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ECOSYSTEMS

Patterns of Privet: Urbanizing Watersheds, Invasive *Ligustrum sinense*, and Performance of Native Plant Species in Piedmont Floodplain Forests

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ABSTRACT

Floodplain forests in rapidly changing landscapes with increased urbanization may reshape habitat conditions to the detriment of native biota and favor invasive species. We assessed whether introduced *Ligustrum sinense* distribution and abundance are causally linked to urbanization and whether mechanisms that promote *L. sinense* cause the demise of native plant species. We surveyed vegetation in 12 independent floodplain forests along an urban to rural gradient in South Carolina, USA. We then used a seedling transplant experiment in nine watersheds to assess how increased urban development affects survival and growth of *L. sinense* and three native species over two growing seasons. Urban development ranged from 1 to 45% and *L. sinense* cover was positively associated with development. However, in our transplant experiment, growth and survival of *L. sinense* did not differ significantly among watersheds. Native species were able to survive at all sites, but performance varied greatly among sites and species but not as a function of urban development. Our results suggest that although *L. sinense* invasion and urbanization are related (likely due to proximity of propagules from urban sources), the demise of native species cannot be explained by increased urbanization or changes in edaphic conditions and points to *L. sinense* as an agent of change in our floodplain forests. These results indicate that all floodplain forests are at risk of invasion if propagules arrive and that land managers need to be vigilant against new species introductions regardless of the proximity to urban areas.

Key words: Chinese Privet; floodplain; forested wetlands; invasion; propagule pressure; transplant experiment; watershed urbanization.

INTRODUCTION

Urbanization is one of mankind's most apparent land use transformations (Grimm and others 2008) that influences not only the land directly occupied, but also other areas that are ecologically connected (Poff and others 1997). Urbanization eliminates existing land cover and increases the extent of impervious

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surfaces (IS) that change water flow regimes, increase stream incision, alter channel geomorphology, and lower ground water tables creating an ''urban stream syndrome'' (Walsh and others 2005) that can lead to hydrologic drought in associated riparian wetlands (Groffman and others 2003). Associated with urbanization are species introductions that increase propagule pressure and facilitate spread of non-native plant species (Cadenasso and Pickett 2001; Levine 2001; McDonald and Urban 2006). Once introduced, lack of specialized natural enemies and other biotic interactions (Keane and Crawley 2002; Mitchell and others 2006), pre-adaptations due to superior traits (Brown and Sax 2004), and functional distinctiveness (Dukes 2001) may further facilitate their spread. A spirited debate about the relative contributions of these factors in promoting plant invasions is ongoing but few generalizations appear possible (Park and Blossey 2008; Bradley and others 2010; Thompson and Davis 2011), and even the assumption that invasive plant species are drivers of ecosystem deterioration is questioned (MacDougall and Turkington 2005; Nuzzo and others 2009; Davis and others 2011). Uncertainty about mechanisms for native species declines complicates management efforts and for many invaders we find rather little, if any, holistic assessments allowing us to determine who drives and who rides along.

Ligustrum sinense Loureiro (Chinese Privet) has spread to more than 1 million ha in riparian forests of the United States (Merriam 2003; Miller and others 2008). Stands have persisted for more than 40 years (Ward 2002) and reduce native plant growth and survival (Osland and others 2009; Greene and Blossey 2012). The species occupies a near vacant shrub niche in the mid canopy of Piedmont floodplain forests and appears to host few herbivores (Morris and others 2002). Previous work linked depauperate plant communities with *L. sinense* invasion (Merriam 2003; Greene and Blossey 2012) and increased urbanization (Kuhman and others 2010). What remains unclear is whether land use changes favor *L. sinense* and prevent growth of native species (Sung and others 2011). Williams and others (2009) proposed a framework that different urban filters (habitat transformation, fragmentation, urban environment, and human preference) create selection pressures facilitating persistence of certain species in urban landscapes. But for land managers to know how to address invasive plant problems, it is critical to know which filter has the largest influence.

We located our study in floodplain forests of the Piedmont ecoregion of South Carolina. The primary disturbance regime in these forests is seasonal floods (Hook and others 1994) that are influenced by land use in the associated watershed. This region experienced intense cotton farming from 1820 to 1930 until abandoned fields reverted to forests, increasing forest cover in some areas up to 30% by 1967 (Trimble and others 1987). Rapid population growth from 1973 to 2000 increased urban land cover in the eastern Piedmont ecoregion from 11.9 to 16.4% and exurban development in the Piedmont of South Carolina increased by 50% (Brown and others 2005). These changes in land cover altered flow regimes (Poff and others 2006) with flashier hydrographs and more frequent elevated peak discharges (Schoonover and others 2006).

We explored the importance of different biotic and abiotic factors in an attempt to explain prevalence and distribution of *L. sinense* and several native species typical for these habitats. We first examined whether *L. sinense* prevalence was related to urbanization within the watershed. We predicted that (1) stem density and cover of *L. sinense* increases with increased urbanization. We then explored potential mechanisms promoting *L. sinense* invasion and declines of native species. If urbanization constitutes an important mechanism then (2) habitat quality or edaphic conditions of invaded and uninvaded watersheds should differ due to altered flood regimes; and (3) growth and survival of *L. sinense* should be greater in urban watersheds compared to forested watersheds, and (4) native species should perform best in watersheds least affected by urbanization. If traits of *L. sinense* explain invasive success, then (5) growth and survival of *L. sinense* should not differ among watersheds along an urbanization gradient and (6) *L. sinense* herbivory and growth rates should differ from native species giving *L. sinense* a competitive advantage.

MATERIALS AND METHODS

Site Selection

We used the 2001 National Land Cover Database (Homer and others 2004) and the National Wetland Inventory (US Fish and Wildlife Service 2009) to initially select palustrine forested wetlands across a rural–urban forested land cover gradient. We visited sites in May 2007 and chose 12 hydrologically independent floodplain forests on public and private lands and their associated watersheds (Figure 1) but rejected sites with livestock grazing, recent logging (<10 years), or with floodplains less than 100 m wide. All sites are secondary hardwood forests with grasses and sedges dominating herbaceous understories and ubiquitous presence of deer (*Odocoileus virginianus*) and non-native earthworms.

