) at the AL site than the BL site ($P < 0.0001$). The dominant tree at both BL and AL was *J. nigra*, but the dominant sapling at BL was *A. altissima* while it was *J. nigra* at AL. The exotic-to-native species ratio was only 0.17 (both trees and saplings) at BL while it was 0.54 at AL. *Ailanthus altissima* was the only exotic species at BL; at AL, *Maclura pomifera* (Raf.) C. K. Schneider was the most abundant exotic species. *Ailanthus altissima* was the third most important tree and fourth most important sapling at AL, while it was the second most important tree and first most important sapling at BL. Though AL had a higher exotic-to-native species ratio than BL, the site with a larger ratio also had more native species (11 in AL vs 6 in BL) so the ratios of exotic to native between sites were almost equivalent.

Table 1
The total number of trees, saplings, advance regeneration, and species in the six 20 m × 50 m plots surveyed. BL = Blandy Experimental Farm, Winchester, VA US; AL the private property site 16 km from BL; BA = basal area; AR = advance regeneration; RP = plot with only *R. pseudoacacia*, no *A. altissima*; AA = plot with only *A. altissima*, no *R. pseudoacacia*; BOTH = plot with both species.

Plot type	Trees #/ha	Tree BA m^2/ha	Saplings #/ha	Sapling BA m^2/ha	AR #/ha	# Tree Species
BL-RP	640	18.03	90	0.38	710	7
BL-BOTH	320	14.15	390	1.15	2,090	9
BL-AA	360	15.37	420	1.18	6,620	9
AL-RP	450	8.66	1,330	3.84	5,860	19
AL-BOTH	540	13.66	620	1.04	11,920	19
AL-AA	410	17.05	720	1.60	31,070	17

Combining the two sites, Chi-square tests of plot type differences showed that RP plots had a greater total number of trees than AA or BOTH plots, but the difference was only marginally significant (P = 0.052). RP plots also had a greater number of saplings than the AA or BOTH plots (P = 0.026). However, AA plots showed greater advance regeneration than RP or BOTH plots (P = 0.0001). Diversity was not significantly different among the plot types for trees, saplings or seedlings, suggesting that most of the advanced regeneration in the AA plots were not *A. altissima* seedlings. However, 91% of the seedlings were *A. altissima* seedlings at the BL site, while only 8% of the seedlings were *A. altissima* at the AL site. Other seedlings, in order of importance, included *M. pomifera*, *R. pseudoacacia*, *Prunus serotina* Ehrh., *Gleditsia triacanthos* L., *M. rubra*, *J. nigra*, *Fraxinus americana* L., and *Platanus occidentalis* L.

When the basal area and density of trees and saplings in all plots at each site are ranked from highest to lowest (Table 2) the RP plots are the highest ranked for the trees and saplings at BL but only for the saplings at AL. The AA plots only ranked highest for advance regeneration but did so for both sites (Table 2).

Table 2

Rank orders (1 = highest) for tree and sapling basal area as well as tree, sapling, and seedling numbers per 0.1 ha plot in plots containing *Ailanthus altissima*, *Robinia pseudoacacia*, or both in the Blandy Experimental Farm (BL), Winchester, VA US and the private property site (AL) 16 km from BL. Ranks are based on the total basal area or numbers for the plot after the target species have been removed from the data set.

Rank	Tree BA	Tree #	Sapling BA	Sapling #	Seedling #
BL Site					
1	BL-RP	BL-RP	BL-BOTH	BL-BOTH	BL-AA
2	BL-BOTH	BL-BOTH	BL-RP	BL-RP	BL-BOTH
3	BL-AA	BL-AA	BL-AA	BL-AA	BL-RP
AL Site					
1	AL-BOTH	AL-RP	AL-RP	AL-RP	AL-AA
2	AL-AA	AL-BOTH	AL-AA	AL-AA	AL-BOTH
3	AL-RP	AL-AA	AL-BOTH	AL-BOTH	AL-RP

The BL site generally had higher basal area of *A. altissima* and *R. pseudoacacia* than that of the AL site (Table 3). However, tree, sapling and advance regeneration density of *A. altissima* and *R. pseudoacacia* was relatively similar for AL and BL sites. In plots with both species, *A. altissima* had more individuals and a higher basal area than that for *R. pseudoacacia.* Also, *A. altissima* had about 118 times the advance regeneration of *R. pseudoacacia* in the BOTH plot type (Table 3).

Table 3
The total number and basal area (BA) of *R. pseudoacacia* (RP) and *A. altissima* (AA) trees, saplings, and advance regeneration (AR) in six 20 m × 50 m plots surveyed. BL = the Blandy Experimental Farm, Winchester, VA US; AL = a site on private property 16 km distant from BL; RP = plot with only *R. pseudoacacia*, no *A. altissima*; AA = plot with only *A. altissima*, no *R. pseudoacacia*; BOTH = plot with both species.

		Trees and saplings combined				AR	
Plot type	Plot #	*RP* #/ha	*RP*-BA m^2/ha	*AA* #/ha	*AA*-BA m^2/ha	*AA* #/ha	*RP* #/ha
BL-RP	1	290	7.1	-	-	-	180
BL-BOTH	2	100	2.1	300	4.2	3,950	20
BL-AA	3	-	-	590	8.2	6,010	-
AL-RP	4	220	1.4	-	-	-	40
AL-BOTH	5	160	0.9	280	2.6	4,340	50
AL-AA	6	-	-	120	2.3	2,560	-

Local approach: Similarity among plots

Combining tree, sapling and seedling data, AL-RP and AL-BOTH plot types shared the most species and BL-BOTH and AL-AA were the least similar plot types. Within the BL site, BL-BOTH and BL-AA were more similar than the other two plot types. Within the AL site, AL-BOTH and AL-RP were the most similar. The similarity tended to be greater within sites than between sites for any plot type comparison (Table 4).

