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Influence of Intensity and Duration of Invasion by Amur Honeysuckle (*Lonicera maackii*) on Mixed Hardwood Forests of Indiana

Joshua M. Shields, Michael A. Jenkins, Michael R. Saunders, Kevin D. Gibson, Patrick A. Zollner, and John B. Dunning, Jr.*

The expansion of populations of invasive species continues to compromise the ecological and economic integrity of our natural resources. The negative effects of invasive species on native biota are widely reported. However, less is known about how the duration (i.e., age of oldest invaders) and intensity (i.e., density and percent cover) of an invasion influences native plant diversity and abundance at the microsite scale. We examined the influence of density, percent cover, and age of Amur honeysuckle (a nonnative invasive shrub), and several environmental factors on native plant taxa at 12 mixed hardwood forests in Indiana, USA. Overall, study sites with the greatest taxonomic diversity (Shannon's Diversity; H′), richness (S), percent cover, and density of native vegetation also had the lowest percent cover of Amur honeysuckle in the upper vertical stratum (1.01 to 5 m). Based on linear mixed model analyses, percent cover of Amur honeysuckle in the upper vertical stratum was consistently and negatively correlated with H′, S, total percent cover, and woody seedling density of native taxa at the microsite scale ($P < 0.05$). Duration of Amur honeysuckle at the microsite scale was not significant when percent cover of Amur honeysuckle in the upper vertical stratum was included in models. However, duration of Amur honeysuckle invasion was significantly correlated with dependent variables and with upper-stratum honeysuckle cover, suggesting that older Amur honeysuckle in a microsite resulted in greater light competition from above for native understory plant species. Beyond increased cover and shading, our results do not provide evidence of duration-related effects from long-term dominance of honeysuckle in our sampled mixed hardwood forest sites.

Nomenclature: Amur honeysuckle, *Lonicera maackii* (Rupr.) Herder.

Key words: Central Hardwoods, diversity, evenness, linear mixed effects model, nonnative shrub, richness, spring ephemerals.

Invasions by nonnative plant species have become one of the most serious threats to the ecological and economic integrity of ecosystems worldwide (Bennett 2014; Chornesky and Randall 2003; Fan et al. 2013; Higgins et al. 1999; Hunter and Mattice 2002; Mack et al. 2000; Mullin et al. 2000; Pimentel et al. 2005; Simberloff et al. 2013). Invasive plants may impact ecosystems in numerous ways, such as causing declines in native plant diversity and growth (Fagan and Peart 2004; Jose et al. 2002; Martin 1999; Pyšek et al. 2012; Webster et al. 2006), altering disturbance regimes and other ecological processes (Brooks et al. 2004; Dukes and Mooney 2004; Ehrenfeld et al. 2001), and even facilitating invasions by other nonnative species (Heimpel et al. 2010; Simberloff and Von Holle 1999). The result of such ecological impacts is often major economic costs. For example, Pimentel et al. (2005) reported that the invasive purple loosestrife (*Lythrum salicaria* L.) costs the United States $45 million per year for control efforts and loss of wildlife forage.

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Management Implications:

Nonnative invasive plants continue to pose one of the most serious threats to ecosystems worldwide. While the negative effects of invasive plants have been well documented, it is still unclear how the combined effect of duration of invasion and intensity (amount of occupied growing space) of an invader can influence native diversity at the microsite scale. We addressed this knowledge gap by examining how the duration and intensity of Amur honeysuckle invasion influenced the diversity and abundance of native plants in hardwood ecosystems of Indiana. Our results indicated that while percent cover of Amur honeysuckle in the upper vertical stratum (1.01 to 5 m) exhibited a strong negative correlation with native plant diversity and abundance at the microsite scale, duration of Amur honeysuckle invasion was not important when honeysuckle percent cover was included in the statistical models. However, when only duration of invasion was considered, it did show a significant negative correlation with native plant diversity and abundance and upper-stratum honeysuckle cover. It therefore appears that microsites where Amur honeysuckle has persisted longer contain a greater percent cover of this invasive shrub, resulting in greater light competition from above and reduced diversity and abundance of native flora. Information about the combined effects of Amur honeysuckle invasion intensity and duration can help forest managers prioritize control efforts in areas where existing sources of native plant propagules are present in microsites where Amur honeysuckle invasion is less intense. Also, our results suggest that the rate of community recovery after honeysuckle removal may not be heavily influenced by cumulative effects related to the duration of invasion. Such information is important for management efforts to support the long-term recovery of native plant communities in invaded ecosystems. Such information may be critical to the long-term recovery of native plant communities in these invaded ecosystems.

The specific response of a native plant community to nonnative plant invasions is influenced by a multitude of factors pertaining to characteristics of both the invader and the invaded ecosystem. For example, numerous investigators have proposed that nonnative plants that become invasive, and therefore capable of displacing native species, possess characteristics that give them an advantage in their invaded environment, such as novel weapons (i.e., allelopathic properties; Callaway and Ridenour 2004) and high numbers of large propagules (Simberloff 2009). Impacts of invaders on native biota also depend on environmental factors such as corridors for effective propagule dispersal (Christen and Matlack 2006), resource availability coinciding with propagule pressure (Davis et al. 2000), disturbances that favor establishment (Stapanian et al. 1998; Sutherland and Nelson 2010), and lack of natural enemies in the invaded range (enemy release; Keane and Crawley 2002).

Equally important is how invasive plants spread in space and time. For plant invasions, it is generally thought that effects on native biota are least severe and control efforts are most effectively implemented during the establishment phase of invasion, prior to the point at which an invader begins to spread exponentially (Sakai et al. 2001; Webster et al. 2006). Abundant populations of invasive plants have been shown to negatively affect native communities through competition (e.g., Gorchov and Trisel 2003; Gould and Gorchov 2000), but less is known about the effects of the sustained presence of invasive plants. Recent research has shown that, in addition to direct competition, established populations of invasive plants may have indirect effects, including altering nutrient cycles and inhibiting fungal associates in native communities (Ehrenfeld et al. 2001; Wilson et al. 2012; Wolfe and Klironomos 2006); these indirect effects may become more acute with long-term exposure. Because density of invasive plants varies at small spatial scales, it is critical to understand the combined effects of intensity and duration of invasions in order to better understand the multitude of impacts on native species that can occur within an invaded area. However, it remains unclear how microsite-level effects on native plants may vary within an invasion and whether these effects are exacerbated where the invader has persisted longer.

Throughout the eastern United States and parts of Canada, the nonnative shrub Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder] has invaded forest ecosystems, expanding its range since its initial introduction in the 1890s; and is considered one of the most aggressive invasive plants in North America (Deering and Vankat 1999; Luken and Thieret 1995). Numerous investigators have shown that Amur honeysuckle has negative impacts on native plants (Cipollini and McClain 2008; Collier et al. 2002; Gorchov and Trisel 2003; Gould and Gorchov 2000; Hartman and McCarthy 2008; Hutchinson and Vankat 1997; McKinney and Goodell 2010; Meiners 2007; Miller and Gorchov 2004), with some research providing insights into its invasion process in time and space (Deering and Vankat 1999; Shields et al. 2014). However, we are unaware of any studies that have examined the combined effects of Amur honeysuckle invasion intensity and duration of invasion on native taxa. As Amur honeysuckle and other long-lived woody invasives continue to expand within native communities and establish in new areas, an improved understanding of the gradient of intensity and duration impacts on native biota within invaded areas could be used to more effectively prioritize control efforts at multiple scales.

