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# Relationships between *Ligustrum sinense* Invasion, Biodiversity, and Development in a Mixed Bottomland Forest

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Invasion of closed canopy forests by shade-tolerant alien plants has the potential to modify species composition, stand structure, ecosystem function, and long-term forest development patterns. *Ligustrum sinense* is a shade-tolerant alien shrub that has invaded bottomland forests throughout the southeastern United States. This species has received comparatively little attention in the literature despite its potential to drastically alter invaded sites. The overarching goal of our study was to document the relationships between *Ligustrum sinense* invasion and woody plant biodiversity and development patterns in an intact southeastern U.S. bottomland forest. The forest was dominated by *Quercus nigra* and *Liquidambar styraciflua. Ligustrum sinense* ranked fifth in basal area contribution, occurred in 97% of our plots, and represented 95% of all understory stems. Spearman's rho for dominance (based on basal area of stems $> 5$ cm diameter at breast height [dbh]) of *L. sinense* and woody plant species richness for each plot revealed a significant negative relationship ($r_s = -0.69$, $P < 0.01$). A similar relationship was revealed between *L. sinense* density and woody plant species diversity ($r_s = -0.78$, $P < 0.01$) and evenness ($r_s = -0.82$, $P < 0.01$). Spearman's rho for *L. sinense* density and native understory stem density (individuals $\geq 1$ m height, $< 5$ cm dbh) also revealed a significant negative association ($r_s = -0.48$, $P < 0.01$). Under the current disturbance regime and without active management, we projected the forest would shift to support a stronger component of *L. sinense* and that structure would transition from tree to shrub dominance for sites within the forest.

**Nomenclature:** Chinese privet, *Ligustrum sinense* Lour; sweetgum, *Liquidambar styraciflua* L.; water oak, *Quercus nigra* L.

**Key words:** Alien shrub, biodiversity, bottomland forest, forest development, shade-tolerant, southeastern United States.

In traditional invasion ecology theory, intact forests have been hypothesized to be resistant to alien plant invasion (Crawley 1987; Elton 1958; Von Holle et al. 2003). This hypothesis is based on the assumption that competition from resident plant communities is a strong control on invasion success (Levine 2000; Levine et al. 2004; Seabloom et al. 2003). Thus, undisturbed forests (i.e., those with closed canopy conditions) should have low invasibility, especially undisturbed forests with high plant diversity (Kennedy et al. 2002). Without question, a major focus in invasion ecology research has been the facilitative role of disturbance on alien plant establishment and recruitment (Lozon and MacIsaac 1997; Rejmánek 1989). Indeed, common traits of successful alien plant invaders have been summarized by multiple authors (e.g., Bazzaz 1986; Reichard and Hamilton 1997; Rejmánek and Richardson 1996) and the traits listed are often characteristic of early successional and often disturbance-obligate species (i.e., *r*-selection species). However, undisturbed closed canopy forests are not immune to alien plant invasions (Martin et al. 2009).

The vast majority of intentionally introduced plant species are shade-intolerant (Martin et al. 2009) because available light is the major limiting factor in closed canopy systems (Oliver and Larson 1996), the invasion of undisturbed forests by these species is dependent on disturbances that create gaps in the forest canopy. Even highly localized canopy disturbance events (such as the death of a single canopy tree) can provide a mechanism for alien plant invasion of forested sites. In the eastern United States for example, the shade-intolerant tree-of-heaven [*Ailanthus altissima* (Mill.) Swingle] has been shown to establish in forest interior locations through gap-phase

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## Management Implications

Invasion of *Ligustrum sinense* on bottomland sites may inhibit forest regeneration and shift structure of invaded stands from tree to shrub dominance. Scatterplots of *L. sinense* density and woody plant diversity measures revealed that 0.05-ha plots with greater than ca. 200 *L. sinense* stems (4,000 stems $ha^{-1}$) had relatively low evenness and Shannon diversity values. Although low biodiversity might not be the result of *L. sinense* invasion, if abiotic conditions of invaded sites are similar to nearby sites with higher biodiversity, then such severely invaded sites may be prioritized for *L. sinense* control. Restoration efforts might be best if focused on sites with mature *L. sinense* stems that have ascended to the uppermost forest stratum and lack the multi-stemmed growth form common for the species in smaller size classes. These areas may be those considered most impacted by *L. sinense* establishment and may be considered priority restoration areas by managers. Based on the potential density of *L. sinense* stems, even relatively small invaded forests might need to be compartmentalized by field crews.

processes (Hart and Grissino-Mayer 2008; Knapp and Canham 2000). Although the number of intentionally introduced plants that are shade-tolerant is much smaller than those that are shade-intolerant, many of these species are disturbance facultative and have the ability to colonize closed-canopy forests (Martin et al. 2009). Forest invasion by shade-tolerant alien plants has the potential to drastically modify species composition, stand structure, and ecosystem function (Pimental et al. 2000; Powell et al. 2011; Vila et al. 2011). These invasions can also have long-term consequences on forest development and succession (Gorchov and Trisel 2003; Reinhart et al. 2005). Shade-tolerant trees, shrubs, and grasses, such as Norway maple (*Acer platanoides* L.), Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder], and Nepalese browntop [*Microstegium vimineum* (Trin.) A. Camus], have the potential to drastically modify forest ecosystems in the eastern United States. One notable shade-tolerant alien shrub in bottomland forests of the southeastern United States is Chinese privet (*Ligustrum sinense* Lour.). Invasion by this species has been shown to have a negative relationship with herb and shrub layer diversity and native tree seedling density in some forests of the region (Kittell 2001; Merriam and Feil 2003; Wilcox and Beck 2007).