The region experienced a drought for the entire time of this study (National Climatic Data Center (NCDC) 2009) but we observed flooding events at several sites during our study.

Land Cover Analysis

We conducted land cover analysis with ArcGIS v9.2 using land cover, forest, and IS data layers obtained from the 2001 National Land Cover Database. Land cover classification followed Homer and others (2004) with classes 21–24 pooled for development, 41–43 for forest, and 90–99 for wetlands. We measured direct distance and stream flow path distance from the field sites to the nearest developed area in kilometers. To be identified as a developed area, land use categories were aggregated into 36 ha grids and classified as developed if more than half the cells inside the grid contained a developed land cover class. We used hydrologic units (HUC 10) obtained from the United States Department of Agriculture Watershed Boundary Dataset for watershed delineation. We grouped watersheds into four categories (three urban, two developing, four mixed, and three forested) representing different dominant land cover patterns (Table 1).

Vegetation Surveys and Forest Stand Measurements

We surveyed sites for vascular plants from 11 June to 15 July 2007. We selected a 200 m stream reach at least 75 m from the nearest forest edge (at Lawson's Fork and Reedy River, sites 1 and 2, Figure 1, we used a 100 m stream reach to ensure contiguous habitat). We randomly located five parallel 100 m transects in each reach running along a compass heading perpendicular to the stream. Along each transect we randomly located six shrub plots (2 × 5 m, $N = 30$ plots/site; for herbaceous vegetation see Greene and Blossey 2012). We used the 10 m^2 area to identify and count all individuals and visually estimate cover (%) for each shrub species and total plot cover. We used the same transect headings and locations to collect forest stand measurements of diameter at breast height (DBH) and basal area. We established a 2 m wide by 100 m long belt transect and identified and measured all woody stems at least 1.5 cm in DBH for each of the five transects per site covering a total area of 1000 m^2 from August to October 2008. For individuals with multiple stems we recorded the largest stem diameter.

Transplant Experiment

To assess performance of native and introduced species we used *L. sinense*, *Acer negundo* L. var. *negundo*, *Chasmanthium latifolium* (Michaux) Yates, and *Allium canadense* L. var. *canadense*. These species represent different life forms and life histories and are common at our sites. *Acer negundo* is a common native floodplain tree whereas *C. latifolium* is a common understory grass; *A. canadense* is a common

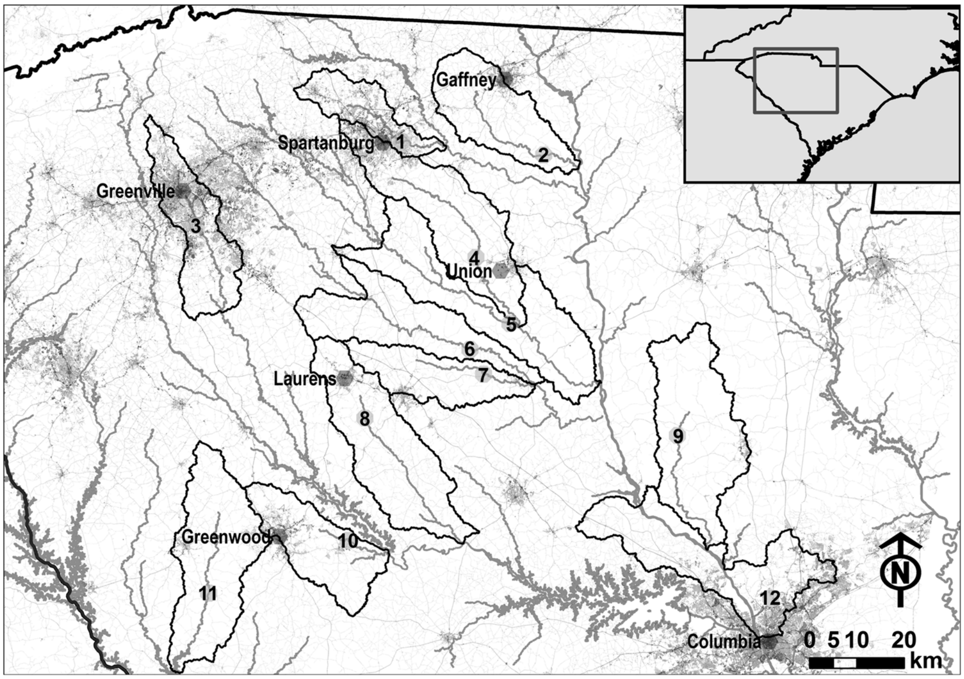


Fig. 1. Field site locations and their associated watersheds, major cities (*hexagon outlines*), and impervious surfaces (*grey*) in the Piedmont ecoregion of South Carolina. *Sites* Lawson's Fork Creek (*1*), Thicketty Creek (*2*), Reedy River (*3*), Fairforest Creek (*4*), Tyger River (*5*), Enoree River (*6*), Duncan Creek (*7*), Little River—Laurens County (*8*), Little River—Fairforest County (*9*), Wilson's Creek (*10*), Long Cane Creek (*11*), Crane Creek (*12*). Sites 1–9 were sites used for the transplant experiment.

Table 1. Individual Sites in Assigned Categories, Land Cover (%) in Their Associated Watersheds, and Summary Values (mean ± 1SE) for the Four Watershed Categories