The primary objective of this study was to examine microsite-level effects of Amur honeysuckle invasion intensity and duration on native plant diversity and abundance in mixed hardwood forests of Indiana. Specifically, we examined the influence of Amur honeysuckle density, percent cover, and duration of invasion, as well as other environmental variables, on the diversity and abundance of native herbaceous and woody ground-layer species and tree seedlings at microsites within 12 mixed

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hardwood forests invaded by Amur honeysuckle. We hypothesized that native diversity and abundance would be lowest at microsites where the density and percent cover of Amur honeysuckle were greatest and where proximate Amur honeysuckle shrubs were oldest (i.e., greatest duration of invasion). Greater percent cover of Amur honeysuckle, especially from the largest shrubs, equates to more light competition from above for native taxa. We predicted that this effect would be especially pronounced for herbaceous plants that flower primarily in the spring given that Amur honeysuckle leafs out earlier in the year than native woody species and therefore captures light that would be available to these spring herbs under the leafless overstory canopy. In terms of duration of invasion, microsites where Amur honeysuckle shrubs have persisted longest may be subjected to greater quantities of allelochemicals found in honeysuckle foliage (McEwan et al. 2010) due to continued exposure to honeysuckle foliage falling to the forest floor compared with microsites where Amur honeysuckle has not persisted as long.

Materials and Methods

Study Area. This study was conducted in 12 mature, second-growth mixed hardwood forests in the glaciated regions of central Indiana (forest locations ranged from 39°20′ N to 40°32′ N, and 86°00′ W to 87°26′W): (1) Fort Harrison State Park (hereafter referred to as Ft. Harrison), (2) Fowler Park (hereafter referred to as Fowler), (3) Hawthorn Park (hereafter referred to as Hawthorn), (4) Pfizer, Inc., Pond 5 eastern forest (hereafter referred to as Pond 5A), (5) Pfizer, Inc., Pond 5 western forest (hereafter referred to as Pond 5B), (6) Pfizer, Inc., Rifle Range woodlot (hereafter referred to as RR), (7) Purdue University, Department of Forestry and Natural Resources Farm (hereafter referred to as FNR Farm), (8) Purdue University, Department of Forestry and Natural Resources Martell Forest (hereafter referred to as Martell), (9) Purdue University, Meigs Farm, south forest (hereafter referred to as Meigs), (10) a private woodlot in Benton County (hereafter referred to as Leuck), (11) a private woodlot in Lafayette (hereafter referred to as Pursell), and (12) Ross Biological Reserve (hereafter referred to as Ross; Figure 1). Landforms across study sites were glacially derived with parent materials consisting of loess, alluvium, and glacial outwash. Soil types ranged from very poorly drained loams to excessively drained sandy loams (Soil Survey Staff 2013).

All 12 study sites were selected using the criteria that (1) Amur honeysuckle was the dominant nonnative shrub in terms of percent cover, density, and size of individuals and (2) sites represented a gradient of Amur honeysuckle percent cover, density, and size. Overstory layers were characterized by mature, second-growth deciduous trees. Overstory species composition varied across study sites and included sugar maple (*Acer saccharum* Marsh.), white ash (*Fraxinus americana* L.), black walnut (*Juglans nigra* L.), osage-orange [*Maclura pomifera* (Raf.) C.K. Schneid.], tuliptree (*Liriodendron tulipifera* L.), black cherry (*Prunus serotina* Ehrh.), elm species (*Ulmus* spp.) and oak species (*Quercus* spp.).



Figure 1. General locations of 12 study sites in central Indiana. One study site (a private woodlot, Leuck) was located in Benton County (upper left star on map); five study sites (Purdue University Department of Forestry and Natural Resources Farm, Purdue University Department of Forestry and Natural Resources Martell Forest, Purdue University Meigs Farm South, a private woodlot [Pursell], and Ross Biological Reserve) were located in Lafayette/West Lafayette (second-highest star on map); one study site (Ft. Harrison State Park) was located near Indianapolis (star near center of map); and five study sites (Fowler Park, Hawthorn Park, Pfizer Inc. Pond 5A forest, Pfizer Inc. Pond 5B forest, and Pfizer Inc. Rifle Range woodlot) were located near Terre Haute (lower left star on map). Indiana image is from IndianaMAP (http://maps.indiana.edu). (Color for this figure is available in the online version of this paper.)

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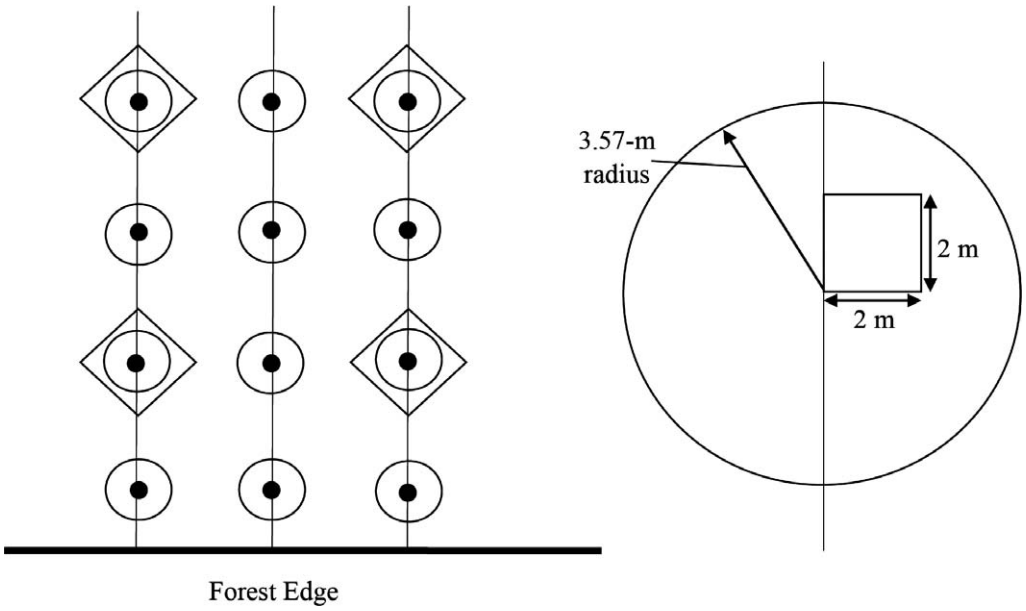


Figure 2. Nested plots for vegetation sampling. In the left diagram, diamonds denote variable-radius plots (basal area factor of 2.296 m^2 ha^{-1} [10 ft^2 ac^{-1}]) for sampling trees $\geq$ 10 cm diameter at breast height (dbh), spaced 40 m apart along transects (used for study site description). Large circles denote 40-m^2 (radius of 3.57 m) sapling/shrub plots spaced 20 m apart along transects. Transects were spaced 20 m apart. In the right diagram, the circle represents a sapling/shrub plot (intersected by a transect) and a 2-m by 2-m quadrat to record percent cover of vascular vegetation and environmental variables. Quadrats were placed either to the upper right, upper left, lower right, or lower left of the sapling/shrub plot center. Canopy cover was measured at each corner of the quadrat, using a spherical densiometer.

