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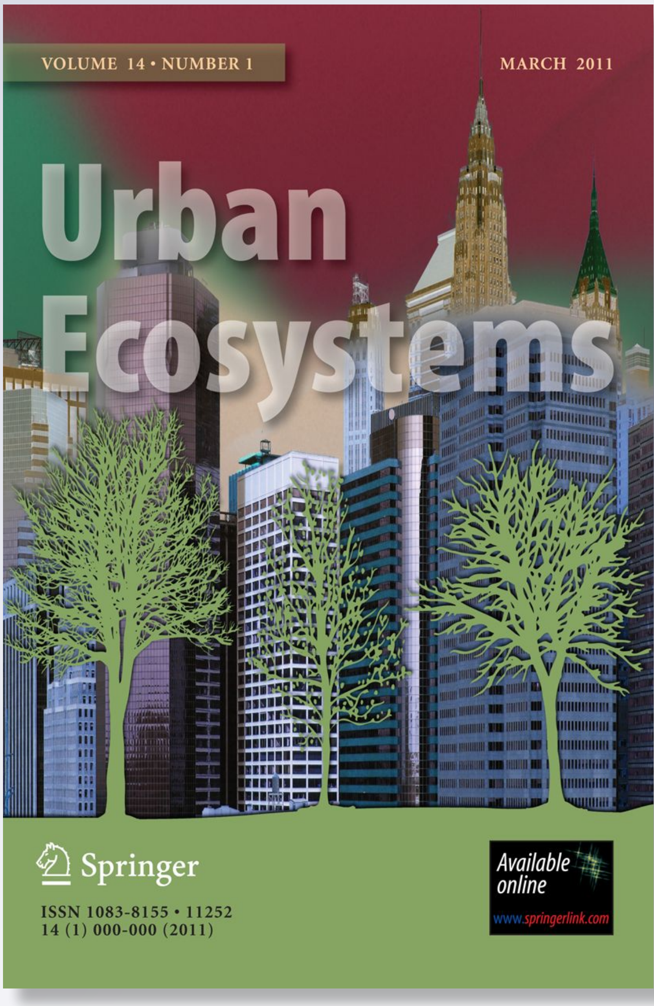

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Vegetation composition and structure of woody plant communities along urban interstate corridors in Louisville, KY, U.S.A.

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Abstract Urban forests adjacent to interstate corridors are understudied ecosystems across cities. Despite their small area, these forests may be strategically located to provide large ecosystem services due to their ability to act as a barrier against air pollutants and noise as well as to provide flood control. The woody vegetation composition and structure of forests adjacent to urban interstates is an important determinant of their ability to provide these services. However, these forest communities may be particularly susceptible to the introduction of exotic invasive species via the interstate and the surrounding city that can potentially alter current and future forest composition. The purpose of this study was to investigate the distribution of native and exotic woody vegetation and tree regeneration in forests along three interstate corridors in Louisville, KY, and to determine potential factors (e.g., traffic density) that are correlated with patterns in the woody vegetation community. We found the most important determinants of vegetation composition along these interstate corridors were the distance from the city center and the presence of an exotic invasive shrub, Amur honeysuckle (*Lonicera maackii*). Compared with forested plots within 10 km of the city center, plots further from the city center had 81% lower stem density of Amur honeysuckle, 96% higher tree seedling regeneration, and 51% greater woody plant species richness. The primarily native species composition of adult trees in forests alongside urban interstates in Louisville and the regeneration of native tree species provide optimism that these forests can maintain native species while experiencing multiple impacts from the interstate as well as from the surrounding city, emphasizing their important potential for maintaining natural forest functions across the urban landscape.

Keywords Urban interstates · Urban forests · Amur honeysuckle · *Lonicera maackii* · Exotic invasive species · Non-metric multidimensional scaling (NMDS) · Ecosystem services · Forest regeneration

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Introduction

Cities, the most human-dominated of all ecosystems, are inhabited by approximately 50% of the world's population (United Nations Department of Economic and Social Affairs, Population Division 2009). In the United States, nearly 80% of the population resides in cities and associated suburban areas (U.S. Census Bureau 2001). The expansion of urban areas in the United States can be partially attributed to the interstate highway system built in the mid-1900s with the purpose of connecting cities across the landscape (Forman et al. 2003). While the total land area covered by roads and cities is a small proportion of the total United States land area, the area ecologically affected by roads and cities is much larger (Folke et al. 1997; Forman 2000; Nowak and Walton 2005). Roads have multiple impacts (e.g., physical compaction, chemical deposition, wildlife mortality) that affect nearby terrestrial and aquatic systems (Spellerberg 1998; Trombulak and Frissell 2000; Forman et al. 2003). Similarly, cities have elevated pollutant loads, altered climate regimes, and increased exotic species presence relative to rural landscapes (Botkin and Beveridge 1997; Gatz 1991; Lovett et al. 2000; Zipperer and Guntenspergen 2009). While previous research has examined the ecological effects of cities and roads on natural areas, to our knowledge no research has investigated the combined effects of the urban environment and major highways on natural terrestrial communities.

Despite their small area, natural and semi-natural areas located adjacent to interstate highways in urban environments are well situated for providing disproportionately large benefits to society by offsetting the ecological impacts of concentrated human activity along roads and in cities. Woody vegetation in cities can provide many ecological benefits such as increased pollutant filtration (Grantz et al. 2003; McPherson et al. 1997; Nowak et al. 1997), carbon storage/sequestration (Jo and McPherson 1995), temperature amelioration (Bolund and Hunhammar 1999; Chen and Jim 2008), and psychological well-being (Smardon 1988). In addition, roadside vegetation enhances the visual perception of the landscape and creates an effective barrier to objectionable views from the roadside (Smardon 1988), potentially improving the commuting experience in increasingly congested urban environments. Vegetation barriers along roads, even if narrow, provide an additional benefit by reducing noise to adjacent residents, a benefit that is improved when the vegetation buffer is closer to the noise source (i.e., highway) (Anderson et al. 1984; Harris and Cohn 1985; Heisler 1977). Vegetation composition and structure is an important determinant of the ability of roadside vegetation buffers to provide these benefits for people in cities and to promote plant and animal movement across harsh urban environments.