Site	Land cover categories (%)					Distance (km)		Area (ha)
	Developed	IS	Forest	Agriculture	Wetland	Direct	Flow	
Forest sites								
Enoree River (ER)	1.2	0.8	65.0	17.5	3.4	10.5	34.9	48,059
Little River (LR)	4.0	0.6	75.1	7.0	2.8	9.3	20.9	62,886
Tyger River (TR)	4.7	0.5	72.7	12.1	3.4	9.5	47.5	63,420
Mixed sites								
Long Can Creek (LC)	7.4	0.8	68.7	13.3	1.7	8.5	12.5	59,112
Little River (LL)	8.2	1.1	61.5	19.2	3.0	6.2	8.6	59,587
Duncan's Creek (DC)	9.5	1.5	69.6	12.1	3.4	6.4	20.8	31,079
Thicketty River (TC)	9.6	1.9	57.6	22.4	1.6	14.7	28.1	40,807
Developing sites								
Wilson's Creek (WC)	15.9	2.8	57.2	16.4	2.8	1.3	5.4	37,242
Fairforest Creek (FC)	17.0	4.1	58.5	13.9	4.0	2.1	30.9	56,560
Urban Sites								
Crane Creek (CC)	21.4	5.2	62.4	6.6	3.0	0.3	0.7	60,183
Lawson's Fork Creek (LF)	38.9	9.5	35.7	19.7	2.1	0.3	0.8	22,034
Reedy River (RR)	44.5	13.7	32.8	15.5	2.8	0.1	1.0	39,106
Watershed category								
Forest	3.3 ± 1.1^{a}	0.6 ± 0.1^{a}	70.9 ± 3.0^{a}	12.2 ± 3.0	3.2 ± 0.2	9.8 ± 0.4^{a}	34.4 ± 7.7^{a}	58,122 ± 5,034
Mixed	8.7 ± 0.5^{b}	1.3 ± 0.2^{ab}	64.4 ± 2.9^{ab}	16.8 ± 2.4	2.4 ± 0.5	8.9 ± 2.0^{a}	17.5 ± 4.4^{ab}	47,646 ± 9,659
Developing	16.5 ± 0.5^{bc}	3.4 ± 0.6^{bc}	57.8 ± 0.6^{ab}	15.1 ± 1.2	3.4 ± 0.6	1.7 ± 0.4^{b}	18.2 ± 12.8^{ab}	46,901 ± 9,659
Urban	35.0 ± 7.0^{c}	9.5 ± 2.4^{c}	43.6 ± 9.4^{b}	13.9 ± 3.9	2.7 ± 0.3	0.2 ± 0.1^{b}	0.8 ± 0.1^{b}	40,441 ± 11,033

Two letter codes in parentheses represent site codes throughout the manuscript. Groups with different letters in a column are significantly different based on a Tukey Post hoc test. Data in developed and IS cover types were log10 transformed to meet the assumptions of normality for the ANOVA.

Direct distance refers to the linear distance between urban area and site, flow refers to the distance via stream between urban area and site. All data based on 2001 National Land Cover Database. Our site categories (urban, developing, mixed, and forested) are distinct for development ($F_{3,8} = 15.64$, $P = 0.001$), IS ($F_{3,8} = 10.72$, $P = 0.004$), forests ($F_{3,8} = 4.82$, $P = 0.03$), direct distance from urbanization ($F_{3,8} = 11.93$, $P = 0.003$), and flow path distance from urbanization ($F_{3,8} = 4.97$, $P = 0.03$; Table 1).

early season forb found in many habitats across the eastern United States. We collected seeds for *A. canadense* in May 2007 and for the remaining species in fall and winter 2007–2008. We stored *A. canadense*, *C. latifolium*, and *L. sinense* seeds dry at 22°C in paper bags and *A. negundo* seeds in the dark at 5°C in plastic bags with moist paper towels. In mid-March 2008 we scattered seeds on a moist 50:50 mixture of potting soil and playground sand in plastic trays in a greenhouse maintained at 25°C (12-h photoperiod). We watered seeds periodically from above to maintain moisture. After 9 weeks we selected 180 individuals of similar size from each species except for *A. negundo* which had insufficient germination. As a replacement, we collected 4-leaved *A. negundo* seedlings on 26 April 2008 at Lawson's Fork Creek. We also collected similar sized *L. sinense* seedlings on 27 April 2008 at Little River Laurens to compare field-grown plants for the two woody species in our experiment.

We selected three field sites each with predominant urban, mixed, and forested land cover (nine total). At each site we established a transplant garden consisting of 80 1 × 1 m cells with seedling identity in each cell determined at random. Each grid consisted of two adjoining rows of ten cells separated by a 1-m wide walkway from the next two adjoining rows for a total of eight rows. Each grid was located in the first terrace of the floodplain forest away from mature *L. sinense*. We divided individuals of each transplant species randomly into groups of 20. We selected an individual at random from this group and planted it bare root into the center of a cell. To avoid immediate plant competition by existing vegetation, we anchored a 20 × 20 cm black plastic sheet (6 mm) to the substrate using metal nails. Each plastic sheet contained a 25 cm^2 center hole where the seedling was planted. We marked all seedlings individually using metal ID tags to ensure proper identification on subsequent visits. Plastic sheets were quickly overgrown by vegetation but made relocation much easier. The local vegetation matrix was representative of the floodplain forest herbaceous community, dominated by grasses and sedges, and included both native and non-native species.

We planted 20 individuals of each species at each site (total = 720 individuals) from 27 April 2008 to 1 May 2008. We watered plants twice, once upon planting and again at the first re-visit. We replaced dead individuals that most likely died due to transplant shock on the first subsequent visit after 1 week. During the first year we monitored sites weekly for the first month and then every other week in June and July, once in mid-August, and once in late October (10 sample periods over 27 weeks). In the second year we visited each site once in February, May, July, and October (four sample periods over 49 weeks). We counted individuals as alive if green photosynthetic tissue was present. We measured height to the apical meristem for *A. negundo* and *L. sinense* and to the height leaves reached when held erect for *A. canadense* and *C. latifolium*. We recorded herbivory qualitatively via presence or absence of visual stem and leaf damage from mammal and insect foraging. When we terminated the experiment and removed all plants in October 2009, we had recorded seedling survival and growth on a total of 14 sampling dates over a period of 76 weeks.

Edaphic Measurements

We measured soil infiltration, soil nutrients, and ground water table depth to assess differences in edaphic conditions at our sites. We measured soil infiltration capacity using a double ring infiltrometer (40 cm and 65 cm diameter) at each site (17 July–7 August 2007) at ten randomly selected vegetation plots. At each test location we drove the two metal rings at least 5 cm into the ground and then twice filled both with a known volume of water and timed (in seconds) how long it took for all the water in the inner ring to infiltrate. The second measurement was used for analysis of saturated soil infiltration capacity (liters/minute).