Data Collection. During 2010 and 2011, we sampled vegetation by placing a series of fixed-area plots along transects that extended from the forest edge into the interior. At each study site, we placed transects $\geq$ 20 m (65.6 ft) apart. Along each transect, we placed two or more 40-m^2 (430.6 ft^2; radius of 3.57 m [11.7 ft]) sapling/shrub plots and two or more 2-m by 2-m (6.6-ft by 6.6-ft) quadrats to quantify seedlings and ground cover (Figure 2). Sapling/shrub plots were spaced 20 m apart along each transect, the first plot was placed 5 to 10 m (16.4 to 32.8 ft) from the forest edge. Each quadrat was placed to the upper right, upper left, lower right, or lower left of the sapling/shrub plot center (direction was chosen randomly), with the quadrat oriented parallel to the transect. The number of transects at a given study site depended on the size of the forest/woodlot. Likewise, the number of plots per transect depended on transect length, where each transect was extended until (1) it reached a distance that was more than halfway between the origin of the transect and another forest edge, (2) it reached a large stream or river, (3) topographic aspect changed $\geq 180^\circ$, or (4) it reached 80 m (262.5 ft) in length. The total number of nested plots (quadrats nested in sapling/shrub plots) placed at FNR Farm, Fowler, Ft. Harrison, Hawthorn, Leuck, Martell, Meigs, Pond 5A, Pond 5B, Pursell, Ross, and RR were 30, 24, 18, 24, 15, 12, 15, 19, 12, 30, 28, and 27, respectively.

In the sapling/shrub plots, we recorded the number of living saplings and shrubs (woody plants $<$ 10 cm (4 in) dbh and $\geq$ 1.37 m [4.5 ft] tall) by species. A sapling/shrub that produced multiple stems from the same rootstock (e.g., Amur honeysuckle and northern spicebush [*Lindera benzoin* (L.) Blume]) was recorded as a single individual. In the quadrats, we recorded number of living seedlings (woody stems $<$ 1.37 m tall) by species and percent cover of living vascular herbaceous species, woody vines, shrubs, seedlings, saplings, coarse woody debris (CWD, midpoint diameter $\geq$ 10 cm), fine woody debris (FWD, midpoint diameter $<$ 10 cm), dead leaves and herbaceous stems, and bare soil. Percent cover was categorized as follows: 1 = at study site but outside quadrats, 2 = 0 to 1%, 3 = 1 to 2%, 4 = 2 to 5%, 5 = 5 to 10%, 6 = 10 to 25%, 7 = 25 to 50%, 8 = 50 to 75%, 9 = 75 to 95%, and 10 $>$ 95% (modified from Peet et al. [1998]). Percent cover was recorded in two vertical strata: lower (0 to 1 m [0 to 3.3 ft) and upper (1.01 to 5 m [3.3 to 16.4 ft]). Percent cover estimates were performed by a single observer to reduce observer bias. Finally, we recorded total percent canopy cover at one meter above ground level using a spherical densiometer (Convex Model A, Forest Densiometers, Bartlesville, OK, USA) averaged from measurements taken at each of the four corners of the quadrat.

Additional data were collected for a subset of Amur honeysuckle individuals in the sapling/shrub plots.

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Specifically, each sapling/shrub plot was divided into four quadrants and the following information was collected for the largest Amur honeysuckle individual (based on diameter at ground level) in each of those four quadrants: diameter at ground level just above the root burl (dia_{burl}; cm), number of living basal stems (n_{stem}), diameter of largest basal stem (dia_{basal}; cm), height (ht; m), and distance to the overstory drip line of the nearest forest edge (edge; m).

Data were collected in 2010 at FNR Farm, Fowler, Ft. Harrison, Hawthorn, Pond 5A, Pond 5B, Pursell, Ross, and RR, and in 2011 at Leuck, Martell, and Meigs. During each year, quadrats were visited in early May to coincide with the growth of spring-flowering herbaceous plants and again in July-August to coincide with growth of summer ground-layer species. Density data for woody stems in quadrats were collected only during the summer sampling period. Sapling/shrub plots were also only visited once in September. We were unable to classify some taxa to species because distinguishable features were not consistently present at all study sites. For those taxa, we grouped them into multiple-species groups or classified them to genus.

Data Analyses. For percent cover data collected in quadrats, we calculated total percent cover and mean percent cover by taxon/variable, quadrat, and study site. Mean percent cover values were calculated separately for each season (spring, summer) and vertical stratum (lower, upper). All mean values were calculated based on midpoint values from the percent cover classes. We also calculated mean individuals ha^{-1} by taxon and study site for woody taxa in the seedling layer and sapling layer. We calculated Importance Values (IV) for herbaceous vegetation, vines, and environmental variables observed in the lower vertical stratum, for woody individuals observed in the seedling layer, and for woody individuals observed in the sapling layer at each study site. Importance values for each herb/vine taxon and each environmental variable were calculated as IV = ([{mean percent cover + frequency based on plots at a given study site}/2] $\times$ 100); spring and summer observations were examined separately. For woody individuals in the seedling and sapling layers, IV = ([{relative density + frequency based on plots at a given study site}/2] $\times$ 100).

We calculated taxonomic richness (S, number of taxa), Pielou's Evenness Index (J'; Pielou 1966), and Shannon's Diversity Index (H'; Shannon 1948) by quadrat and study site (mean value) using midpoint values from percent cover data of native herbaceous and woody plants in the lower vertical stratum. Calculations of H', S, and J' for summer data included any native herbaceous and woody taxa observed. However, calculations for plants observed during spring included only native herbaceous taxa that flower primarily during the spring and early summer (March to June), based on descriptions from Yatskievych (2000).

We used linear mixed effects models (see Laird and Ware [1982] for formulation of model) to examine the influence of environmental variables on nine dependent variables (Table 1): spring H' (H'_{sp}), spring S (S_{sp}), spring J' (J'_{sp}), spring native percent cover in the lower vertical stratum (species combined as a group; $NLow_{sp}$), summer H' (H'_{su}), summer S (S_{su}), summer J' (J'_{su}), summer native percent cover in the lower vertical stratum (species combined as a group; $NLow_{su}$), and native seedlings ha^{-1} (species combined as a group; N_{seed}). With traditional linear regression techniques, one assumes that all observations are independent (often not the case with ecological data). Linear mixed effects models are appropriate when data have a nested structure (Crawley 2013; Pinheiro and Bates 2000), such is the case in our study, where multiple plots were placed at each study site.