Table 4
The community similarity (Sørensen's index) between each pair of the six plots surveyed. BL = the Blandy Experimental Farm, US; AL = a private property site 16 km distant from BL; RP = plot with only *R. pseudoacacia*, no *A. altissima*; AA = plot with only *A. altissima*, no *R. pseudoacacia*; BOTH = plot with both species.

	BL-RP	BL-BOTH	BL-AA	AL-RP	AL-BOTH	AL-AA
BL-RP	1.000	0.500	0.500	0.462	0.462	0.417
BL-BOTH		1.000	0.667	0.357	0.429	0.308
BL-AA			1.000	0.429	0.429	0.385
AL-RP				1.000	0.895	0.556
AL-BOTH					1.000	0.556
AL-AA						1.000

The Bray-Curtis ordination, which used importance values that included abundance and density measures of tree and saplings but not seedlings, revealed three groupings with BL-BOTH and BL-AA in one and associated most closely with Axis 1, AL-BOTH and AL-AA in a second and associated most closely with Axis 2, and AL-RP and BL-RP in a third and associated most closely with Axis 3 (Fig. 1). Axis 1 represented 49.34% of the variance, Axis 2 with 23.23%, and Axis 3 with 15.49% resulting in a total of 88.06% of variance explained by the three axes. The BOTH plots tend to be between the AA and RP plots on the ordination plot.

Local approach: Spatial analysis of trees and saplings

The mapped locations of individual trees and saplings of both target species indicated that both species tended to be clumped (Fig. 2). At the AL-BOTH site the target species were clumped together (Fig. 2B) while in the BL-BOTH site the target species were more independently distributed (Fig. 2B). A nearest neighbor analysis for a combined data set of all plots indicated that for both trees and saplings of *A. altissima* (119 in total), the nearest species was itself (Fig. 3A), and the average distance to the nearest neighbors was 1.26 ± 0.09 m. *Robinia pseudoacacia* was the third most frequent nearest neighbor to *A. altissima*. For trees and saplings of *R. pseudoacacia* (79 in total), the nearest species was itself (Fig. 3B), and the average distance between neighbors was 1.35 ± 0.13 m. Among the other trees associated with *R pseudoacacia* only *J. nigra* was the nearest neighbor over 5% of the time. *Ailanthus altissima* was the second most likely nearest neighbor to *R. pseudoacacia*. For the BOTH plot type, *A. altissima* (Fig. 3C) was nearest to itself (64.42%) followed by *M. pomifera* (20.34%) and *R. pseudoacacia* (3.39%). Also, the nearest neighbor to *R. pseudoacacia* (Fig. 3D) was itself (69.23%) followed by *A. altissima* (11.4%) and *J. nigra* (7.69%).

Local approach: Spatial analysis of advance regeneration

Looking at all plot types together, within the 10 × DBH (m) radius circle, there was significantly more advance regeneration under *M. rubra* ($P < 0.0001$) than the mean for all other tree species. There was significantly less advance regeneration under *J. nigra* ($P < 0.0001$), *R. pseudoacacia* ($p = 0.0009$), *C. occidentalis* ($P = 0.0008$), *M. pomifera* ($P = 0.0019$), and *G. triacanthos* ($P = 0.0111$) trees than the mean for all trees. Also for trees that had *A. altissima* as its closest neighbor, there was significantly less advance regeneration than the mean for all trees ($P = 0.0112$). In contrast, when the nearby closest tree was *Asimina triloba* (L.) Dunal. ($P = 0.0072$) or *J. virginiana* ($P = 0.0101$), there was significantly more advance regeneration than compared to the mean for all trees. Within the 20 × DBH (m) radius circle (which was approximately 7 m^2 in area), advance regeneration was also significantly greater under *M. rubra* ($P < 0.0001$) than the mean for all other tree species, and less advance regeneration also was found under *J. nigra* ($P = 0.0018$) and *R. pseudoacacia* ($P = 0.0488$). Similarly, when the closest neighbor to the target tree was *A. altissima*, there was less advance regeneration ($P = 0.017$) compared to the mean for all tree species, and when the closest neighbor was *A. triloba* ($P = 0.0049$) or *J. virginiana* ($P = 0.0143$), there was significantly more advance regeneration. Within the 50 × DBH (m) radius circle (which was

approximately 45 m^2 in area) advance regeneration again was significantly greater under *M. rubra* (P = 0.0014), but also greater under *A. altissima* (P = 0.0206) than the mean for all other tree species. When the closest neighboring tree was *J. nigra* (P = 0.0256) or *C. occidentalis* (P = 0.0256), advance regeneration was significantly less than that when other species (including *A. altissima*) were closest. When the closest neighboring tree was *A. triloba* (P < 0.0001), there was significantly more advance regeneration.

Regional approach: The association between the target species

We evaluated 4,958 FIADB plots within the native range of *R. pseudoacacia.* The most common tree species in these plots were *Quercus prinus* L., *A. rubrum*, and *Liriodendron tulipifera* L. More than 5% of the plots sampled had *R. pseudoacacia*, while less than 1% of the plots contained *A. altissima* (Table 5). There were 50 plots and only 32 subplots that contain both species. Although *A. altissima* appeared in less than 1% of the total plots, 5.2% of these plots and 23% of the subplots contained only *A. altissima;* in these subplots, *A. altissima* accounted for more than 50% of total basal area. *Robinia pseudoacacia had a* similar percentage of pure stand plots (5.5%), but only 15% of the subplots with more than 50% of the basal area composed of *R. pseudoacacia*. Both the Chi-square test of Independence and the Phi coefficient test showed a significant positive association between *A. altissima* and *R. pseudoacacia* for both subplots and plots (Table 6).