We installed seven ground water table wells in June 2008 at each of the nine transplant sites. We randomly choose two transects from the vegetation survey and placed one well each at 15, 50, and 100 m from the stream and an additional one adjacent to the transplant grid. Each well consisted of a capped 3-m long PVC pipe (3.8 cm diameter) with 1-cm diameter holes drilled every 10 cm along 2.6 m of the pipe and then 2.75 m of the pipe was wrapped in cloth to prevent sedimentation. We used a 5-cm auger, to drill to a depth of 2.75 m and installed wells leaving 0.25 m of the pipe above ground. We refilled holes initially with sand and then packed the top 15 cm with clay. We manually measured water table depth ten times (June 2008–May 2009). When the water table dropped below 2.75 m we recorded 2.75 m for the maximum value of affected wells. We collected soil for nitrate, P, and K soil concentration analysis from each site used for transplant experiments in February 2009 by removing the upper 10 cm of a 10-cm diameter soil core at three locations directly adjacent to transplant gardens. We thoroughly mixed samples from each site, and had them evaluated at the Cornell Nutrient Analysis Laboratory (USDA 2004).

Statistical Analysis

To ensure that our sites varied on an urban to forested gradient we compared land cover of different watershed categories using ANOVA followed by multiple pairwise comparisons using Tukey's HSD. To analyze our first prediction we examined relationships between *L. sinense* stem density and cover to land cover and forest stand measurements using linear regression. To examine differences in edaphic conditions (prediction 2) we compared soil infiltration rates using ANOVA and Tukey's HSD. We examined relationships between soil nutrients and plant species growth using linear regression. To avoid pseudoreplication, we used a derived variable analysis for comparing mean water table depth by site with ANOVA and Tukey's HSD. We report transplant experiment data for two growing seasons (April–October 2008 and October 2008–October 2009). We analyzed *A. canadense* survival rates for the second season from week 53 because plants were dormant in October 2009. We calculated maximum growth as largest height increase from initial height of surviving individuals for each growing season. To examine if species performed better in certain watersheds we analyzed survival and maximum growth data of *L. sinense* (prediction 3 and 5) and native plants (prediction 4) by land use and watershed categories using linear regression, ANOVA, and Tukey's HSD. To analyze survival (prediction 3, 4, and 5) we created survival curves for each species at each site and analyzed final survival by site using a binomial Generalized Linear Model. To analyze if *L. sinense* has a competitive advantage over natives (prediction 6) we used a binomial generalized estimating equation model with site as a random effect to analyze results of herbivory among three species from the transplant experiment. We also used Mann–Whitney tests to compare maximum growth rates of all living *A. negundo* and *L. sinense* for both growing seasons.

We inspected normality and homoscedasticity with both graphical and statistical methods to ensure test assumptions were met. In cases with non-normally distributed data we used log10 transformations. We conducted all analyses using R (R Development Core Team 2008, Packages: stats and gee:geepack).

RESULTS

Our site selection resulted in strong gradients in different land cover categories, which enabled comparisons among replicate watersheds (Table 1).

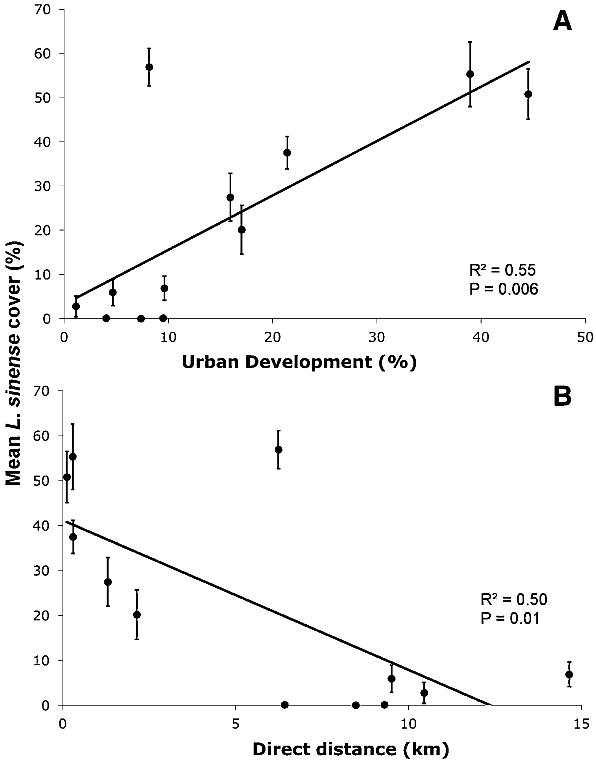


Fig. 2. Cover (%) of *L. sinense* as a function of (**A**) urban development (%) and (**B**) direct distance to developed area (km). Data are means ± 1SE of 12 field sites (30 plots per site).

There was no difference among watershed categories for agriculture, wetland, or watershed area and we omitted these cover types from subsequent analyses. Percent development and forest cover were inversely correlated. We classified Fairforest Creek as an urban watershed for our transplant experiment because developing watersheds showed large similarities with urban ones.

Mean *L. sinense* cover varied 0.1 to 56.9% and increased in watersheds with more development ($R^2 = 0.55$, $P = 0.006$; Figure 2) and at sites located nearer to urban development ($R^2 = 0.50$, $P = 0.01$; Figure 2). Mean stem density of *L. sinense* varied from 0 to 4.36 stems per m^2 among the 12 study areas and did not vary with any of the land use in the watersheds (all $P > 0.05$). *L. sinense* maximum DBH ranged from 0 to 23.1 cm and was positively related to stem density ($R^2 = 0.52$, $P = 0.007$) and cover ($R^2 = 0.76$, $P = 0.0002$; Figure 3). We found a similar result between *L. sinense* total basal area at each site to stem density ($R^2 = 0.41$, $P = 0.01$) and cover ($R^2 = 0.81$, $P > 0.0001$; Figure 3). We found no significant relationships of *L. sinense* stem density or mean cover to native tree DBH or basal area (all $P > 0.05$).