*Ligustrum sinense* is a semievergreen to evergreen shrub or small tree that can reach ca. 9 m height and is often multistemmed (Miller 2003). The species is native to China, Laos, and Vietnam and was first introduced into the United States in 1852 as an ornamental (Merriam and Feil 2003). The species is now naturalized in the United States where its range extends along the Atlantic Coast from Massachusetts to Florida and westward to Texas, Oklahoma, and Missouri (USDA NRCS 2012a). *Ligustrum sinense* is a prolific seed producer; mature plants can produce on average 1,300 fruits $m^{-2}$ of canopy, typically with one seed per fruiting body (Westoby et al. 1983). Fruits are common on larger plants (e.g., plants $\geq$ 5 m height), but fruit can also occur on plants as small as 1 m height (Grove and Clarkson 2005). Germination rates are ca. 40%, and seeds can germinate under a variety of environmental conditions (Panetta 2000). The seeds are readily dispersed by birds and do not require the removal of berry flesh for germination (Panetta 2000). The species is capable of clonal growth and it commonly produces basal and root sprouts (Nesom 2009; Swarbrick, Timmins, and Bullen 1999). *Ligustrum sinense* has a low light compensation point and readily invades closed canopy forests (Hanula et al. 2009; Miller 2003; Morris et al. 2002; Ward 2002); thus, the species is an excellent model to provide information on the potential effects of forest invasion by shade-tolerant alien shrubs.

Richardson and Rejmánek (2011) created a global list of invasive trees and shrubs and noted that the importance of woody plant invasions is rapidly increasing worldwide. They also provided a list of research priorities, such as a focus on invasion dynamics and mapping and assessing potential impacts (Richardson and Rejmánek 2011). Relatively few studies have analyzed the ecological consequences of *L. sinense* invasion in bottomland forests of the southeastern United States, and fewer still have analyzed the potential ecological consequences of *L. sinense* invasion on biodiversity and forest development along an invasion gradient. The paucity of quantitative data is surprising, based on the attention recently given to the role of shade-tolerant alien invaders (Martin et al. 2009), the spatial extent of the *L. sinense* invasion in the southeastern United States (USDA NRCS 2012a), the level of invasion in many forests (i.e., high relative densities), and the potential ecological impacts. A relatively small foundation of *L. sinense* invasion literature is available for the southeastern United States (e.g., Brantley 2008; Hanula and Horn 2011; Kittell 2001; Merriam and Feil 2003; Mitchell et al. 2011; Morris et al. 2002; Wilcox and Beck 2007), but additional quantitative data are needed to document the potential impacts of invasion in this region (Boyce 2010). Our specific objectives were to: (1) quantify forest composition and stand structural attributes for a southern U.S. bottomland forest invaded by *L. sinense*, (2) examine the relationships between *L. sinense* invasion intensity as measured by density (stems $plot^{-1}$) and dominance (basal area contribution $plot^{-1}$) and biodiversity measures for the woody plant assemblage, and (3) project the development and successional trajectory of the forest under the current disturbance regime based on forest composition and structure data.

## Methods

**Study Site.** Our study was conducted in Sokol Park in west-central Alabama (33°16′09″N, 87°31′58″W). The 132 ha (326 ac) periurban park is managed by the



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Tuscaloosa County (Alabama) Parks and Recreation Authority. Sokol Park is located within the City of Tuscaloosa, which has a metropolitan population of ca. 200,000 (U.S. Census 2010). The park was formally established in 1979 when the property was donated to the County of Tuscaloosa from private ownership. In the early 1900s the property was intensively used for row cropping and grazing, and in 1949 the property was purchased by Morris Sokol. At that time, land-use intensity decreased and fields succeeded to forest. Since park establishment, land uses have been restricted to recreation. Our study was specifically focused within a ca. 50 ha forest in the eastern section of the park.

Sokol Park occurs in the Fall Line Hills (Fenneman 1938). The Fall Line separates the Appalachian Highlands and the Interior Low Plateau from the Gulf and Atlantic Coastal Plains. The Fall Line Hills represent a transitional zone where streams have eroded through Coastal Plain sediments to expose previously underlain Appalachian formations (Fenneman 1938; Shankman and Hart 2007). The topography of the region is described as moderately hilly, and most streams have wide, level terraces (Harper 1943). Our study plots occurred across the Smithdale-Flomaton soil complex and the Smithdale fine sandy loam (USDA NRCS 2012b). The Smithdale-Flomaton complex consists of small areas of Smithdale and Flomaton soils intermixed to the extent that they are not mapped separately at a scale of 1 : 20,000. Approximately 45% of each area mapped as the Smithdale-Flomaton complex is comprised of Smithdale fine sandy loam and approximately 20% is the Flomaton very gravelly loamy sand (USDA SCS 1981). Both soil series are low in fertility and organic matter content, are acidic, and are well drained.

The climate of this region is classified as humid mesothermal with long, moderately hot summers and short, mild winters (Thornthwaite 1948). The annual average temperature is 17 C with a January average of 7 C and a July average of 27 C (US NCDC 2012). The region typically has no distinct wet or dry season and prolonged periods of water deficit are rare (USDA SCS 1981). Mean annual precipitation is 134 cm (PRISM Climate Group 2012). Mean precipitation during the wettest month (March) is 15 cm, and during the driest month (October) is 8 cm (PRISM Climate Group 2012). Thunderstorms with intense periods of rainfall and sometimes hail occur ca. 60 d $yr^{-1}$ and are most common in summer. Average annual snowfall is less than 2.5 cm and accumulation is rare (USDA SCS 1981).

The study site occurs in the oak-pine (*Quercus–Pinus*) transitional region between the Central Hardwood Forest to the north and the Southern Evergreen Forest to the south. The Fall Line marks the southern range boundaries for some Appalachian tree species, as well as the northern range limits for some Coastal Plain tree species (Shankman and Hart, 2007). Harper (1943) classified the region as part of the shortleaf pine (*Pinus echinata* Mill.) belt, which is characterized by mixed stands of *Quercus* spp. and *P. echinata* on upland sites, and swamp hardwood stands in alluvial and nonalluvial valleys. Our study plots all occurred in alluvial valleys.

**Field Methods.** To examine relationships between *L. sinense* invasion, biodiversity, and forest development, we subjectively established 30, 0.05-ha fixed-radius plots (r = 12.7 m) across the study site to represent a range of *L. sinense* densities (Figure 1). In locating plots, we avoided trails, forest edges, areas of possible *L. sinense* removal (i.e., control efforts), and locations of recent canopy disturbance based on visual observation (e.g., closed forest canopy without gaps and devoid of gapmaker trees or large fallen branches). One goal was to document forest conditions across a range of *L. sinense* densities (including plots free of *L. sinense*) and we attempted to hold other biophysical variables, such as moisture availability and canopy cover, relatively constant. To this end, we concentrated our plots within a 50-ha area and the greatest distance between two plots was ca. 400 m. We acknowledge that physical site conditions varied across our plots, but we contend that the density of *L. sinense* (i.e., the degree of invasion) was the major difference between study plots. Slope angle ranged from 0 to 20% with a mean of 4% ± 1 (SE). Elevation ranged from 78 to 105 m above mean sea level (amsl) with a mean of 95 m ± 2 (SE). Based on field observations, we are confident that our sampling captured site heterogeneity such that our results provide information on the general conditions of the mixed bottomland forest.