Table 5. Two by two contingency tables of number of subplots (a) and plots (combined subplots) (b) containing *A. altissima* or *R. pseudoacacia* in FIADB plots within the native range of *R. pseudoacacia.*

(a)

		A. altissima	
		0	>0
R. pseudoacacia	0	18,636	133
	>0	1,031	32

(b)

		A. altissima	
		0	>0
R. pseudoacacia	0	4,007	94
	>0	807	50

Table 6

Chi-square test (χ^2) and Phi coefficient results of the association between *A. altissima* and *R. pseudoacacia* based on contingency tables of number of plots with either or both species present in the FIADB within the native range of *R. pseudoacacia.*

		A. altissima	
		0	> 0
R. pseudoacacia	0	4,007	94
	> 0	807	50

Regional approach: The Influences of target species on tree species abundance and diversity

The mean, median, and maximum number of *A. altissima* individuals in each subplot in which it was present was 2.2, 1.0 and 15, respectively. The mean, median, and maximum number of *R. pseudoacacia* individuals in each subplot in which it was present was 1.7, 1.0, and 12, respectively. There were more species associated with *R. pseudoacacia* (2.948 ± 1.605) on average in the subplots than *A. altissima* (2.376 ± 1.439).

The total basal area of other tree species in the plots was significantly higher for plots with *R. pseudoacacia* than those with *A. altissima* only for plots with < 35% dominance of either target species (Table 7). Plots with *R. pseudoacacia* had higher tree species richness than plots with *A. altissima*. In fact, only plots with *A. altissima* had fewer other tree species compared with the expected when there is no additional effect of the target species, i.e., the percent of other species decreases at the same rate the target species increases. (Fig .4).

Table 7. The Welch Two Sample T-test results of the total number and basal area of other species in the plots stratified based on 5% increments of total basal area of *A. altissima* (AA plot) or *R. pseudoacacia* (RP plot) using FIADB plots within the native range of *R. pseudoacacia*. Significant p-values are shown in bold.

Minimum relative basal area of *A. altissima* or *R. pseudoacacia* in the plot	p-value for t-test of total basal area of other species	p-value for t-test of total number of other species
5%	**1.096e-10**	**2.41e-7**
10%	**8.146e-9**	**3.044e-4**
15%	**9.143e-8**	**4.794e-3**
20%	**3.244e-5**	**6.707e-3**
25%	**2.722e-4**	**0.032**
30%	**4.55e-3**	0.222
35%	**5.135e-3**	0.358
40%	0.011	0.596
45%	0.172	0.746
50%	0.788	0.397

Tree species richness in the plots with *R. pseudoacacia* was not significantly different from that of plots with *A. altissima* when either target species had more than 25% dominance (Table 7). The mean diversity for the four plot types were 0.7869 ± 0.0806 for AA plots, 0.7955 ± 0.0925 for RP plots, 0.7995 ± 0.0894 for BOTH plots, and 0.7647 ± 0.1280 for Reference plots. Diversity differed significantly among the plot types (P = 5.86e-12). However, this difference was strongly influenced by the difference between Reference and RP plots (P = 6.4e-10), with the RP plots having the highest diversity and the Reference plots having the lowest diversity of plot types. There was no significant difference between the other pairs of plot types.

Discussion

Generalities of local and regional vegetation of sampled plots.

Tree density in the six local plots (320–640 trees ha^{-1}) was similar to the range for mature forests (398–496 trees ha^{-1}) in eastern North America forests (Keddy and Place 1994), but lower than that (800–1000 ha^{-1}) in another report conducted in New York state (Schuster et al. 2008). However, the basal area of canopy trees in the sampled plots (8.6–18.0 m^2ha^{-1}) was at the low end for mature stands (15–25 m^2ha^{-1}) in other eastern North American forest (Keddy and Place 1994; Schuster et al. 2008), supporting their description as mid- to late-successional forests. FIADB plots averaged approximately 20–30 m^2/ha, somewhat higher than our local plots but similar to other mature eastern deciduous mature forests with data; these data are mixtures of early-, mid-, and late-successional forests. FIA defines a forested area,

which must be 0.4 ha or larger in size with the narrowest width being 36.6 m or greater, as at least 10% of its area covered by tree canopies (McRoberts 2005).

Spatial dispersion of target tree species (Hypothesis one)

Both target species were spatially clumped within their own mapped local plots and in plots that had both species present. Moreover, the two species preferentially grew together in the plots where they were co-located. A few other species in the mapped local plots also had spatial distributions exhibiting contagion but none as consistent as the two target species. Similarly, the association between *A. altissima* and *R. pseudoacacia* was significantly greater than what would be expected at random in the FIADB plots. Clumped distributions may be a consequence of vegetative reproduction and because both species characteristically establish in disturbed forest sites (Bray 1962; Call and Nilsen 2003). These results support a high likelihood that these two species interact in early- to late-successional forests, when present. Plant species exhibiting contagion in their distribution may also be prone to having invasive tendencies especially in landscapes with complex shapes and high patch densities that increase opportunities for dispersal and access to disturbed edges (Boscutti et al. 2022). Contagion is not uncommon and has been documented as the most common distribution pattern for several species, including *A. altissima*, in Western Himalaya where it is also considered an invasive exotic (Haq et al. 2022) though right on the border with its native region. Interestingly, *R. pseudoacacia*, which is also nonnative to Western Himalaya, had a uniform distribution (Ahmad et al. 2016; Thakur et al. 2020); both species are documented as plantation and roadside species in the region (Haq et al. 2022), though *A. altissima* may dominate more on the roadsides.

In our study, the clumped dispersion pattern was most evident for *A. altissima*. Clumps of *A. altissima* trees were often associated with clumps of *A. altissima* saplings and abundant *A. altissima* seedlings at the local scale. At the regional scale, *A. altissima* trees covered 50% or more of the subplots in which it was present. This strong clumping of trees, saplings and advance regeneration suggests over time *A. altissima* will be able to establish dominance in disturbed patches more so than *R. pseudoacacia* and other less aggressive native trees. The dominance of *A. altissima* in the tree, sapling and advance regeneration layers indicates *A. altissima* may be able to maintain its abundance during succession, effectively altering the successional trajectory to a mature forest with an *A. altissima* canopy, subcanopy, and understory. Thus, while in early succession these two target species may both dominate, over time *R. pseudoacacia* declines faster than *A. altissima* (Nilsen et al. 2018) indicating the impact of *A. altissima* on forest structure and processes may increase over time relative to impacts of *R. pseudoacacia*. The fact that there were many more FIADB plots within *R. pseudoacacia*'s native range that contained or were dominated by *A. altissima* compared with that for *R. pseudoacacia* further supports the predicted future increased dominance of *A. altissima.*