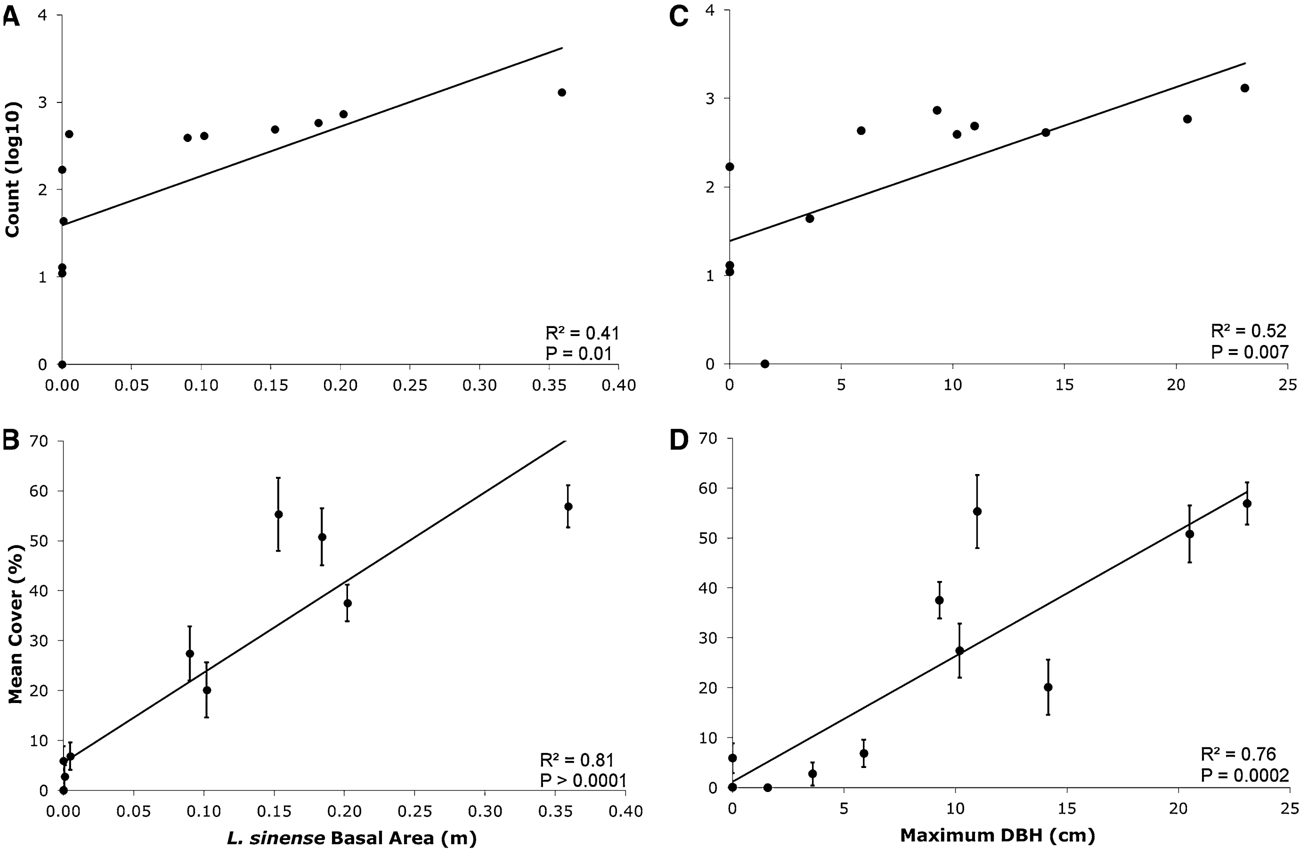


Fig. 3. Number of *L. sinense* individuals (log10 transformed) and mean *L. sinense* cover (%) as a function of **A**, **B** basal area and **C**, **D** maximum *L. sinense* DBH (cm) at each site. Data are means ± 1SE of 12 field sites (30 plots/site).

Among edaphic characteristics we measured, infiltration capacity varied among watershed classes (6.1 l/min in Forest, 10.9 l/min in Mixed, 5.6 l/min in Developing, 7.3 l/min in Urban) but was significant only between forested and mixed watershed categories (Supplemental Figure A1). Depth to water table did not vary significantly by watershed category and soil nutrient concentrations were not related to species growth (Supplemental Table 1).

When we analyzed survival and growth of individual species among watershed categories and individual field sites we found significant differences, but no consistent patterns indicating idiosyncratic interactions of species with local site conditions (Supplemental Figure A2, Figures 4, 5). Seedling survival rates did not differ between watershed categories for any species or year. Survival rates differed among species by site (75–5% *A. canadense*, 90–20% *A. negundo*, 60–5% *C. latifolium*, 85–50% *L. sinense*) but only *A. canadense* was positively related to urbanization in year one ($R^2 = 0.51$, $P = 0.03$) and *C. latifolium* negatively related ($R^2 = 0.44$, $P = 0.05$) to urbanization in year two (Figure 4). Seedling growth was not related to urbanization (Figure 4), but second year seedling growth did differ by watershed category, although first year growth did not (Figure 5). Species differed in their responses with median growth highest for *A. canadense* in mixed watersheds, *A. negundo* in urban, *C. latifolium* and *L. sinense* in forested watershed (Figure 5).

We examined if *L. sinense* had a competitive advantage over the native species by comparing survival, growth, and herbivory among species. Survival rates were significantly different among species (Yr 1: $F_{3,32} = 80.47$, $P < 0.0001$; Yr 2: $F_{3,32} = 7.91$, $P = 0.0004$) where the woody species *A. negundo* and *L. sinense* had higher survival than the herbaceous species *A. canadense* and *C. latifolium* (Figure 6). Comparing the growth of the two woody species there was no significant difference in the first year, but a highly significant difference in year two (Mann–Whitney $W = 6218$, $P < 0.0001$, Supplemental Figure A3). We found large and significant differences in herbivore attack among three species with *L. sinense* consistently experiencing the lowest herbivory (Figure 7). After