To quantify forest species composition and structural characteristics, we documented crown class and diameter at breast height (dbh, ca. 1.4 m above the root collar) of all stems ≥ 5 cm dbh (hereafter referred to as the overstory). Crown class categories (dominant, codominant, intermediate, and overtopped) were based on the amount and direction of intercepted light, vertical position, and crown crowding (Oliver and Larson 1996). Dominant individuals occupied positions in the uppermost forest stratum for their spatial location and had crowns that expanded laterally. Codominant individuals occupied positions in the uppermost forest stratum for their spatial location, but had crowded crowns. Intermediate individuals were those that were not directly overtopped, but were not in the uppermost forest stratum for their location. Overtopped stems were directly beneath a closed forest canopy. Based on these crown classifications, shrubs such as *L. sinense* could be considered dominant without reaching typical canopy tree height. To quantify the understory layer, we tallied all stems ≥ 1 m height and < 5 cm dbh by species. Multistemmed individuals were counted as one individual if the stems separated above ground, and as multiple



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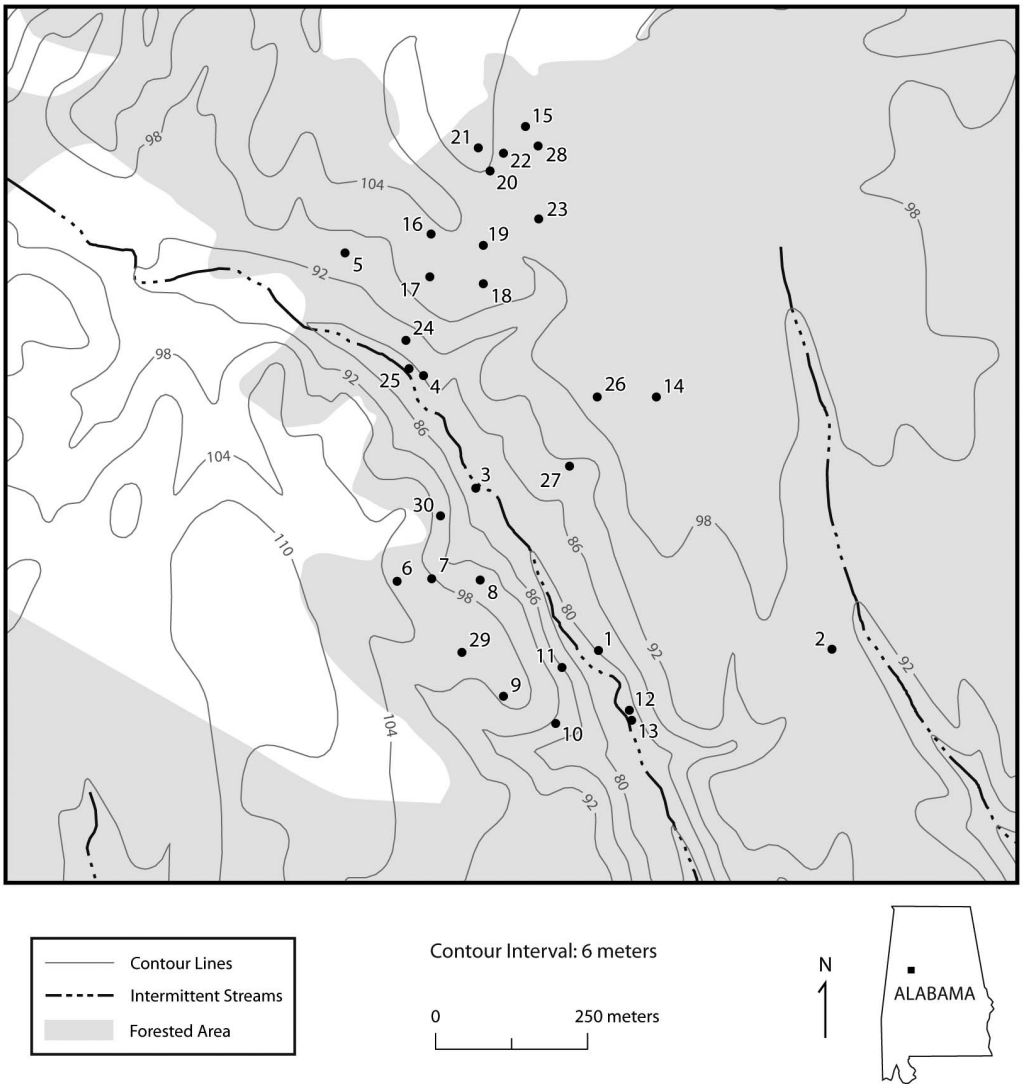



Figure 1. Map of the study area in Sokol Park, Tuscaloosa, AL. Plots are shown to within 3 m of absolute locations. Area of detail is shown on the Alabama inset map.

individuals if the stems separated below ground (i.e., the connection between shoots was not visible). The coordinate pair of each plot center was recorded with a handheld global positioning system (GPS) receiver (< 3 m accuracy). Canopy cover for each plot was measured using a densiometer at 5 m from plot center in each cardinal direction. Densiometer measures were converted to percentages and averaged by plot to determine percentage canopy cover. Canopy cover ranged from 85 to 99% with a mean of 95% ± 1 (SE).