Target trees and advance regeneration (Hypothesis two)

We predicted that advance regeneration of other tree species would be enhanced near *R. pseudoacacia* and inhibited near *A. altissima*. However, we found fewer seedlings near *R. pseudoacacia* than compared

to other tree species, including *A. altissima*, at the sites. This unexpected finding contradicts the assertion that the nitrogen-fixing *R. pseudoacacia* could facilitate the development of other tree seedlings (Boring et al. 2014; Von Holle et al. 2006; Castro-Díez et al. 2008) at least in this mid- to late-successional system. It is possible that other neighboring tree species may have influenced soil nutrition near *R. pseudoacacia*, thereby diluting the effect of *R. pseudoacacia*. However, increased soil nitrogen often increases plant productivity that can be manifested in the increased growth of existing dominant species rather than increased richness via greater germination of one or more new or less common species (Temperton et al. 2007). Similar to our findings, understory plant species richness in a *R. pseudoacacia* plantation in Japan did not differ from that of a *Betula platyphylla* Sukaczev (not a nitrogen fixer) plantation (Masaka et al. 2013). The physical dormancy of *R. pseudoacacia* seeds may delay responses to increased nutrient levels that may trigger germination in some species but inhibit germination in others (Zhong et al. 2019). Also, water extractions of *R. pseudoacacia* leaves have been found to have allelopathic effects on herbaceous species when evaluated in lab experiments (Nasir et al. 2005). But the allelopathic effect of *R. pseudoacacia* has not been documented in field studies.

Although we hypothesized that advance regeneration would be inhibited (both in number and diversity) near *A. altissima* trees, the amount of advance regeneration was significantly greater in the two AA plots compared with other plot types within the same site, though diversity was not significantly greater in the AA plots. Having more seedlings near *A. altissima* target trees is counterintuitive because previous research has shown that *A. altissima* inhibits germination and seedling growth, though less so for individuals pre-exposed to the allelopathic compounds (Lawrence et al. 1991). Our results also show the importance of proximity concerning whether advance regeneration will be impacted by *A. altissima*; negative impacts are noted if within 10-20x the radius of the target *A. altissima* tree but are positive at greater distances. As a comparison, less advance regeneration was found under *J. nigra* as well, which was expected based its documented allelopathy (Rietveld 1983).

Ailanthus altissima's presence may increase soil fertility primarily due to rapid decomposition of its leaf litter, which is high in N and other nutrients (Gómez-Aparicio and Canham 2008b). For larger *A. altissima* trees, which required the larger virtual circle in our study, the decomposing leaf litter from the canopy may have a greater effect on the advance regeneration than allelopathic compounds, which become less effective the further distance from the tree base regardless of tree size (Gómez-Aparicio and Canham 2008a). Lastly, the advance regeneration near *A. altissima* plants was dominated by *A. altissima*, especially at the BL site. Thus, when there was a positive association of *A. altissima* trees with advance regeneration it is not indicative of a healthy native seedling bank, but rather a lack of system resilience. Similarly, the other species making up the advance regeneration in the AA plot type at the AL site were primarily other nonnative invasive woody species (e.g., *M. pomifera*, *M. rubra*, *Ulmus pumila* L., *Elaeagnus angustifolia* L., and *E. umbellata* Thunb.), providing some evidence of the formation of a novel plant community dominated by nonnative species (Simberloff and Von Holle 1999) at least in the understory.

Impacts on Forest productivity and richness/diversity (Hypothesis 3)

Local plots with *A. altissima* or both target species present had relatively high compositional similarity and separated out in ordination space from plots with *R. pseudoacacia*, indicating that *A. altissima* had a significant effect on community composition that also surpassed any effect of *R. pseudoacacia.* These findings also support Maskell et al.'s (2006) assertion that regional impacts of invasive species are less evident than local impacts because disturbance and land-use change are the drivers of change at the regional scale with invasions being only symptoms of these drivers. Our results show that *A. altissima*-dominated plots did not differ significantly in diversity from reference plots but plots dominated by *R. pseudoacacia* did. Thus, *A. altissima* appears to be a driver of invasion at the local scale but a passenger at the regional scale, whereas *R. pseudoacacia*'s role in succession is evident at both scales in terms of diversity (MacDougall and Turkington 2005).

At the local scale, productivity was site-dependent with the plots dominated by *R. pseudoacacia* having the most basal area trees and saplings in one site (BL – 40 year old site) and having the least in the other (AL – 100 year old site). These results support expectations of *R. pseudoacacia* as an early-successional species, but *A. altissima*'s larger basal area values than *R. pseudoacacia* in both sites highlights how *A. altissima* can maintain its dominance in older forests. Maintaining dominance in older forests via gap dynamics (Knapp and Canham 2000) and clonal growth (Kowarik 1995) is attributed to *A. altissima*, which has an ability to survive as ramets under shady conditions and then rapidly grow in response to a canopy opening. Some *A. altissima* populations may exhibit greater shade-tolerance than once thought with evident growth under light conditions below typical of shade-intolerant species (Martin et al. 2010; Knüsel et al. 2017). In fact, the microsite conditions that favor *A. altissima* colonization of forests once dominated by *Castanea sativa* were the same for recently undisturbed forests or post-fire forests (Knüsel et al. 2019). Such a capacity has not been established for *R. pseudoacacia*.

Our regional-scale results show that the basal area of other species in a community decreases more than expected in relation to the basal area of either target species. Thus, both target species reduce the basal area of other species in mid- to late-sere communities. Yet, the effect of *A. altissima* on other species basal area is more severe than that for *R. pseudoacacia*. In fact, at 5% basal area of *A. altissima* the basal area of other species was reduced by an average of 50%, while at 5% basal area of *R. pseudoacacia* basal area of other species was reduced by an average of only 25%. Our stratification of relative effects based on invader abundance provides greater insight into potential effects of an invader and does not suffer from the weaknesses associated with studies that compare invaded and uninvaded patches or sites (Stolgren and Rejmanek 2013). We did not attempt to evaluate impacts of these species at the regional scale in terms of different forest types; several studies including Mason and French (2008) and Huebner (2021) indicate that impacts will vary across different land types.