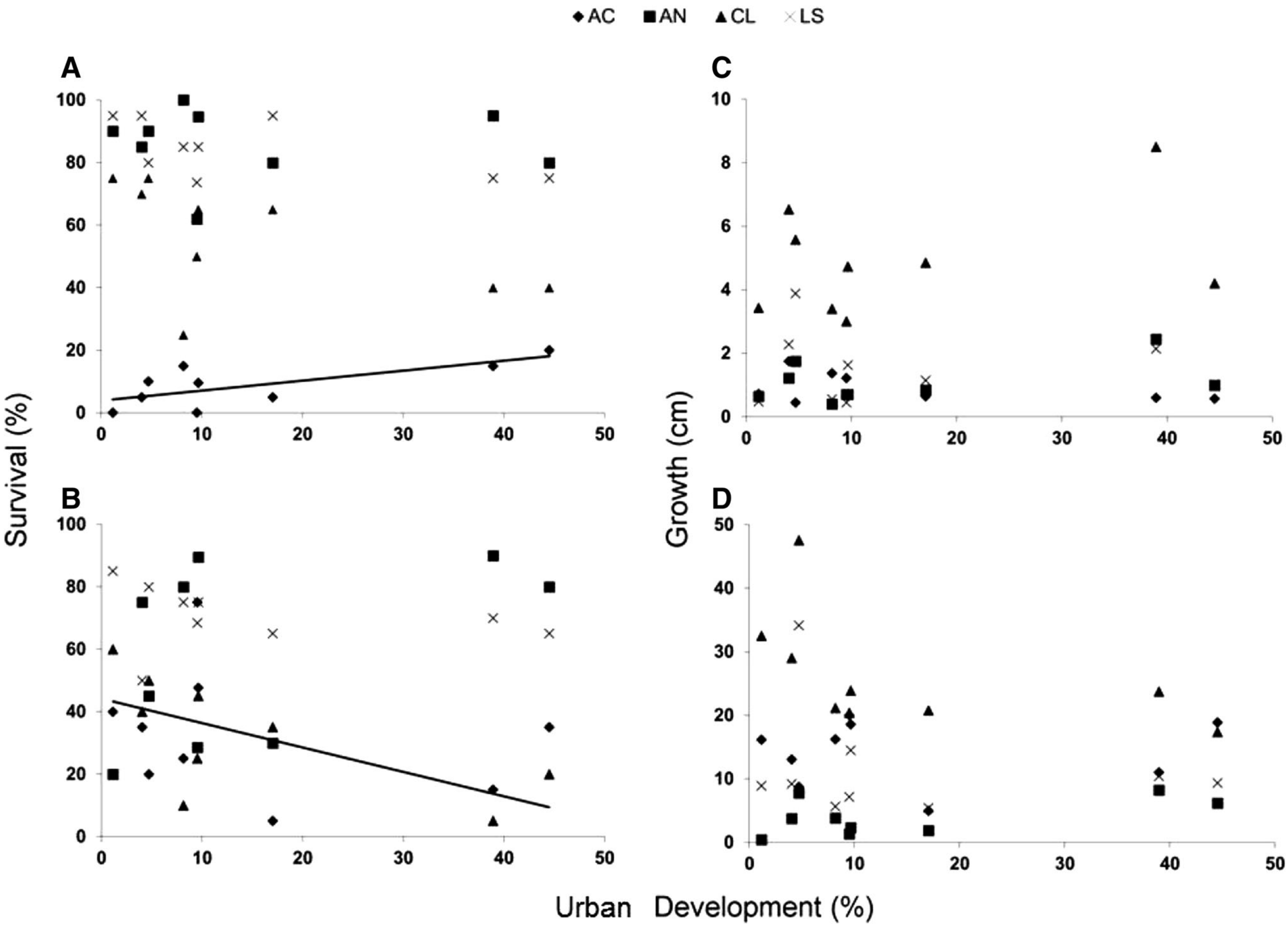


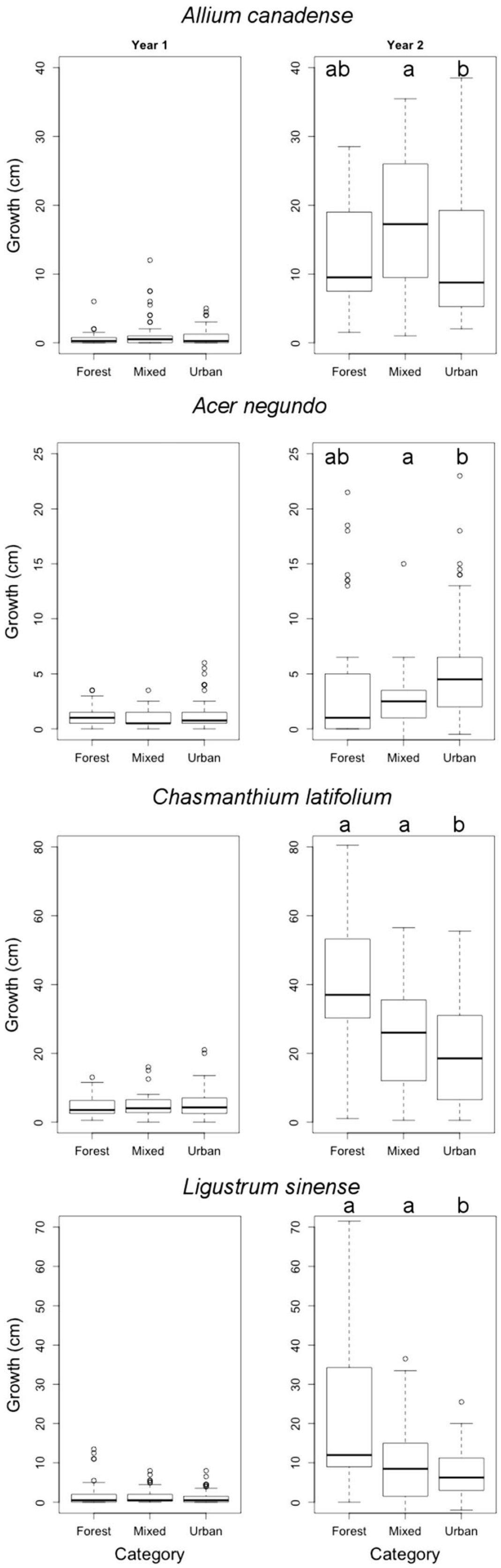
Fig. 4. Seedling survival (%) and growth (cm) in the first (**A**, **C**) and second (**B**, **D**) growing season for four different species in nine different floodplain forests as a function of urban development (%). $N = 20$ individuals/species/site; *error bars* removed for clarity. AC—*Allium canadense* (Survival: Yr 1: $R^2 = 0.51$, $P = 0.03$; Yr 2: $R^2 = 0.07$, $P = 0.50$; Growth: Yr 1: $R^2 = 0.15$, $P = 0.31$; Yr 2: $R^2 = 0.00$, $P = 0.91$); AN—*Acer negundo* (Survival: Yr 1: $R^2 = 0.00$, $P = 0.90$; Yr 2: $R^2 = 0.22$, $P = 0.21$; Growth: Yr 1: $R^2 = 0.24$, $P = 0.18$; Yr 2: $R^2 = 0.32$, $P = 0.11$); CL—*Chasmanthium latifolium* (Survival: Yr 1: $R^2 = 0.31$, $P = 0.12$; Yr 2: $R^2 = 0.44$, $P = 0.05$; Growth: Yr 1: $R^2 = 0.19$, $P = 0.24$; Yr 2: $R^2 = 0.23$, $P = 0.19$); LS—*Ligustrum sinense* (Survival Yr 1: $R^2 = 0.33$, $P = 0.11$; Yr 2: $R^2 = 0.06$, $P = 0.54$; Survival: Yr 1: $R^2 = 0.00$, $P = 0.99$; Yr 2: $R^2 = 0.04$, $P = 0.62$).