**Analytical Methods.** Overstory and understory vegetation layers were analyzed using standard descriptors. For overstory stems we calculated density (number of stems $ha^{-1}$), relative density (contribution to total stems), dominance (basal area [$m^2$] $ha^{-1}$), relative dominance (contribution to total basal area), and relative importance (average of relative density and relative dominance) of each species. The understory was characterized by frequency (number of plots on which the species occurred), relative frequency (percentage of plots on which the species occurred), density, relative density, and relative importance (average of relative frequency and relative density). Species richness, Shannon diversity ($H'$), and species evenness ($J$; Ludwig and Reynolds, 1988) were calculated for the overstory stratum, the understory stratum, and for both layers collectively at the plot and forest levels. Size structure was analyzed across five taxonomic categories based on relative importance values (*L. sinense*, sweetgum [*Liquidambar styraciflua* L.], water oak [*Quercus nigra* L.], loblolly pine [*Pinus taeda* L.], and other species present) using diameter class distributions. Individuals were categorized



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and tallied into 5-cm-diam classes (Nyland 2007). Crown class distributions were also examined across the same taxonomic categories to analyze vertical forest structure. Projections of forest development and successional trends were based on these measures.

To document the relationships between *L. sinense* invasion and woody plant biodiversity, we analyzed species richness, Shannon diversity, and species evenness against *L. sinense* density and dominance using Spearman's correlation on a per plot basis. We used Spearman's correlation because scatterplots revealed that these relationships were not linear. Spearman's correlation was also used to examine the associations between native sapling density (stems $\geq$ 1 m height, $<$ 5 cm dbh) and *L. sinense* density. Native tree establishment was also examined via analysis of forest composition and stand structure data. All statistical tests were performed using SAS v. 9.2.

## Results

Total documented woody species richness for all plots combined was 39 (Table 1). *Ligustrum sinense* was the only alien woody plant documented in our study plots. Density of overstory stems ($\geq$ 5 cm dbh) was 1,009 ha$^{-1}$ and the basal area for such stems was 30.36 m$^2$ ha$^{-1}$. The two most dominant overstory species based on basal area were *Quercus nigra* and *Liquidambar styraciflua* (Table 2). Collectively, these species comprised 49% of the total basal area. These species were followed by *Pinus taeda*, tulip-poplar [*Liriodendron tulipifera* L.], and *L. sinense*. The most abundant overstory species was *L. sinense*, which represented 36% of overstory stems. This species was followed by *L. styraciflua*, *Q. nigra*, *P. taeda*, and black cherry [*Prunus serotina* Ehrh]. The most important species (based on relative density and dominance) was *L. styraciflua* and the second most important species was *L. sinense*.

*Ligustrum sinense* occurred in 97% of our plots and represented 95% of all understory stems (Table 3). As a result, the relative importance value (based on relative frequency and relative density) for the species was 96%. Mean density of *L. sinense* across our study plots was 372 stems 0.05 ha$^{-1}$ $\pm$ 51 (SE) with a minimum and maximum of 0 and 1,214 stems ha$^{-1}$, respectively. The second most frequently encountered species on our plots was *L. styraciflua*. This species was also the second most abundant in the understory stratum, but only accounted for 2% of all woody stems. No other understory species comprised more than 1% of the understory stem density of 7,429 ha$^{-1}$.

Table 1. Diversity, structural, and compositional measures of all stems $\geq$ 1 m height (total), stems $\geq$ 5 cm diameter at breast height (dbh) (overstory), and stems $\geq$ 1 m height, $<$ 5 cm dbh (understory) in a southeastern U.S. bottomland forest.

| Parameter | Total | Overstory | Understory |
|---|---|---|---|
| Richness (*S*) | 39 | 35 | 26 |
| Diversity (*H*′) | 0.63 | 2.01 | 0.29 |
| Evenness (*J*) | 0.17 | 0.56 | 0.09 |
| Density (stems ha$^{-1}$) | 8,438 | 1,009 | 7,429 |
| Basal area (m$^2$ ha$^{-1}$) | — | 30.36 | — |

The diameter structure of all overstory stems (i.e., all stems $\geq$ 5 cm dbh) in the forest revealed an inverse J-shaped distribution from small size classes to large size classes (Figure 2). When species were grouped into the five taxonomic categories, establishment and recruitment patterns were apparent. For *L. sinense* and *L. styraciflua*, the number of individuals declined with increased size, indicative of continuous regeneration. We documented 41 overstory *L. sinense* stems ha$^{-1}$ and 90 overstory *L. styraciflua* stems ha$^{-1}$. The "others" category also exhibited this diameter structure, but density in the smaller size classes was lower than for the two abovementioned species. *Quercus nigra* and *P. taeda* exhibited uniform distributions. Notably, *P. taeda* was absent from the smallest and largest size classes. No single species occurred in all size classes. Stems of the "others" category occurred in all diameter classes. Species from this category that occurred in the largest size classes included southern red oak (*Quercus falcata* Michx.), *L. tulipifera*, black walnut (*Juglans nigra* L.), and white oak (*Quercus alba* L.). The smaller size classes of this category were largely comprised of red maple (*Acer rubrum* L.), blackgum (*Nyssa sylvatica* Marsh.) and *P. serotina*.

The mean diameter of overstory stems in the forest was 15 cm, the mean diameter of canopy stems (those with dominant or codominant crown classes) was 28 cm, and the largest tree documented was a *Q. falcata* at 116 cm dbh. Mean diameter for *Ligustrum sinense* overstory stems was 8 cm. The largest *L. sinense* stem documented was 24 cm dbh; thus, the species was absent from the large size classes. Mean diameter for *L. sinense* stems with dominant or codominant positions in the forest canopy was 13 cm. Mean diameter for overstory *L. styraciflua* was 15 cm, for overstory *Q. nigra* was 34 cm, and for *P. taeda* was 35 cm.