Hypothesis 3 is based on the supposition that *A. altissima* inhibits advance regeneration and gains dominance in the community over time while *R. pseudoacacia* fertilizes the community and decreases in dominance over time enhancing the dominance of other species. In its native range in China, *A. altissima* is negatively related to forest cover, while in the U.S., there is a preference for intermediate forest cover based on Albright et al.'s (2010) comparison of ecological niches in each country. Albright et al. (2010)

proposed that *A. altissima* has broadened its ecological niche into later successional sites in the U.S. possibly in response to less intense competition, increased allelopathic potency, and the presence of novel genotypes due to multiple introductions (Albright et al. 2010). In contrast, *R. pseudoacacia* is most successful in early successional sites and rapidly loses dominance as succession proceeds (Boring et al. 2014).

Our local scale results did not show a difference in diversity among plots occupied by one or both the target species, but plots dominated by *R. pseudoacacia* at the regional level were more diverse than the Reference plots. Our local scale sites had no Reference plots with which to compare the *R. pseudoacacia* sites. Thus, this regional pattern may reflect the greater diversity often associated with early to mid-successional sites where both ruderal species and K-selected species co-occur but may also reflect the presence of many more exotics in the AA, RP, and BOTH plots. However, the FIA data for these sites show no other exotic tree species.

Moreover, differentiating relative impacts on native species of other exotic invasive species in addition to *A. altissima* would require sequential removals of each exotic species with high potential of increased spread of present invasives, new invasions, or reinvasion of the species removed. Several studies reveal a reduction in native plant richness or diversity in response to the presence of *A. altissima* at a local scale (Motard et al. 2011; Constan-Nava et al. 2015; Sladonja et al. 2015; Brooks et al. 2021). *Robinia pseudoacacia* also can reduce native species diversity but published cases appear to be limited to its nonnative range (Benesperi et al. 2012) and negative impacts become less likely with age of the invaded site (Staska et al. 2014).

Antagonistic relationship between A. altissima and R. pseudoacacia (Hypothesis 4)

We were particularly interested in the interaction of these two species and predicted that the interaction would be antagonistic. Previous research on invasive species has shown that invaders interact strongest with native species that are in the same functional group as the invader (e.g. Case et al. 2016). In our study, *A.altissima* is invading the native range of *R. pseudoacacia* yet both trees share similar functions. We were not able to document a strong negative interaction between these two species suggesting that competition between these two species is relatively weak. Both species are characteristically clumped together and grow to within 1 m of each other commonly in disturbed forest sites (Call and Nilsen 2003). Our current study shows that both species have a negative effect on the basal area of other species and when they cohabit a site the effect is similar, though *A. altissima*'s impact is stronger. *Ailanthus altissima*'s allelopathic effects may also differ by species and developmental stage, with a measurable negative effect on *A. rubrum* and no effect on *Q. rubra* documented in one study, but such effect was primarily demonstrated by *A. altissima* saplings and not trees (Gómez-Aparicio and Canham 2008a). Although both species can grow to maturity together, as the forest canopy develops, *R. pseudoacacia* will be extirpated from the site due to increased shading. In contrast, *A. altissima* may persist later in community development as clonal sprouts and a subsequent rapid response to canopy openings

(Kowarik 1995; Knapp and Canham 2000) or possibly due to greater shade tolerance than typical of many ruderal plants (Martin et al. 2010; Knüsel et al. 2017). Consequently, any effect that *R. pseudoacacia* had on the community (its legacy) will be negated by the potential longevity of *A. altissima* at the site. Our data support this idea on a regional scale because sites with both species present were most like those with only *A. altissima* and significantly different from sites with only *R. pseudoacacia*. However, the eventual canopy dominance of *A. altissima* vs. another species may depend on the initial site conditions. For instance, Pickett et al. (2001) found that *A. altissima* became the dominant canopy trees in an old field that was left unplowed at the time of abandonment whereas *A. rubra* became the dominant canopy trees in an old field that was plowed the year it was abandoned. Castro-Díez et al. (2014), in their comparison of the invasive nonnative *A. altissima* and *R. pseudoacacia* interactions with the native *Populus alba* L. in floodplain forests of central Spain, found that *A. altissima* could outcompete *P. alba* by retaining great height growth capacity over time and overtopping *P. alba*, whereas *R. pseudoacacia* would not outcompete coexisting adult trees of *P. alba* because of a reduced growth rate over time but would more efficiently invade new sites because of its higher reproductive capacity that it retains as an adult tree.

Conclusions

Our research documented contagion between *R. pseudoacacia* and *A. altissima* in mid- to late-successional temperate deciduous forests at both local and regional scales. In addition to this positive association, both species had a negative effect on other associated species at the local scale with *A. altissima* also negatively impacting other species at the regional scale. The relative longevity and ability to rapidly respond to small disturbances of *A. altissima* allow it to influence the presence and growth of other species through late succession, whereas *R. pseudoacacia*'s impacts on associated vegetation occur in earlier stages of succession in which negative effects on diversity are evident locally but with positive effects on diversity when comparing *R. pseudoacacia*-dominated sites (younger forests) with reference sites (more mature forests without either target species) regionally.

Declarations

Acknowledgements: We thank Zhe Bao and Angang Zhang for their help with data collection and analyses. This project was funded with USDA Forest Service Joint Venture Agreement 12-JV-11242303-03.

Funding: This research was funded by a USDA Forest Service Joint Venture Agreement 12-JV-11242303-03.

Competing Interests: *The authors have no relevant financial or non-financial interests to disclose.*

Author Contributions: Nilsen and Huebner conceived the idea, designed the study, collected, and analyzed the data, and wrote the paper.