the 42nd week, the vast majority of *A. negundo* and *C. latifolium* seedlings had visual signs of herbivory whereas few *L. sinense* individuals were attacked. The odds coefficients from the binomial generalized estimating equation indicate that *A. negundo* is 5.4 and *C. latifolium* is 3.6 times more likely to experience attack than *L. sinense*, when controlling for site.

DISCUSSION

We conducted landscape and local analyses of factors that may facilitate *L. sinense* invasion success and declines of native species in floodplain forests. Our results confirm previously reported associations of *L. sinense* with increased urbanization (Loewenstein and Loewenstein 2005; Burton and Samuelson 2008; Kuhman and others 2010), a pattern reported for many other invasive species (McKinney 2002). However, contrary to expectations, the proportion of the watershed that was urbanized was not associated with differences in local edaphic conditions nor with differences in performance of *L. sinense* or native species.

Although we cannot rule out effects of past habitat modification (Walter and Merritts 2008), or climate change induced drought (Zhang and others 2007) in eliminating or reducing native plant populations in our watersheds, it appears that current urban development (and the assumed resulting alterations in abiotic conditions) is not the mechanism promoting *L. sinense* invasion and



◀ **Fig. 5.** Boxplot of species growth by watershed category over two growing seasons. Species with *identical letters* are not significantly different (Tukey's HSD). The *line* in *each box* represents the median, the *box* encompasses the 25–75% range of data, and the *whiskers* show the non-outlier range. *A. canadense* Yr 1: $F_{2,177} = 1.93$, $P = 0.15$; Yr 2: $F_{2,97} = 4.59$, $P = 0.01$; *A. negundo* Yr 1: $F_{2,177} = 1.64$, $P = 0.20$; Yr 2: $F_{2,150} = 4.59$, $P = 0.01$; *C. latifolium* Yr 1: $F_{2,177} = 0.68$, $P = 0.51$; Yr 2: $F_{2,91} = 10.51$, $P < 0.0001$; and *L sinense* Yr 1: $F_{2,177} = 2.53$, $P = 0.08$; Yr 2: $F_{2,145} = 16.87$, $P < 0.0001$).

preventing recolonization of native vegetation. Although we did not directly manipulate disturbance regimes, we expected but did not find differences in watershed land cover to cause variance in survival or growth favoring *L. sinense* in developed watersheds. Moreover, forested watersheds do not appear resistant to *L. sinense* advancement because the species is equally abundant regardless of forest age, a finding similar to work on other non-native shrub species (Flory and Clay 2009). Our results support the notion that *L. sinense* is a strong invader of floodplain forests and all Piedmont floodplain forests appear at risk. None of the sites we investigated appear to have inherent resistance to prevent *L. sinense* invasion.

Our transplant experiment using *L. sinense* and three native species provided further insights into local versus watershed factors that may drive abundance of invader and native flora. Overall, growth and survival varied by species and among sites, but there was no consistent pattern on a landscape level and no association with increasing development. Survival of *L. sinense* seedlings was significantly higher than for *A. canadense* and *C. latifolium* (Figure 6), but this is more reflective of differences in life form (woody shrub vs. herbaceous forb and grass). A better comparison is with the functionally similar *A. negundo*; still *L. sinense* had higher mean survival, the least variation of survival among sites, and higher growth in year two (Supplemental Figure A3). If the experiment had continued these small but accumulating differences in survival and growth rates should increase *L. sinense*'s competitive edge over native woody species illustrating a long-term threat to southeastern floodplain forests.

This performance advantage is further enhanced through an apparent release from natural enemies. We found significantly reduced herbivory on *L. sinense* compared to native *A. negundo* and *C. latifolium* (Figure 7) which promotes invasiveness

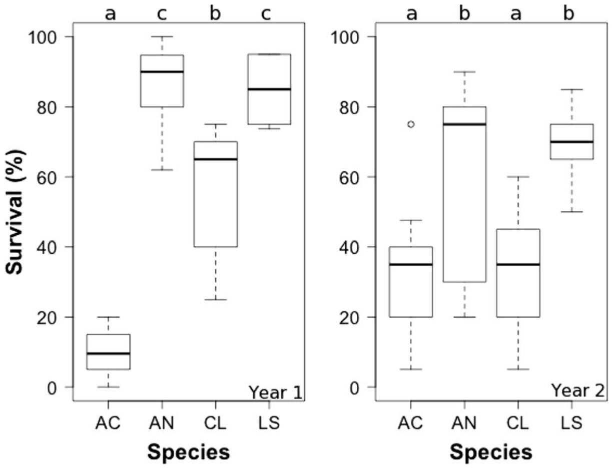


Fig. 6. Boxplot of species transplant survival (%) combined for all sites for growing seasons (Yr 1 $F_{3,32} = 80.47$, $P < 0.0001$; Yr 2 $F_{3,32} = 7.91$, $P = 0.0004$). Species with *identical letters* are not significantly different (Tukey's HSD). The *line* in *each box* represents the median, the *box* encompasses the 25–75% range of data, and the *whiskers* show the non-outlier range.