For the models with H'_{sp}, S_{sp}, J'_{sp}, and $NLow_{sp}$ as dependent variables, we examined the following predictor variables: spring percent cover of Amur honeysuckle in the lower vertical stratum ($AhLow_{sp}$), spring percent cover of Amur honeysuckle in the upper vertical stratum ($AhUp_{sp}$), age of the oldest Amur honeysuckle shrub in the sapling/shrub plot (duration of invasion; Ah_{age}), spring percent cover of other nonnative species in the lower vertical stratum (species combined as a group; $OELow_{sp}$), spring percent cover of other nonnative species in the upper vertical stratum (species combined as a group; $OEUp_{sp}$), spring percent cover of native species in the upper vertical stratum (species combined as a group; NUp_{sp}), spring canopy cover (based on densiometer; $canopy_{sp}$), spring percent cover of bare soil ($soil_{sp}$), spring percent cover of CWD (CWD_{sp}), spring percent cover of FWD (FWD_{sp}), spring percent cover of dead leaves and herbaceous stems ($litter_{sp}$), Amur honeysuckle saplings ha^{-1} (Ah_{sap}), saplings ha^{-1} of other nonnative shrubs (species combined as a group; OE_{sap}), and native saplings ha^{-1} (species combined as a group; N_{sap}). For the models with H'_{su}, S_{su}, J'_{su}, and $NLow_{su}$ as dependent variables, we examined the following predictor variables: summer percent cover of Amur honeysuckle in the lower vertical stratum ($AhLow_{su}$), summer percent cover of Amur honeysuckle in the upper vertical stratum ($AhUp_{su}$), Ah_{age}, summer percent cover of other nonnative species in the lower vertical stratum ($OELow_{su}$), summer percent cover of other nonnative species in the upper vertical stratum ($OEUp_{su}$), summer percent cover of native species in the upper vertical stratum (NUp_{su}), summer canopy cover (based on densiometer; $canopy_{su}$), summer percent cover of bare soil ($soil_{su}$), summer percent cover of CWD (CWD_{su}), summer percent cover of FWD (FWD_{su}), summer percent cover of dead leaves and herbaceous stems ($litter_{su}$), Ah_{sap}, OE_{sap}, and N_{sap}. For the model with N_{seed} as the

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Table 1. Explanation of codes, as well as minimum, mean, and maximum values, for diversity and abundance measures at 12 mixed hardwood forests in central Indiana. Mean values were calculated based on all 254 plots across all 12 study sites. Minimum and maximum values were based on the plot with the lowest and highest values for a given variable (i.e., these are not minimum and maximum mean values at the study site scale). For density values, plot level variables were scaled up to a per hectare value.

Description	Code	Minimum	Mean	Maximum
Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder]				
Diameter at ground level (cm)	dia_{burl}	0.4	7.9	27.3
Diameter of largest basal stem (cm)	dia_{basal}	0.4	3.9	15.5
Number of living basal stems	n_{stem}	1	3	13
Height (m)	ht	< 0.5	2.8	7.1
Minimum age of largest individual (years)	Ah_{age}	0	13.2	32
Percent cover in lower stratum, spring	$AhLow_{sp}$	0	10.9	62.5
Percent cover in lower stratum, summer	$AhLow_{su}$	0	11.7	62.5
Percent cover in upper stratum, spring	$AhUp_{sp}$	0	34.1	85
Percent cover in upper stratum, summer	$AhUp_{su}$	0	36.0	85
Saplings ha^{-1}	Ah_{sap}	0	1,913	7,250
Distance to overstory drip line forest edge (m)	edge	9.0	51.4	187.0
Other Vegetation				
Spring native diversity	H'_{sp}	0	0.62	2.12
Summer native diversity	H'_{su}	0	1.78	2.91
Spring native richness	S_{sp}	0	2.72	15
Summer native richness	S_{su}	0	9.49	25
Spring native evenness	J'_{sp}	0	0.51	1.00
Summer native evenness	J'_{su}	0	0.83	1.00
Spring native percent cover, low stratum	$NLow_{sp}$	0	29.5	> 100.0
Summer native percent cover, low stratum	$NLow_{su}$	0	36.3	> 100.0
Spring native percent cover, high stratum	NUp_{sp}	0	8.8	80.0
Summer native percent cover, high stratum	NUP_{su}	0	13.1	87.5
Spring nonnative percent cover (not Amur honeysuckle), low stratum	$OELow_{sp}$	0	4.0	67.5
Summer nonnative percent cover (not Amur honeysuckle), low stratum	$OELow_{su}$	0	3.9	67.5
Spring nonnative percent cover (not Amur honeysuckle), upper stratum	$OEUp_{sp}$	0	0.9	35.0
Summer nonnative percent cover (not Amur honeysuckle), upper stratum	$OEUp_{su}$	0	1.0	35.0
Native seedlings ha^{-1}	N_{seed}	0	12,923	85,000
Native saplings ha^{-1}	N_{sap}	0	1,286	7,500
Nonnative shrubs ha^{-1} (not Amur honeysuckle)	OE_{sap}	0	184	3,000
Environmental Variables				
Bare soil percent cover, spring	$soil_{sp}$	0	15.6	85.0
Bare soil percent cover, summer	$soil_{su}$	0	16.9	85.0
Coarse woody debris percent cover, spring	CWD_{sp}	0	4.3	62.5
Coarse woody debris percent cover, summer	CWD_{su}	0	4.4	62.5
Fine woody debris percent cover, spring	FWD_{sp}	0	10.0	62.5
Fine woody debris percent cover, summer	FWD_{su}	0	10.3	62.5
Percent cover of dead leaves and herbaceous stems, spring	$litter_{sp}$	0	27.8	85.0
Percent cover of dead leaves and herbaceous stems, summer	$litter_{su}$	0	22.4	85.0
Canopy cover, spring	$canopy_{sp}$	22.8	83.4	93.8
Canopy cover, summer	$canopy_{su}$	75.0	91.0	95.1

dependent variable, we examined the following predictor variables: $NLow_{summer}$, $AhLow_{su}$, $AhUp_{su}$, Ah_{age}, $OELow_{su}$, $OEUp_{su}$, NUp_{su}, $canopy_{su}$, $soil_{su}$, CWD_{su}, FWD_{su}, $litter_{su}$, Ah_{sap}, OE_{sap}, and N_{sap}.