Data Availability: Data used in these analyses will be available *are available from the corresponding author on reasonable request*.

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Figures

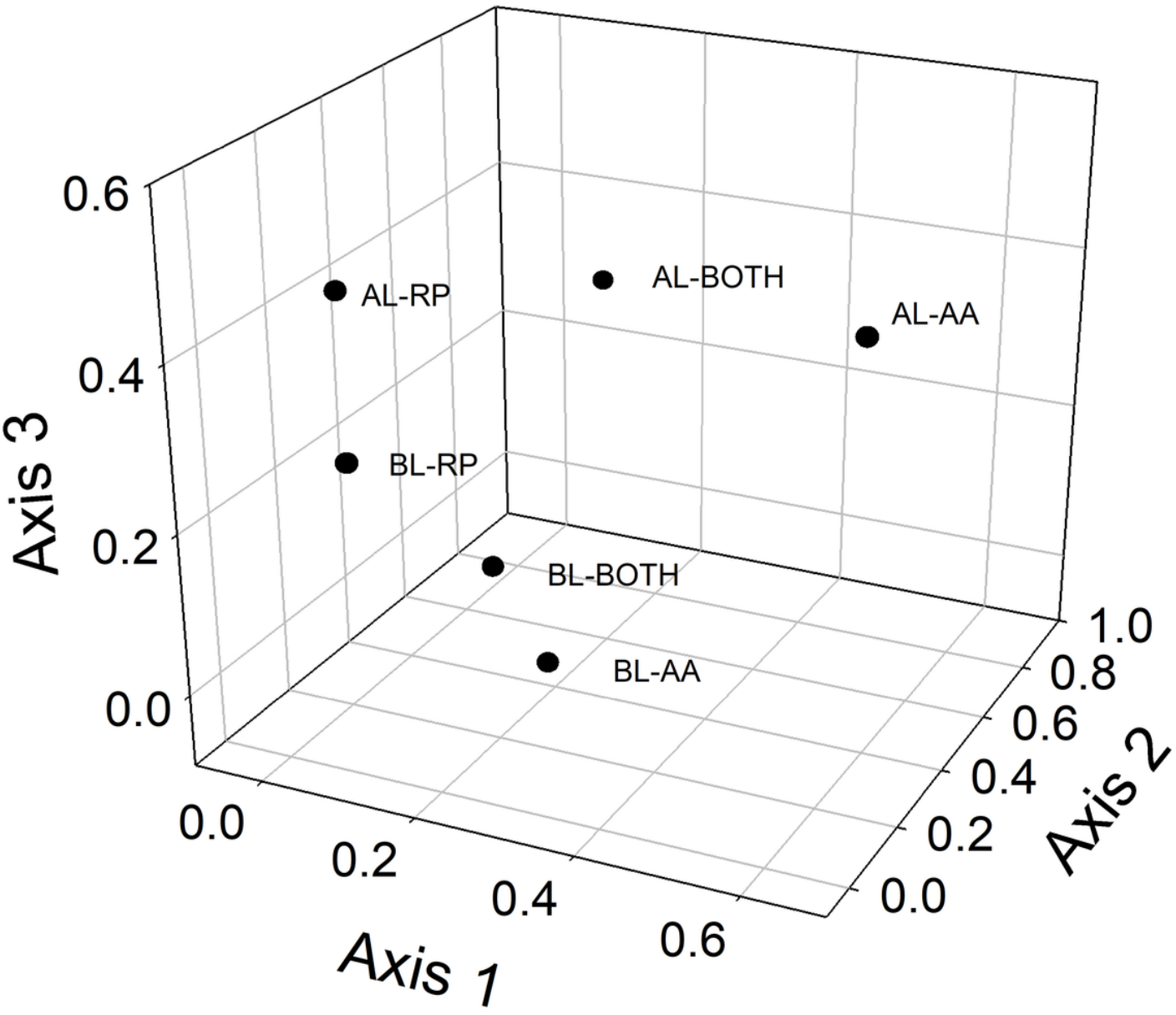

Figure 1

Bray Curtis ordination of six, 0.1 ha plots at two locations in Virginia US. Locations are identified as AL and BL. Plot types are identified as containing at least 20% *A. altissima* (AA) or *R. pseudoacacia* (RP) or a sum of 40% of *A. altissima plus R. pseudoacacia*(BOTH). The three most important axes are shown.