The majority of overstory stems in the forest were overtopped (465 ha$^{-1}$). We documented 89 individuals ha$^{-1}$ with canopy dominant positions and 203 trees ha$^{-1}$ with codominant positions in the canopy. A total of 17 species were represented in canopy-dominant positions. Crown class distributions varied by taxonomic classification (Figure 3). The majority of *L. sinense* individuals were overtopped and the frequency of stems with intermediate, codominant, and dominant positions was relatively similar. The crown class distribution for *L. styraciflua* was similar across overtopped, intermediate, and codominant categories, but relatively few individuals of this species occupied



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Table 2. Density, dominance, and importance (average of relative density and relative dominance) measures for all live stems ≥ 5 cm diameter at breast height [dbh] in a southeastern U.S. bottomland forest. The "other" category contains species with stem density less than 1 $ha^{-1}$.

| Species | Density | Relative density | Dominance | Relative dominance | Relative importance |
|---|---|---|---|---|---|
| | stems $ha^{-1}$ | | $m^2$ $ha^{-1}$ | | |
| *Liquidambar styraciflua* | 265 | 26.20 | 7.36 | 24.22 | 25.21 |
| *Ligustrum sinense* | 359 | 35.58 | 2.15 | 7.08 | 21.33 |
| *Quercus nigra* | 121 | 11.95 | 7.47 | 24.60 | 18.27 |
| *Pinus taeda* | 49 | 4.88 | 5.27 | 17.34 | 11.11 |
| *Liriodendron tulipifera* | 32 | 3.17 | 2.32 | 7.64 | 5.40 |
| *Prunus serotina* | 37 | 3.63 | 1.11 | 3.64 | 3.64 |
| *Acer rubrum* | 33 | 3.23 | 0.35 | 1.16 | 2.20 |
| *Nyssa sylvatica* | 23 | 2.24 | 0.34 | 1.12 | 1.68 |
| *Quercus falcata* | 1 | 0.13 | 0.73 | 2.41 | 1.27 |
| *Quercus alba* | 5 | 0.53 | 0.45 | 1.48 | 1.01 |
| *Tilia americana* L. (American basswood) | 11 | 1.12 | 0.19 | 0.63 | 0.88 |
| *Ulmus alata* Michx. (winged elm) | 11 | 1.06 | 0.20 | 0.66 | 0.86 |
| *Ilex opaca* Aiton (American holly) | 8 | 0.79 | 0.27 | 0.90 | 0.84 |
| *Juglans nigra* | 3 | 0.33 | 0.35 | 1.16 | 0.74 |
| *Ulmus rubra* Muhl. (slippery elm) | 5 | 0.46 | 0.30 | 0.99 | 0.73 |
| *Quercus phellos* L. (willow oak) | 7 | 0.73 | 0.15 | 0.50 | 0.61 |
| *Carya* spp. | 5 | 0.46 | 0.21 | 0.70 | 0.58 |
| *Quercus marilandica* Münchh. (blackjack oak) | 5 | 0.53 | 0.18 | 0.58 | 0.55 |
| *Juniperus virginiana* L. (eastern redcedar) | 4 | 0.40 | 0.21 | 0.69 | 0.54 |
| *Magnolia virginiana* L. (sweetbay) | 5 | 0.46 | 0.10 | 0.34 | 0.40 |
| *Cornus florida* L. (dogwood) | 5 | 0.53 | 0.03 | 0.11 | 0.32 |
| *Oxydendrum arboreum* (L.) DC. (sourwood) | 1 | 0.13 | 0.05 | 0.15 | 0.14 |
| *Fagus grandifolia* Ehrh. (American beech) | 2 | 0.20 | 0.01 | 0.05 | 0.12 |
| *Fraxinus pennsylvanica* Marsh. (green ash) | 2 | 0.20 | 0.01 | 0.04 | 0.12 |
| *Ostrya virginiana* (Mill.) K. Koch (hophornbeam) | 1 | 0.13 | 0.01 | 0.03 | 0.08 |
| Other | 9 | 0.86 | 0.54 | 1.78 | 1.32 |
| Total | 1,009 | 100 | 30.37 | 100 | 100 |

dominant canopy positions (11 $ha^{-1}$). *Pinus taeda* was largely restricted to dominant and codominant canopy positions with a total of only 3 stems $ha^{-1}$ in overtopped and intermediate positions. *Quercus nigra* revealed a relatively even crown class distribution, but was least common in the intermediate crown class. The "others" category showed slight and gradual decline from overtopped to dominant crown classes.

Spearman's rho for dominance (based on basal area of stems > 5 cm dbh) of *L. sinense* and woody plant species richness for each plot revealed a significant negative relationship ($r_s = -0.69$, $P < 0.01$, Figure 4). A similar relationship was revealed between *L. sinense* density and woody plant species diversity ($r_s = -0.78$, $P < 0.01$, Figure 5A). As the density of *L. sinense* increased across our plots, plot-level diversity decreased. Similarly, we found a significant negative relationship between *L. sinense* density and evenness ($r_s = -0.82$, $P < 0.01$, Figure 5B). Spearman's rho for *L. sinense* density and native understory stem density (individuals ≥ 1 m height, < 5 cm dbh) revealed a



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Table 3. Frequency (percent of plots on which species occurred), density, and importance (average of relative frequency and relative density) measures for all live stems ≥ 1 m height, < 5 cm diameter at breast height (dbh) in a southeastern U.S. bottomland forest.

| Species | Frequency | Relative frequency | Density | Relative density | Relative importance |
|---|---|---|---|---|---|
| | | | stems $ha^{-1}$ | | |
| *Ligustrum sinense* | 29 | 96.67 | 7,076.00 | 95.24 | 95.96 |
| *Liquidambar styraciflua* | 16 | 53.33 | 157.33 | 2.12 | 27.73 |
| *Ilex opaca* | 12 | 40.00 | 38.00 | 0.51 | 20.26 |
| *Juniperus virginiana* | 9 | 30.00 | 16.00 | 0.22 | 15.11 |
| *Ulmus* spp. | 9 | 30.00 | 14.67 | 0.20 | 15.10 |
| *Prunus serotina* | 8 | 26.67 | 11.33 | 0.15 | 13.41 |
| *Acer rubrum* | 7 | 23.33 | 40.00 | 0.54 | 11.94 |
| *Nyssa sylvatica* | 7 | 23.33 | 10.00 | 0.13 | 11.73 |
| *Quercus nigra* | 7 | 23.33 | 7.33 | 0.10 | 11.72 |
| *Magnolia virginiana* | 5 | 16.67 | 22.67 | 0.31 | 8.49 |
| *Cornus florida* | 4 | 13.33 | 4.00 | 0.05 | 6.69 |
| *Carya* spp. | 4 | 13.33 | 4.00 | 0.05 | 6.69 |
| *Ostrya virginiana* | 3 | 10.00 | 4.67 | 0.06 | 5.03 |
| *Callicarpa americana* L. (American beautyberry) | 2 | 6.67 | 6.67 | 0.09 | 3.38 |
| *Fagus grandifolia* | 2 | 6.67 | 4.67 | 0.06 | 3.36 |
| *Diospyros virginiana* L. (common persimmon) | 2 | 6.67 | 2.67 | 0.04 | 3.35 |
| *Liriodendron tulipifera* | 2 | 6.67 | 2.00 | 0.03 | 3.35 |
| *Fraxinus pennsylvanica* | 2 | 6.67 | 1.33 | 0.02 | 3.34 |
| *Tilia americana* | 2 | 6.67 | 1.33 | 0.02 | 3.34 |
| *Quercus alba* | 1 | 3.33 | 2.67 | 0.04 | 1.68 |
| *Asimina triloba* (L.) Dunal (pawpaw) | 1 | 3.33 | 0.67 | 0.01 | 1.67 |
| *Oxydendron arboreum* | 1 | 3.33 | 0.67 | 0.01 | 1.67 |
| *Quercus marilandica* | 1 | 3.33 | 0.67 | 0.01 | 1.67 |
| Total | | | 7,429.33 | 100 | 276.67 |