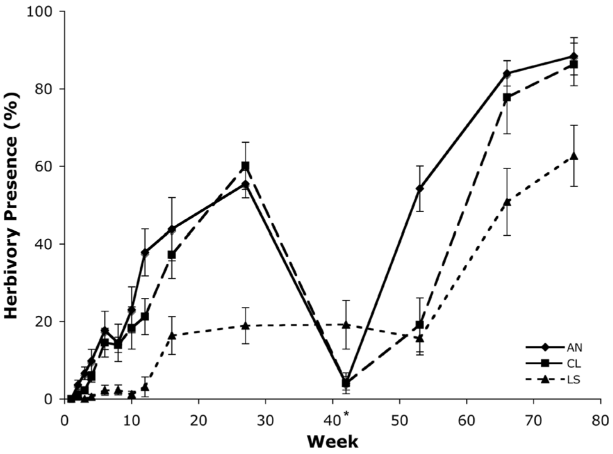


Fig. 7. Herbivory (%) of *A. negundo* (AN), *C. latifolium* (CL), and *L. sinense* (LS) over a 2-year period. Data are means ± 1SE of mean herbivory rates for nine sites each starting with 20 individual plants/site. The *asterisk* at week 40 indicates a winter time sampling event during winter when *A. negundo* and *C. latifolium* had no leaves to assess.

in other introduced species (Carpenter and Cappuccino 2005). The final outcome of the interaction of site conditions with native species and *L. sinense* are heavily invaded floodplain forests where a dense mid level canopy prevents recruitment of native species (Greene and Blossey 2012) despite apparently suitable growing conditions.

If *L. sinense* is competitively dominant over native species and able to survive and grow equally well in all watersheds, why is *L. sinense* cover strongly related with development (Figure 2)? Traditional explanations have focused on disturbance induced by urbanization, but our results show little differences in a variety of measures that should affect plant growth between urban and forested watersheds. This requires consideration of other factors associated with development that may promote invasive species. These could include additional factors that we did not directly measure in this study, such as propagule pressure, light availability, non-native predators, or altered soil microbial communities. Propagule pressure is considered an important factor promoting spread and abundance of invasive species (Levine 2001; Lockwood and others 2005; Von Holle and Simberloff 2005; Eschtruth and Battles 2009; Gavier-Pizarro and others 2010). As a horticultural introduction, it is likely that large *L. sinense* populations in developed watersheds are sources of initial introductions into riparian corridors as reported for other species (Hutchinson and Vankat 1997; Bartuszevige and others 2006; McDonald and Urban 2006; Gavier-Pizarro and others 2010; Dolan and others 2011). Once propagules arrive and establish, it appears only a matter of time before *L. sinense* is able to become competitively dominant and able to transform riparian habitats.

Results of our forest stand surveys show that size class is a significant predictor for both cover and stem density of *L. sinense* (Figure 3). Moreover, size of the single largest *L. sinense* individual had a much higher explanatory power than any landscape metric in predicting *L. sinense* prevalence. Because our transplant experiment indicated that survival and growth of *L. sinense* are generally similar at all sites, we assume that the largest individuals are also the oldest. Increased *L. sinense* stem density and cover are not the result of more favorable conditions, but are a result of invasion history, making time since first arrival the most important factor in explaining *L. sinense* invasion success. Although growth and survival rates are likely to change over the lifespan of *L. sinense*, we studied a critical life stage and individuals that pass through this filter are likely to persist on the landscape. The association of *L. sinense* and human development is likely the result of horticultural legacies (Williams and others 2009; Dolan and others 2011), higher propagule pressure close to human settlements, and time since invasion, not disturbance or alterations of habitat quality in floodplain forests. Sites with high *L. sinense* abundance or cover outside of developed watersheds are likely results of past chance long distance dispersal events.

Our results have important implications for conservation of native and management of invasive species. Although urbanization creates sources (ornamental plantings) of propagules that invade riparian areas in our study region, urbanization does not benefit *L. sinense* or handicap native species by changing edaphic conditions or hydrology, at least not for the species we investigated. In our particular example, *L. sinense* appears to be the ''driver'' and not a ''passenger'' in transformations of floodplain forests. Urban environmental conditions appear to be secondary in effect to human preference, propagule pressure, and *L. sinense* traits in explaining distribution patterns.

By looking into the past, we are afforded a clear view of the future. At sites where *L. sinense* has been present for long periods of time, *L. sinense* is able to become highly abundant and dense leading to reduced native plant growth and survival (Osland and others 2009; Greene and Blossey 2012). Even though *L. sinense* is currently most dominant in developed watersheds, more distant and forested watersheds are not resistant to *L. sinense* invasion. There are no ''safe sites'' for native plant species. Assumptions that *L. sinense* has invaded all suitable habitats are premature. Land managers need to focus their attention on newly invaded areas since sites with current lower *L. sinense* stem density and cover are likely incipient invasions. These should be focal points for removal because elimination of *L. sinense* effectively resets the invasion trajectory and prevents negative effects on native species (Greene and Blossey 2012). But neither of these steps will ultimately be successful without addressing the apparent root cause of *L. sinense* invasion, that is, propagule sources. This should inherently change ecologist's view of urban areas as not the cause of, but the source of invasive species. Management strategies preventing spread and introduction of invasive species should be more effective than alleviating urbanization effects.

Studies like ours and others (Chytry and others 2008; Predick and Turner 2008; Eschtruth and Battles 2009; Flory and Clay 2009) that simultaneously examine local dynamics and landscape level factors provide critical insights into mechanisms promoting species invasions. Our study also offers a more positive outlook for management of floodplain forests, even if *L. sinense* cannot be completely controlled or eradicated. Urbanization, despite creating habitat loss and many other associated changes, did not have devastating effects on downstream conditions for native plants. Managers should promote establishment of native vegetation as they are trying to prevent initial establishment of *L. sinense*.

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