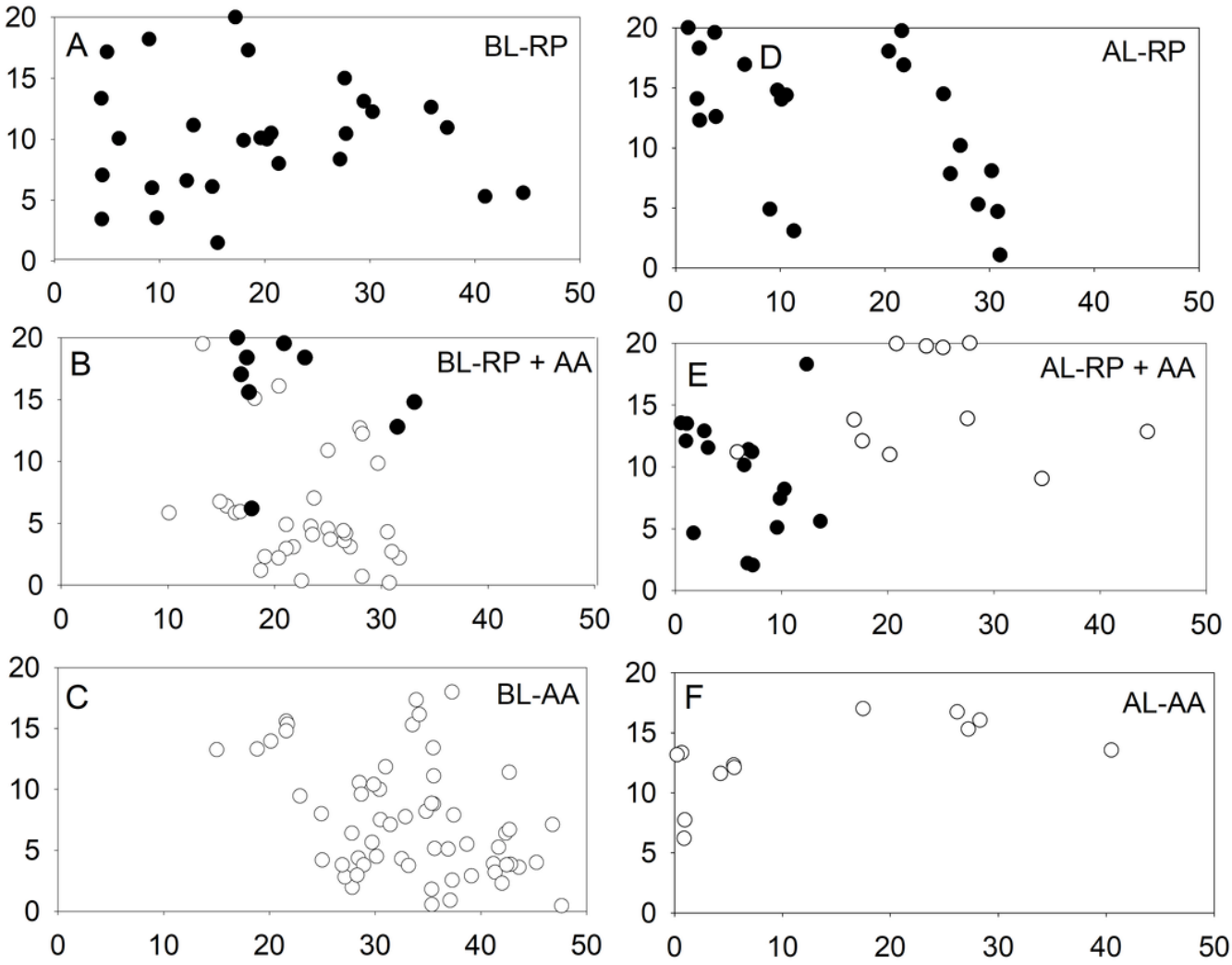

Figure 2

Spatial distribution of *A. altissima (AA* open circles*)* and *R. pseudoacacia (RP* filled circles*)* in six, 0.1 ha plots at two locations (AL and BL) in Virginia US. Plot types are identified as containing at least 20% *A. altissima* (AA) or *R. pseudoacacia*(RP) or a sum of 40% of *A. altissima plus R. pseudoacacia* (BOTH). Plots are designated by site target species. (A) represents the spatial location of RP trees in plot BL-RP, (B) the spatial location of RP and AA trees in plot BL-BOTH, (C) the spatial location of AA and in plot BL-AA, (D) the spatial location of RP trees in plot AL-RP, (E) the spatial location of RP and AA trees in plot AL-BOTH, and (F) the spatial location of AA and in plot AL-AA.