significant negative association ($r_s = -0.48$, $P < 0.01$, Figure 6).

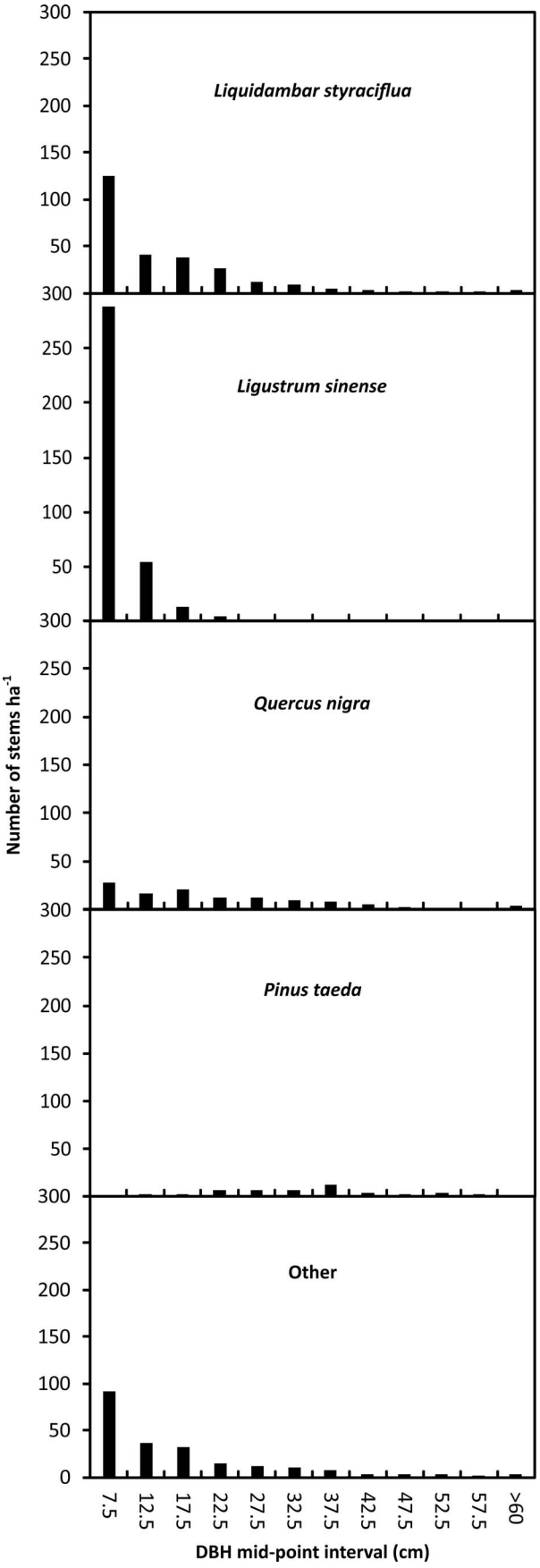
## Discussion

The forest, established ca. 1950, was in the stem exclusion stage of forest development (Oliver and Larson 1996). At this stage of forest development, basal area increases, but tree density decreases. Few stems are added to the overstory during the stem exclusion stage (Nyland 2007; Oliver and Larson 1996). Mortality is high, and thus canopy gap formation is more frequent in this developmental period compared to later stages (Zeide 2005). Gaps formed early in development largely result from endogenous disturbance and are typically filled by canopy trees that spread their crowns laterally into the void space rather than by subcanopy trees (Hart et al. 2011; Richards and Hart 2011). However, even during this stage of development, some large gaps form when multiple canopy trees are removed by exogenous disturbance. In addition, small, single tree gaps can still provide a means for subcanopy trees to recruit to larger size classes (Hart and Grissino-Mayer 2009).

The understories of stands in the stem exclusion stage are typically sparse, but in the forest examined here, the invasion of *L. sinense* resulted in high understory stem density. In fact, the stocking level was > 110% (Goelz 1995). As a result of the high understory stem density, the diameter structure of the stand exhibited an inverse J-shaped distribution indicative of forest regeneration (Nyland 2007), but *L. sinense* comprised 95% of understory stems. Thus, the small size classes were largely comprised of *L. sinense* rather than native arboreal species such that would be expected in a regenerating stand. We hypothesized the high density of *L. sinense* would reduce the likelihood of native tree establishment following local disturbance, because almost all growing space in the understory layer was filled by this species. In overstocked stands, all growing space is utilized and new stems are not added to the system (Nyland 2007). Based on composition



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of the understory layer, we projected that under the current disturbance regime the forest would transition to support a stronger component of *L. sinense* and portions of the forest would move from tree to shrub cover. Some researchers have hypothesized that without active management, some southeastern U.S. bottomland sites invaded by *L. sinense* could move toward monotypic stands of this alien species (e.g., Brantley 2008; Kittell 2001).