For each model, Ah_{age} was calculated by using a linear mixed effects model to predict the ages of the honeysuckle shrubs from which we collected additional structural information. The model used to determine age was based

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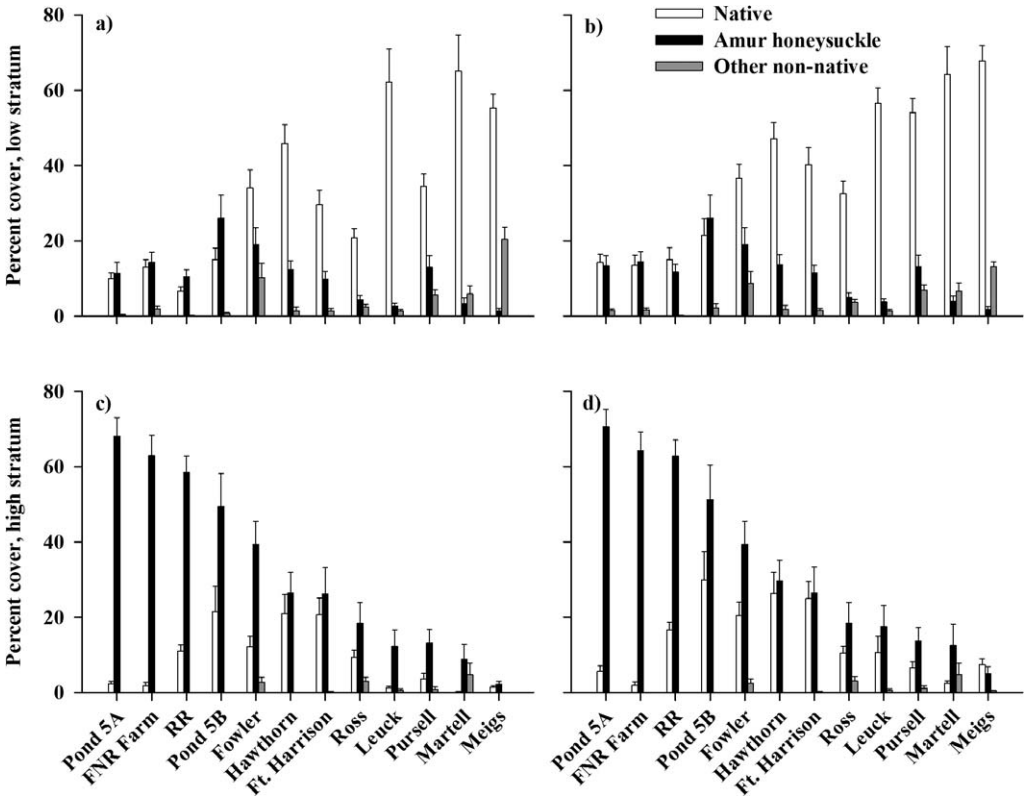


Figure 3. Mean percent cover (± 1 SE) of native plants (species combined as a group), Amur honeysuckle, and other nonnative plants (species combined as a group) in the lower vertical stratum (≤ 1 m) during spring (a) and summer (b), and the upper vertical stratum (1.01 to 5 m) during spring (c) and summer (d) at 12 mixed hardwood forests in central Indiana.

on the minimum ages (age_{min}; age of the oldest basal stem) of Amur honeysuckle shrubs that were measured and destructively sampled at six of the study sites (FNR Farm, Fowler, Hawthorn, Pursell, Ross, RR) in a separate study by Shields et al. (2014). The specific model used to predict minimum age was $age_{min} = 0.12 + 0.04edge + 0.18dia_{burl} + 1.40dia_{stem} + 1.17ht$ + random effects for study sites (n = 442, AIC = 2301.12, $P < 0.001$ for all predictor variables; Shields et al. 2014). The accuracy of the age model was validated by using Spearman's rank correlation coefficient (ρ; Myers and Well 2003) to compare predicted minimum ages to actual minimum ages of 35 destructively sampled Amur honeysuckle cross-sections that were not used to build the model. The resultant ρ of the age model was 0.84 (Shields et al. 2014). All random effects coefficients for the age model were < 2, but for FNR Farm, Fowler, Hawthorn, Pursell, Ross, and RR, we added the study site random effects coefficients when calculating minimum age of Amur honeysuckle. However, for study sites where Amur honeysuckle was not destructively sampled (Ft. Harrison, Leuck, Martell, Meigs, Pond 5A, Pond 5B), only the fixed-effects coefficients from the age model were used.

For the linear mixed effects models with H'_{sp}, S_{sp}, J'_{sp}, $NLow_{sp}$, H'_{su}, S_{su}, J'_{u}, $NLow_{su}$, N_{seed} as dependent variables, we examined data at the plot level, with study site as a random effect. To determine which predictor variables to include in the linear mixed effects model for each dependent variable, we first pooled data across all 12 study sites and developed a full multiple regression model. When necessary, variables were transformed to minimize deviations from normality and constant variance (Zar 1999). Furthermore, a Variance Inflation Factor (VIF) was calculated for each predictor to assess multicollinearity (VIF values ≥ 5 were considered problematic). Using the best subsets regression approach (Miller 1984), we then examined all subsets of the full multiple regression model. We then selected those models with the lowest delta Akaike information criterion (AIC; Akaike 1974) and all significant predictor variables ($P \leq 0.05$) and re-ran the multiple regression model as a linear mixed effects model with study site as the random effect. We observed normality and residual plots to examine distributional assumptions for within-group errors and random effects for each linear mixed effects model.

Statistical analyses were performed using the program R (R Core Team, R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria). Specifically, we used the R package MuMIn (Barton 2013) for best subsets regression and the R package car (Fox and Weisberg 2011) to

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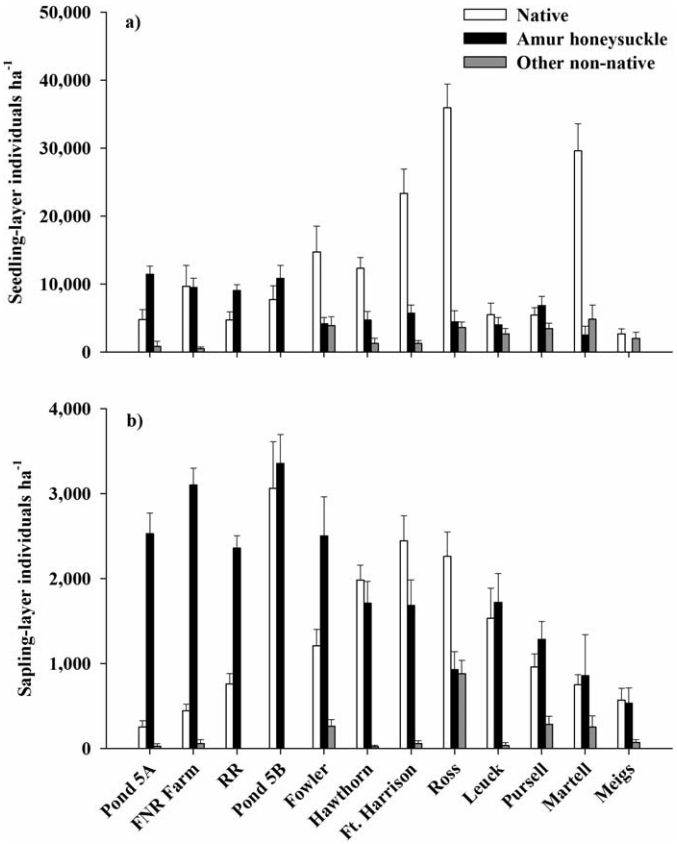


Figure 4. Mean seedling layer density (a) and mean sapling layer density (b) for native woody plants, Amur honeysuckle, and other nonnative woody plants (species combined as a group) at 12 mixed hardwood forests in central Indiana. Seedling layer density included woody individuals < 1.37 m tall and sapling layer density included woody individuals ≥ 1.37 m tall and < 10 cm diameter at breast height (dbh). Error bars are $\pm$ 1 SE.

calculate VIF values. The R package vegan (Oksanen et al. 2013) was used to calculate H′, S, and J′. Linear mixed effects models were built using the R package nlme (Pinheiro et al. 2012). All plant names and native/nonnative classifications were based on the USDA Plants Database (USDA, NRCS 2013).