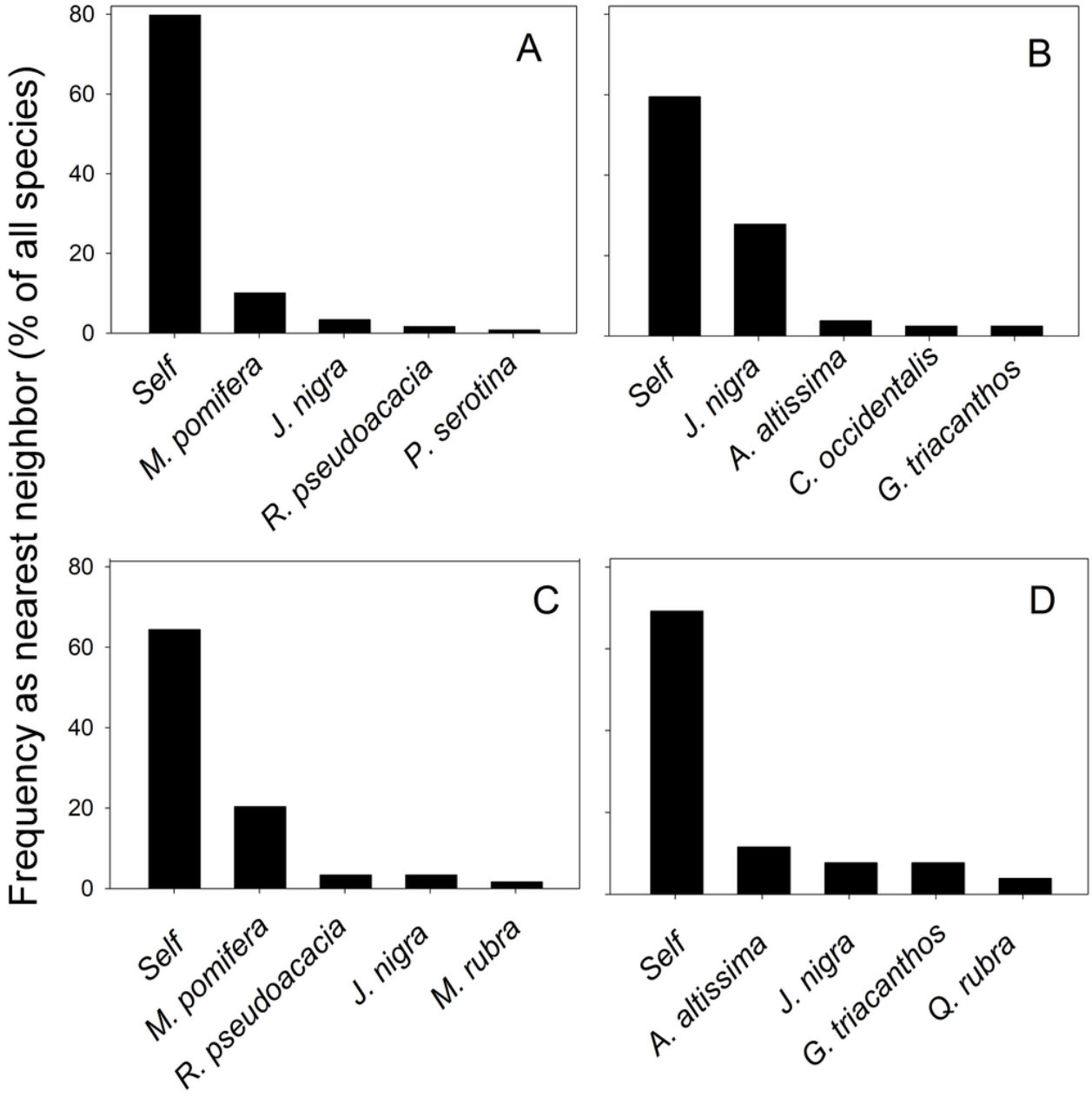

Figure 3

Results of a nearest-neighbor analysis for *R. pseudoacacia* and *A. altissima*trees at two sites in Virginia US. In the combined data set of six mapped plots, the five species most often found as nearest-neighbor to (A) *A. altissima* and (B) *R. pseudoacacia* are shown. In the combined data set from the two plots with both target species present, the five species most often found as nearest neighbor to (C) *A. altissima* and (D) *R. pseudoacacia*are shown. Nearest neighbor species names in alphabetical order refer to: *Ailanthus altissima, Celtis occidentalis, Gleditsia triacanthos, Juglans nigra, Maclura pomifera, Morus rubra, Prunus serotina, Robinia pseudoacacia* and *Quercus rubra.*

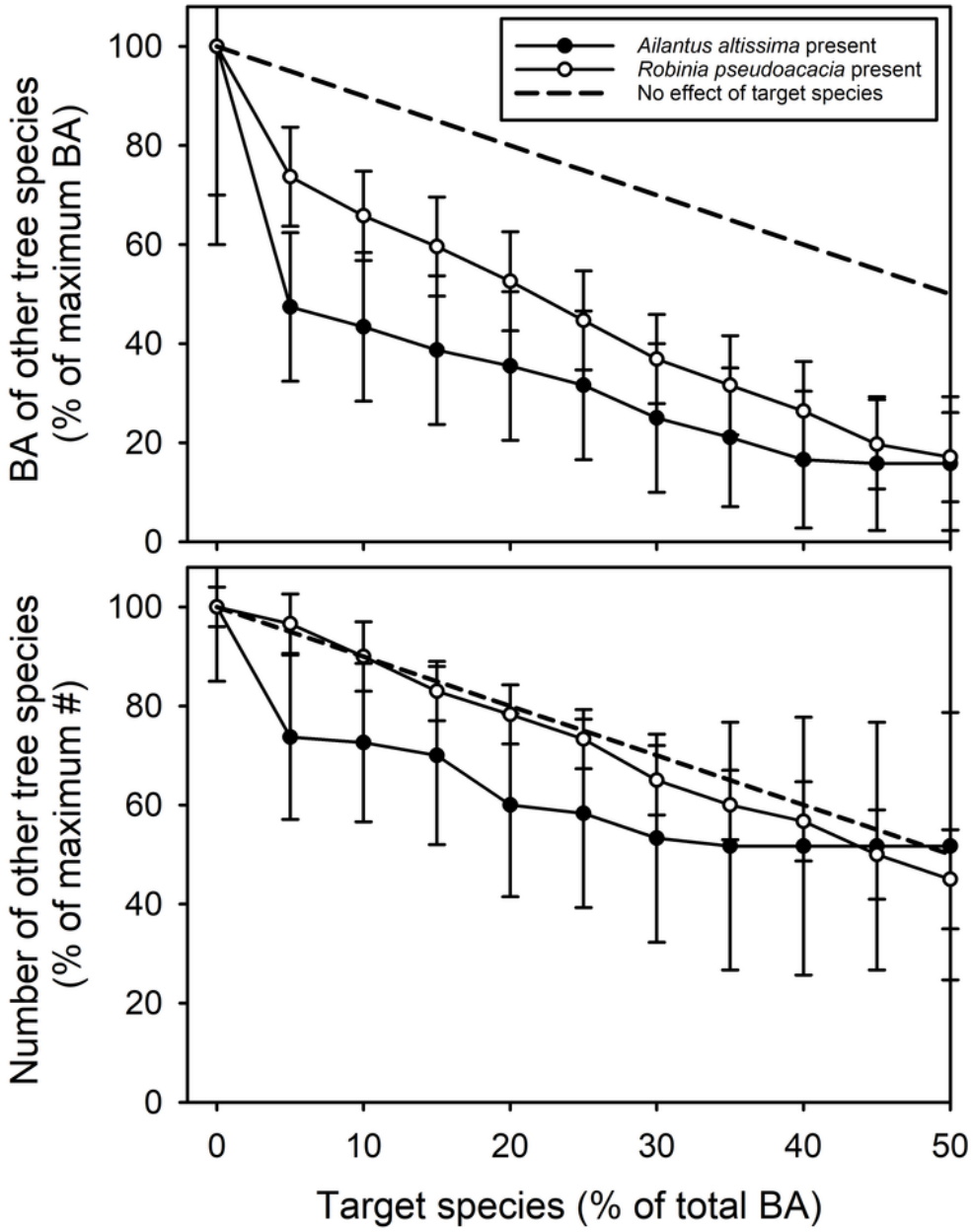

Figure 4

Plots of basal area and number of species for all other species in FIADB plots with the target species (*Ailanthus altissima* or *Robinia pseudoacacia*) present within the native range of *R. pseudoacacia*. (A) shows basal area of other species as a % of the maximum for plots with either *A. altissima* or *R. pseudoacacia*present in 5% increments of basal area; (B) shows the number of other species as a % of the maximum for plots with either *A. altissima* or *R. pseudoacacia*present in 5% increments of basal area.

Dashed line indicates the proportional decrease if there is no effect of target species on basal area or number of other species in the plots.