Notable for a species classified as a shrub or small tree was the number of *L. sinense* stems with positions in uppermost forest stratum (41 stems $ha^{-1}$). These individuals were classified in the field as canopy-dominant or codominant, not because they reached unusual heights for the species, but because they represented the uppermost stratum of vegetation and their crowns were expanding laterally. We projected these stems would remain in the main forest canopy during their lifespans. Based on horizontal spacing of stems, we did not project these *L. sinense* that represented the uppermost vegetation stratum would be overtopped by adjacent trees capable of achieving greater heights, thus sites within the forest had moved from tree to shrub dominance. We noted morphological differences in *L. sinense* stems based on size and canopy position. *Ligustrum sinense* with canopy positions and large stem diameters rarely exhibited multistemmed growth forms. Indeed, the areas immediately underneath these larger *L. sinense* stems were sparse of any woody or herbaceous vegetation. In contrast, *L. sinense* stems without positions in the canopy were often multistemmed. Additional research is needed, but our data and observations indicate that the growth form of the species changes with size and crown position.

Although the forest was dominated by *Q. nigra* and *L. styraciflua*, *Ligustrum sinense* ranked fifth in basal area contribution of overstory stems and was by far the most abundant species in the understory. Our results revealed significant negative relationships between *L. sinense* density and dominance, and species richness, evenness, and diversity of woody plants. We also noted a significant negative relationship between the abundance of *L. sinense* and Shannon diversity and evenness of the understory. Using different approaches, others have noted similar relationships in other locations of the southeastern United States (Kittell 2001; Merriam and Feil 2003; Wilcox and Beck 2007).

←

Figure 2. Number of trees (≥ 5 cm diameter at breast height [dbh]) per hectare divided into five groups in a southeastern U.S. bottomland forest. For a list of species in the "others" group see Table 2.



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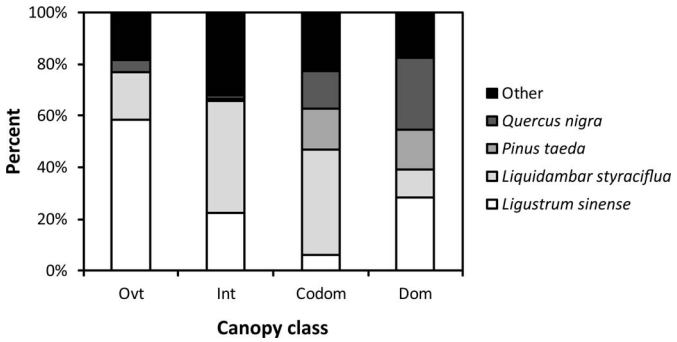



Figure 3. Canopy class percentages by group. Canopy class categories are based on the amount and direction of intercepted light (Oliver and Larson, 1996). Dom: dominant, Codom: codominant, Int: intermediate, Ovt: overtopped. See Table 2 for a list of species in the "others" group.

Our study was not designed to demonstrate causality, but rather to examine the relationships between density and dominance of a shade-tolerant alien shrub and biodiversity measures. The inverse relationships between *L. sinense* and biodiversity might be explained by two mechanisms. The local establishment of *L. sinense* within the forest might have reduced species richness, evenness, and Shannon diversity of the woody plant assemblage relative to preinvasion levels (i.e., *L. sinense* invasion reduced biodiversity). *Ligustrum sinense* has a low light compensation point and can establish in the understory of a closed canopy forest (Miller 2003; Morris et al. 2002; Ward 2002). Once established, the high leaf surface area of *L. sinense* stems further restrict light in low vertical strata and on the forest floor. Because it is semievergreen to evergreen, insolation is restricted throughout the year and thus, its

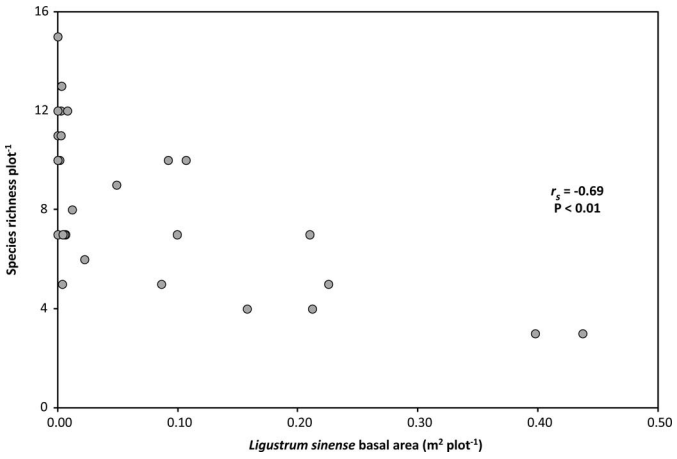



Figure 4. Relationship between *Ligustrum sinense* dominance (measured by basal area of stems ≥ 5 cm diameter at breast height [dbh]) and species richness of woody plants ≥ 1 m height across 30 circular plots of 0.05 ha size in a southeastern U.S. bottomland forest.

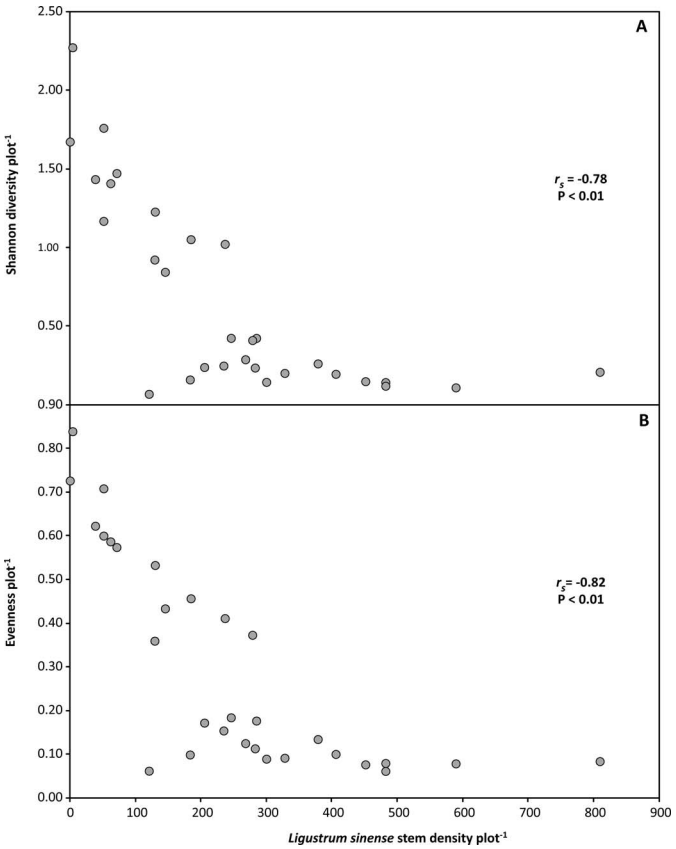



Figure 5. Relationship between *Ligustrum sinense* density (stems ≥ 1 m height plot$^{-1}$), and (A) Shannon diversity and (B) evenness of woody plants ≥ 1 m height across 30 circular plots of 0.05 ha size in a southeastern U.S. bottomland forest.