Results and Discussion

The variation in Amur honeysuckle percent cover, density, and age across study sites reflected our initial site selection criteria. During spring, mean $AhLow_{sp}$ ranged (mean $\pm$ 1 standard error) from 1.4 $\pm$ 0.7 at Meigs to 26.03 $\pm$ 6.1 at Pond 5B (Figure 3). A similar trend was observed in the upper vertical stratum during spring, where the greatest mean $AhUp_{sp}$ was observed at Pond 5A (68.0 $\pm$ 4.9) and the lowest at Meigs (2.2 $\pm$ 0.8; Figure 3). During summer, mean $AhLow_{su}$ was greatest at Pond 5B (26.0 $\pm$ 6.1) and lowest at Meigs (1.7 $\pm$ 0.8; Figure 3).

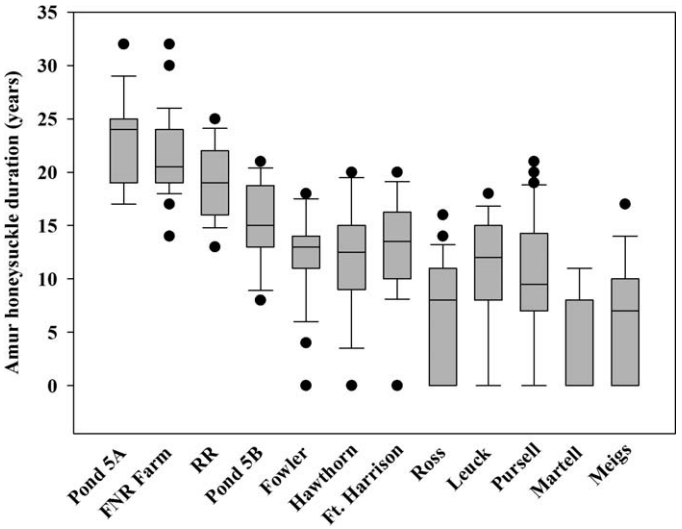


Figure 5. Box plots showing Amur honeysuckle duration of invasion (years) in fixed-area plots at 12 mixed hardwood forests in central Indiana. Sample size (number of plots) for FNR Farm, Fowler, Ft. Harrison, Hawthorn, Leuck, Martell, Meigs, Pond 5A, Pond 5B, Pursell, Ross, and RR were 30, 24, 18, 24, 15, 12, 15, 19, 12, 30, 28, and 27, respectively.

Conversely, greatest mean $AhUp_{su}$ was observed at Pond 5A (70.5 $\pm$ 4.7) and the lowest at Meigs (5.0 $\pm$ 1.8; Figure 3). Ah_{seed} followed a similar pattern as observed for percent cover, where mean density ha^{-1} ranged from 0 (Meigs) to 11,447 $\pm$ 1,167 (Pond 5A; Figure 4). Likewise, mean density ha^{-1} of Ah_{sap} were lowest at Meigs (533 $\pm$ 179) and greatest at Pond 5B (3,354 $\pm$ 340; Figure 4). In terms of age as predicted from the linear mixed effects model, the oldest Amur honeysuckle shrubs (maximum predicted age = 32 years) were observed at FNR Farm and Pond 5A, with the youngest shrubs found at Martell, Meigs, and Ross (Figure 5).

Study sites with the greatest diversity, percent cover, and density of native vegetation also had the lowest percent cover of Amur honeysuckle in the upper vertical stratum (Figure 3, Figure 6). At the plot level, percent cover of Amur honeysuckle in the upper vertical stratum was consistently negatively correlated with native H′, native S, and total native percent cover during the spring and summer, as well as N_{seed} (linear mixed effects models $P < 0.05$; Table 2). Environmental variables such as percent cover of bare soil and FWD were also important, but this varied depending on the response variable (Table 2). For example, bare soil was an important predictor of five response variables: H'_{su}, S_{su}, J'_{su}, $NLow_{sp}$, and $NLow_{sp}$ (Table 2). FWD was an important predictor of H'_{sp}, J'_{sp}, and $NLow_{sp}$, whereas CWD was only an important predictor of $NLow_{su}$ (Table 2). Ah_{age}, when measured at the plot level, was negatively correlated ($P \leq 0.05$) with native H′, S, and total native percent cover in spring and

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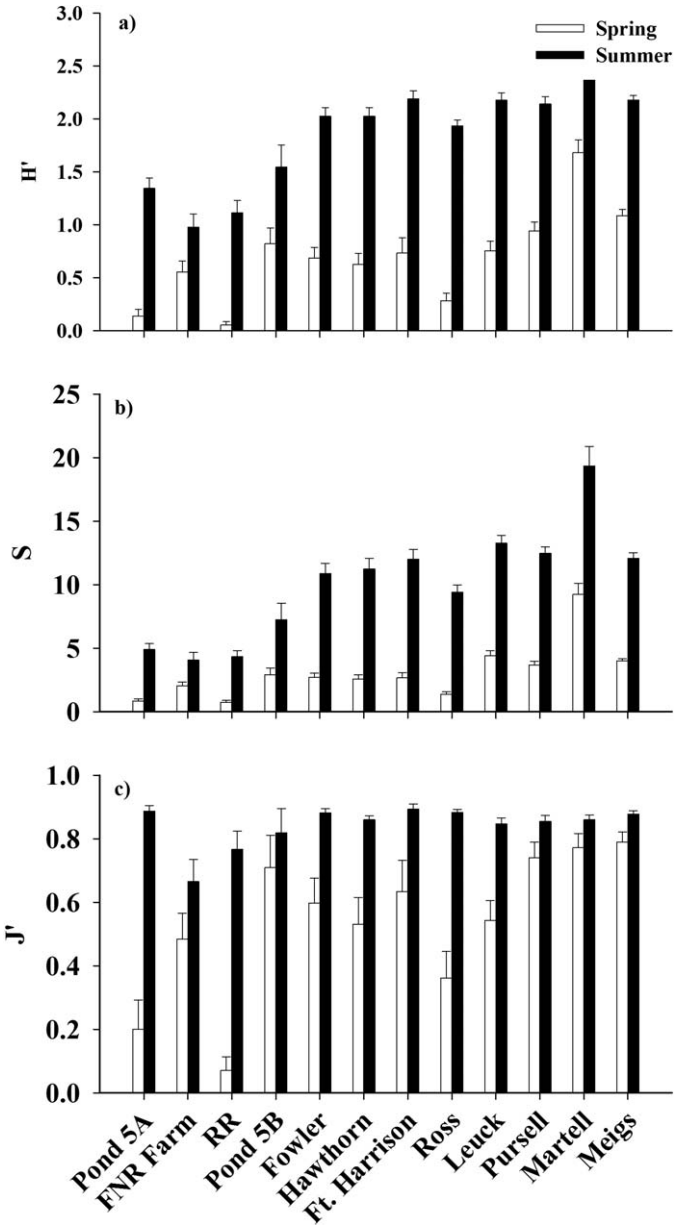


Figure 6. Mean Shannon's Diversity Index (H′) (a), mean taxonomic richness (S) (b), and mean Pielou's Evenness Index (J′) (c) during the spring and summer at 12 mixed hardwood forests in central Indiana. For spring, indices were based on percent cover of native herbaceous plants that flower from March-June. For summer, indices were based on percent cover of all native herbaceous and woody taxa. Error bars are ± 1 SE.

summer, as well as N_{seed}. However, Ah_{age} did not significantly contribute to regression models when the percent cover of Amur honeysuckle in the upper vertical stratum was also included as a predictor variable (Table 2, Table 3). Ah_{age} was positively correlated with percent cover of Amur honeysuckle in the upper stratum during both spring and summer (Table 3).

In the lower vertical stratum, we observed 92 native forb taxa, eight native grass taxa, four native sedge taxa, five native fern taxa, 10 native vine taxa, 48 native tree/shrub taxa, 12 nonnative forb species, one nonnative grass species, five nonnative vine species, and six nonnative shrub species in quadrats across all study sites and both seasons. Across all study sites and seasons, environmental variables such as dead leaves/dead herbaceous stems, bare soil, and FWD had the greatest Importance Value (IV). Herbaceous/vine taxa with the greatest IV during spring were sanicle (*Sanicula* spp.), Virginia creeper [*Parthenocissus quinquefolia* (L.) Planch.], and Virginia springbeauty (*Claytonia virginica* L.). During summer, herbaceous/vine taxa with the greatest IV in the lower vertical stratum were sanicle, Virginia creeper, and jumpseed (*Polygonum virginianum* L.). In terms of IV based on seedling layer density, the most important woody taxa in the seedling layer across study sites were Amur honeysuckle, white ash/green ash (*Fraxinus americana* L./*Fraxinus pennsylvanica* Marsh.), and multiflora rose (*Rosa multiflora* Thunb.). In the sapling/shrub plots, we observed 46 native sapling/shrub taxa and eight nonnative sapling/shrub taxa; taxa with the greatest IV across study sites were Amur honeysuckle, sugar maple (*Acer saccharum*), and hawthorn (*Crataegus* spp.).

In our study, it appears that microsite-level diversity and abundance of native vegetation in mixed hardwood forests is largely driven by competition from above due to percent cover of Amur honeysuckle canopies, supporting our hypothesis that native diversity and abundance would be lowest at microsites with the greatest percent cover of Amur honeysuckle. Differences in percent cover of Amur honeysuckle in the upper vertical stratum within a study site translated to differences in plant diversity and abundance across the gradient of Amur honeysuckle dominance in the invading population. This was likely due to decreased light levels near the forest floor at heavily infested microsites, resulting in little available light for native herbaceous vegetation, vines, and seedlings to germinate and grow. Another possible contributing factor is that microsites with a greater percent cover of Amur honeysuckle may contain greater amounts of honeysuckle foliage containing allelochemicals (McEwan et al. 2010), which could impede the germination and growth of native ground-layer taxa. The effects of honeysuckle allelopathy have not been directly examined in a field study, but the possibility of this phenomenon warrants further investigation.

While we predicted that the effect of Amur honeysuckle cover would be more pronounced for spring-flowering herbaceous plants as compared to summer-flowering herbaceous plants, the spring linear mixed effects models contained different predictor variables than summer linear mixed effects models so were therefore not directly comparable. However, when holding all other predictor variables constant and accounting for the random effect of

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Table 2. Linear mixed-effects models, random effects coefficients by study site, and Akaike information criterion (AIC) for nine dependent variables (spring Shannon's Diversity Index for native ground flora [H'_{sp}], spring taxonomic richness for native ground flora [S_{sp}], spring Pielou's Evenness Index for native ground flora [J'_{sp}], spring native percent cover in the lower vertical stratum [species combined as a group; $NLow_{sp}$], summer H′ [H'_{su}], summer S [S_{su}], summer J′ [J'_{su}], summer native percent cover in the lower vertical stratum [species combined as a group; $NLow_{su}$], and native seedlings ha^{-1} [species combined as a group; N_{seed}]) at 12 mixed hardwood forests in central Indiana. Significant ($P \leq 0.05$) predictor variables included spring percent cover of Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder] in the upper vertical stratum ($AhUp_{sp}$), spring canopy cover (based on densiometer; $canopy_{sp}$), spring percent cover of bare soil ($soil_{sp}$), spring percent cover of FWD (FWD_{sp}), Amur honeysuckle saplings ha^{-1} (Ah_{sap}), summer percent cover of Amur honeysuckle in the lower vertical stratum ($AhLow_{su}$), summer percent cover of Amur honeysuckle in the upper vertical stratum ($AhUp_{su}$), summer canopy cover (based on densiometer; $canopy_{su}$), summer percent cover of bare soil ($soil_{su}$), summer percent cover of CWD (CWD_{su}). Values were calculated for each nested plot within a study site, with study site treated as a random effect. Sample size (number of plots) for FNR Farm, Fowler, Ft. Harrison, Hawthorn, Leuck, Martell, Meigs, Pond 5A, Pond 5B, Pursell, Ross, and RR were 30, 24, 18, 24, 15, 12, 15, 19, 12, 30, 28, and 27, respectively.

	Random effects coefficients											
Model	FNR Farm	Fowler	Ft. Harrison	Hawthorn	Leuck	Martell	Meigs	Pond 5A	Pond 5B	Pursell	Ross	RR	AIC
$H'_{sp} = 0.90 - 0.01FWD_{sp} - 0.005AhUp_{sp}$ + random effects													346.6
	−0.007	0.005	−0.007	−0.09	−0.03	0.78	0.20	−0.29	0.24	0.14	−0.47	−0.48	
$S_{sp} = 3.61 - 0.02AhUp_{sp}$ + random effects													962.3
	−0.55	−0.25	−0.50	−0.58	0.96	5.55	0.41	−1.62	0.10	0.27	−1.90	−1.88	
$J'_{sp} = 0.66 - 0.004FWD_{sp} - 0.003AhUp_{sp}$ + random effects													240.1
	0.02	0.06	0.06	−0.02	−0.03	0.13	0.12	−0.14	0.20	0.13	−0.19	−0.33	
$H'_{su} = 2.14 - 0.006AhUp_{su} - 0.006soil_{su}$ + random effects													336.7
	−0.52	0.17	0.25	0.09	0.15	0.38	0.08	−0.13	−0.09	0.14	−0.07	−0.45	
$S_{su} = 12.37 - 0.05AhUp_{su} - 0.03soil_{su}$ + random effects													1325.3
	−3.65	0.88	1.33	0.60	1.86	7.14	0.08	−2.43	−1.34	1.15	−1.84	−3.78	
$J'_{su} = 0.88 - 0.003soil_{su}$ + random effects													−113.6
	−0.08	0.02	0.02	−0.002	−0.01	−0.005	0.005	0.06	0.01	0.004	0.01	−0.03	
$(NLow_{sp} + 0.5)^{0.5} = 8.39 - 0.03canopy_{sp} - 0.02AhUp_{sp} - 0.02FWD_{sp} - 0.01soil_{sp}$ + random effects													968.9
	−0.95	0.44	−0.09	1.17	0.91	1.46	0.67	−0.54	−0.45	0.13	−1.10	−1.66	
$NLow_{su} = 183.74 - 1.45canopy_{su} - 0.21AhUp_{su} - 0.18CWD_{su} - 0.12soil_{su} - 0.002Ah_{sap}$ + random effects													2156.1
	−11.81	0.66	−1.07	7.20	7.68	17.70	12.22	−9.47	−5.77	7.88	−12.72	−12.51	
$(N_{seed} + 0.5)^{0.5} = -47.17^{*} - 1.86canopy_{su} - 0.69AhUp_{su} - 0.57AhLow_{su}$ + random effects													2738.8
	3.46	5.44	46.51	6.93	−41.46	46.76	−66.16	−16.08	4.64	−42.56	74.60	−22.07	