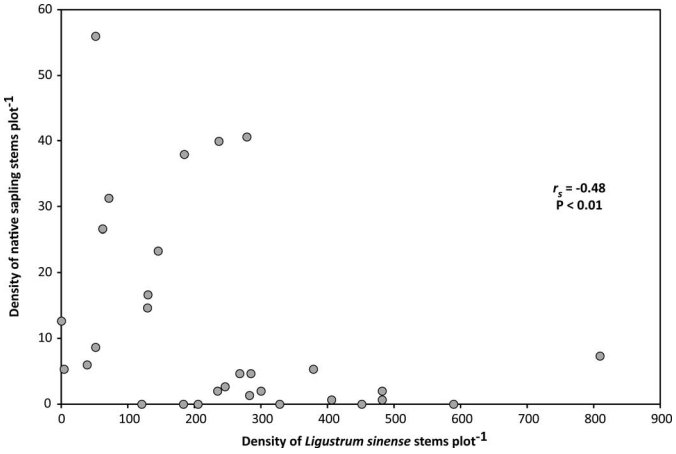



Figure 6. Relationship between *Ligustrum sinense* density (stems ≥ 1 m height plot$^{-1}$) and stem density of native woody plants ≥ 1 m height across 30 circular plots of 0.05 ha size in a southeastern U.S. bottomland forest.



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establishment can influence a range of plant species. Once *L. sinense* is established, it alters the light regime, and although little quantitative data are available, some studies indicate that forest hydrology and nutrient cycling are also modified (Brantley 2008; Mitchell et al. 2011) such that *L. sinense* can be considered a foundation species (Ellison et al. 2005). These feedback mechanisms can impede the establishment of competing native species. Without the establishment of new native germinates, local plant diversity will decline. If *L. sinense* does result in decreased biodiversity on intensively invaded sites, those sites could become more vulnerable to additional invasion (i.e., invasion meltdown; Simberloff and Von Holle 1999).

Alternatively, intraforest biodiversity might have influenced the establishment of *L. sinense* (i.e., *L. sinense* might have invaded microsites with relatively low alpha diversity and been inhibited on microsites with relatively high alpha diversity). An extension of the biotic resistance theory is the diversity resistance hypothesis that states there is a positive relationship between community biodiversity and resistance to alien invasion (Kennedy et al. 2002). This bottomland forest was characterized by relatively high woody plant species richness, but fine-scale, intrastand biodiversity patterns varied spatially (i.e., some plots had relatively high and some plots had relatively low woody plant diversity, including plots in close proximity). To what extent fine-scale woody plant diversity was driven by abiotic conditions was unknown. To test a cause-effect relationship between intrastand biodiversity and invasibility, the invasion process would have to be documented using permanent plots or reconstructive techniques, which were beyond the scope of this study. We suggest future research be targeted at establishing potential causal relationships between biodiversity and invasion success of *L. sinense* and *L. sinense* establishment and potential biodiversity alterations.

Although not quantified, the propagule pressure for this periurban forest was hypothesized to be relatively high, given its proximity to suburban development and the fact that many alien plant invaders are commonly established for ornamental purposes (Bradley et al. 2012; Richardson and Rejmánek 2011). Interestingly, *L. sinense* was the only woody alien plant documented in our study plots. This finding could indicate that invasibility of this intact bottomland forest was low, with the exception of *L. sinense* (Richards and Pyšek 2006).

Active management is needed to remove *L. sinense* from this bottomland forest. Without silvicultural treatments, we hypothesize that composition will shift to support a much stronger *L. sinense* component and structure will be further altered as sites within the forest move from tree to shrub dominance. Control methods for this shrub have been tested and discussed by several researchers (e.g., Hanula et al. 2009; Klepac et al. 2007; Miller 2003). Common *L. sinense* control methods include chainsaw felling with subsequent herbicide application, mowing followed by a foliar herbicide treatment, mechanical removal using an uprooting tool, and basal bark application of herbicide in oil (Hanula et al. 2009). Scatterplots of *L. sinense* density and woody plant diversity measures revealed that 0.05-ha plots with greater than ca. 200 *L. sinense* stems (4,000 stems $ha^{-1}$) had relatively low evenness and Shannon diversity values. Although low biodiversity might not be the result of *L. sinense* invasion, if abiotic conditions of invaded sites are similar to nearby sites with higher biodiversity, then such severely invaded sites could be prioritized for *L. sinense* control. Management goals might be easiest to achieve on sites with mature *L. sinense* stems that have ascended to the uppermost forest stratum and lack the multi-stemmed growth form. These areas may be those considered most impacted by *L. sinense* establishment and may be considered priority restoration areas by managers. Regardless of the method, *L. sinense* control on a site is a multiyear project. Based on the potential density of *L. sinense* stems, even relatively small invaded forests might need to be compartmentalized by field crews. However, local control in forest compartments could be problematic, because of *L. sinense* prolific seed production and avian dispersal and treated areas would require constant monitoring.

## Conclusions

The overarching goal of our study was to investigate the relationships between *L. sinense* invasion, woody plant diversity, and the future development and successional trajectory of a bottomland forest in southeastern United States. We noted significant negative associations between *L. sinense* basal area and density and woody plant species richness, evenness, and diversity. Spearman's correlation for *L. sinense* density and native understory stem density also revealed a significant negative association. *Ligustrum sinense* represented 95% of saplings, and under the current disturbance regime, we projected that the forest would shift to support a stronger component of this species and structure would move from tree to shrub dominance on specific sites within the forest. Future research should investigate causal relationships between biodiversity and invasion success of *L. sinense* and between *L. sinense* establishment and alterations to woody plant diversity.

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