*Intercept was not significant ($P = 0.58$)

Table 3. Linear mixed-effects models (study site = random effect), *p* values, and Akaike information criterion (AIC) for models comparing native plant diversity and abundance measures to Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder] age (Ah_{age}), as well as spring ($AhUp_{sp}$) and summer ($AhUp_{su}$) percent cover of Amur honeysuckle in the upper vertical stratum (1.01 to 5 m) to Ah_{age}, at 12 mixed hardwood forests in central Indiana. Diversity and abundance measures included spring Shannon's Diversity Index for native ground flora (H'_{sp}), spring taxonomic richness for native ground flora (S_{sp}), spring Pielou's Evenness Index for native ground flora (J'_{sp}), spring native percent cover in the lower vertical stratum (species combined as a group; $NLow_{sp}$), summer H′ (H'_{su}), summer S (S_{su}), summer J′ (J'_{su}), summer native percent cover in the lower vertical stratum (species combined as a group; $NLow_{su}$), and native seedlings ha^{-1} (species combined as a group; N_{seed}).

Model	P	AIC
$H'_{sp} = 0.84 - 0.01Ah_{age}$ + random effects	0.04	347.6
$S_{sp} = 3.60 - 0.04Ah_{age}$ + random effects	0.04	973.5
$J'_{sp} = 0.63 - 0.008Ah_{age}$ + random effects	0.07	233.5
$(NLow_{sp} + 0.5)^{0.5} = 5.96 - 0.06Ah_{age}$ + random effects	< 0.01	985.6
$AhUp_{sp} = 0.08 + 2.54Ah_{age}$ + random effects	< 0.01	2326.6
$H'_{su} = 2.02 - 0.01Ah_{age}$ + random effects	0.02	368.3
$S_{su} = 11.16 - 0.09Ah_{age}$ + random effects	0.04	1370.5
$J'_{su} = 0.88 - 0.004Ah_{age}$ + random effects	0.07	−104.5
$NLow_{su} = 47.10 - 0.68Ah_{age}$ + random effects	< 0.01	2217.3
$AhUp_{su} = 0.92 + 2.64Ah_{age}$ + random effects	< 0.01	2327.3
$(N_{seed} + 0.5)^{0.5} = 116.51 - 1.99Ah_{age}$ + random effects	< 0.01	2760.9

study site, increasing AhUp results in a similar change in herbaceous diversity and richness. For example, at Meigs (the site with the lowest Amur honeysuckle sapling density), if FWD is held constant at 20% in the spring and soil is held constant at 20% in the summer, increasing AhUP from 50% to 80% decreases H'_{sp} from 0.65 to 0.50 (change = −0.15) and decreases H'_{su} from 1.8 to 1.62 (change = −0.18), based on linear mixed effects models. Likewise, at Pond 5B (the site with the greatest Amur honeysuckle sapling density), if FWD is held constant at 20% in the spring and soil is held constant at 20% in the summer, increasing AhUP from 50% to 80% decreases H'_{sp} from 0.69 to 0.54 (change = −0.15) and decreases H'_{su} from 1.63 to 1.45 (change = −0.18), based on linear mixed effects models. It is important to note that such changes may still have a more pronounced effect on spring ephemerals given that diversity and richness of spring-flowering herbaceous plants were consistently lower in spring than summer at all study sites (Figure 6; Table 1).

The influence of competition from Amur honeysuckle canopies is further supported by work from Shields et al. (unpublished data), who found that removing 80-m by 80-m areas of Amur honeysuckle and other nonnative shrubs at FNR Farm, Fowler, Hawthorn, Pursell, Ross, and RR resulted in subsequent significant increases in native plant diversity. Several other studies have documented a negative effect of Amur honeysuckle on ground-layer vegetation. For example, Gorchov and Trisel (2003) found that competition with Amur honeysuckle led to increased mortality of native tree seedlings in an American beech (*Fagus grandifolia* Ehrh.)-sugar maple forest in Ohio. Likewise, Collier et al. (2002) found that species richness, percent cover of herbaceous and woody species, and tree seedling density were lower below the crowns of Amur honeysuckle compared to away from the crowns of Amur honeysuckle. Unlike previous investigators, we examined microsite-level differences in native plant diversity and abundance across a gradient of Amur honeysuckle percent cover within a forest and across multiple forests. To our knowledge, we are the first to demonstrate that changes in native taxa diversity and abundance in response to Amur honeysuckle invasion intensity and duration of invasion are heterogeneous within an invaded community.

When percent cover of Amur honeysuckle in the high vertical stratum was included in the linear mixed effects models, Ah_{age} was not important, which does not support our original hypothesis that duration of invasion would be a significant predictor, at least not standalone (Tables 2 and 3). However, it is important to note that we also found significant negative correlations between the duration of Amur honeysuckle presence and measures of native diversity and abundance, as well as between duration of invasion and percent cover of Amur honeysuckle in the upper vertical stratum (Table 3). It is important to note that while Ah_{age} and percent cover of Amur honeysuckle in the high vertical stratum were correlated, VIF was consistently < 5 when Ah_{age} was included with AhU_{sp} or AhU_{su} in models. Thus, it appears that Amur honeysuckle duration of invasion at the microsite scale is important inasmuch that, at microsites where Amur honeysuckle has persisted longer, light competition from above is more intense for native-ground layer species. This is likely because older Amur honeysuckle shrubs may have larger, more

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developed crowns that induce more light competition from above or because longer duration of invasion equates to more sub-canopy growing space being filled due to the coalescing of the crowns from multiple shrubs as invasion progresses from establishment to saturation phases. It is widely acknowledged that plant invasions reaching the expansion and saturation phases at the landscape scale incur greater ecological and economic costs, especially in terms of control efforts (Sakai et al. 2001; Webster et al. 2006). However, to our knowledge we are the first investigators to examine the combined influence of invasive species duration and other environmental factors on native vegetation at the local scale within forests. From a management standpoint, information about microsite-level differences in diversity and abundance within an invaded area may help managers better prioritize control efforts. In particular, some sites may contain existing sources of native propagules at microsites where Amur honeysuckle invasion is less intense; information about microsite-level diversity and abundance may therefore be critical to the long-term recovery of native communities after control efforts are implemented.

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