Compared with forest communities in many rural areas, those located in urban environments, particularly alongside roads, are susceptible to the introduction and spread of exotic invasive species. In addition to direct planting of exotics next to forested verges, vehicles can disperse viable seeds from many plant species (Schmidt 1989; Wace 1977) and thus roadside environments and urban areas may be more susceptible to introduced plant species than habitat types in other locations. Many studies have shown an increased abundance of exotic invasive species in urban forests compared with rural forests (e.g., Arévalo et al. 2005; Duguay et al. 2007). Transportation corridors have also been shown to increase the presence of exotic invasive species in protected areas in the United States (Gelbard and Belnap 2003; Watkins et al. 2003), Canada (Hansen and Clevenger 2005), and South America (Pauchard and Alaback 2004). Studying the distribution of exotic plant species across road networks in urban environments is important for understanding their potential impacts on native plant species, the future integrity of the native forest community, and the ability of these forests to provide ecosystem services in the urban environment.

The wooded verges alongside major highways have been understudied "forgotten forests" in urban areas and across the landscape in general. Therefore, the goal of this study was to determine the composition and structure of the woody vegetation (trees, shrubs and woody vines) adjacent to three interstates (I-64, I-65, and I-71) in Jefferson County (Louisville), Kentucky. At the larger landscape-scale, our goal was to determine the changes in woody vegetation composition and structure along interstate highway corridors across an urbanization gradient from Louisville's city center to the more suburban and rural Jefferson County boundary. We addressed the following specific questions: 1) What are the distribution and abundance patterns of native and exotic woody plant species across three interstate highways in Jefferson County, KY?, 2) What factors (plot-scale and landscape-scale) are correlated with the distribution of vegetation along these forested urban interstates?, 3) What are the patterns of tree species regeneration in highway forest communities in Jefferson County, KY?, and 4) What are the differences in native species distributions, exotic species abundance, and tree regeneration between forested verges located close to the city center versus those further away? Based on previous studies (e.g., Gelbard and Belnap 2003) that demonstrated the ability of roads to facilitate the spread of exotic invasive species, we expected greater abundance of exotic invasive species in forested plots adjacent to highway stretches with greater traffic density. Previous research also showed that exotic species were more numerous and abundant closer to urban centers (e.g., Zipperer and Guntenspergen 2009), so we expected greater exotic species abundance along highways closer to downtown Louisville.

Methods

Study area

The study area (Jefferson County, KY) is located in the Interior Low Plateau, Bluegrass Section and in the Eastern Broadleaf Forest biome (National Atlas of the U.S. 2009). The city of Louisville, founded in 1778, is located in north-central Kentucky along the Ohio River (38° 15′ N, 85° 45′ W). In 2003, Louisville merged with Jefferson County to form the Louisville-Jefferson County Metro Government and ranks 16th in the nation as a city with a population of 713,877 and a mean density of 695 people km^{-2} (U.S. Census Bureau 2008). The mean annual temperature is 13.8°C, with a mean minimum temperature in January of −3.9°C and a mean maximum temperature in July of 30.6°C (National Climate Data Center 2009). Mean annual precipitation is 113 cm, and is evenly distributed throughout the year. The total inorganic nitrogen in wet deposition ranged from 4.6 to 6.2 kg N ha^{-1} from 2006 to 2009 (National Atmospheric Deposition Program 2010).

Louisville interstates

The Louisville metropolitan area has three interstate highways that extend east (I-64), south (I-65), and northeast (I-71) from the city center and pass through Jefferson County. The total highway length within the county from the city center along I-64 is 18.9 km, along I-65 is 13.3 km, and along I-71 is 11.3 km. Construction of I-64, I-65, and I-71 within Jefferson County was completed approximately 40 years ago (1968–1972) (KYTC Projects Archive 2008). To characterize patterns in woody vegetation structure, twenty-one 100-m^2 (10 m ×10 m) study plots were established in forested verges alongside I-64, I-65, and I-71 within the Louisville metropolitan area (Fig. 1). Plots were selected in a stratified random manner within 1 km intervals from the city center to the county boundary (metropolitan area), and located where the vegetation canopy was at least 20-m wide (perpendicular to the interstate). In some locations along each interstate, plots were established at similar distances along the interstate from the city center, but on opposite sides of the highway (Fig. 1). These plots were treated as independent points along each interstate due to differences in plot characteristics (e.g., vegetation composition, dominant tree species, topography). Due to more intense urban development close to the city center along I-65, no forested verges existed within 10 km of the city center along this highway (Fig. 1). Consequently, a more even plot distribution was possible along I-64 (n=10) and I-71 (n=7) than along I-65 (n=4).

Traffic density values were obtained from the Kentucky Transportation Cabinet (KYTC Traffic Count Program 2007) to provide an index for current road impact (e.g., vehicle emission concentrations). The traffic density along the interstate corridor from the city center extending to the county boundary is not similar between the three interstates. I-65 has the highest average daily traffic density (52,406 vehicles km^{-1} d^{-1}) with a maximum of 141,000 vehicles d^{-1} 14 km from the city center. I-64 is intermediate in traffic density (29,129 vehicles km^{-1} d^{-1}) and has a maximum of 131,282 vehicles d^{-1} at the intersection

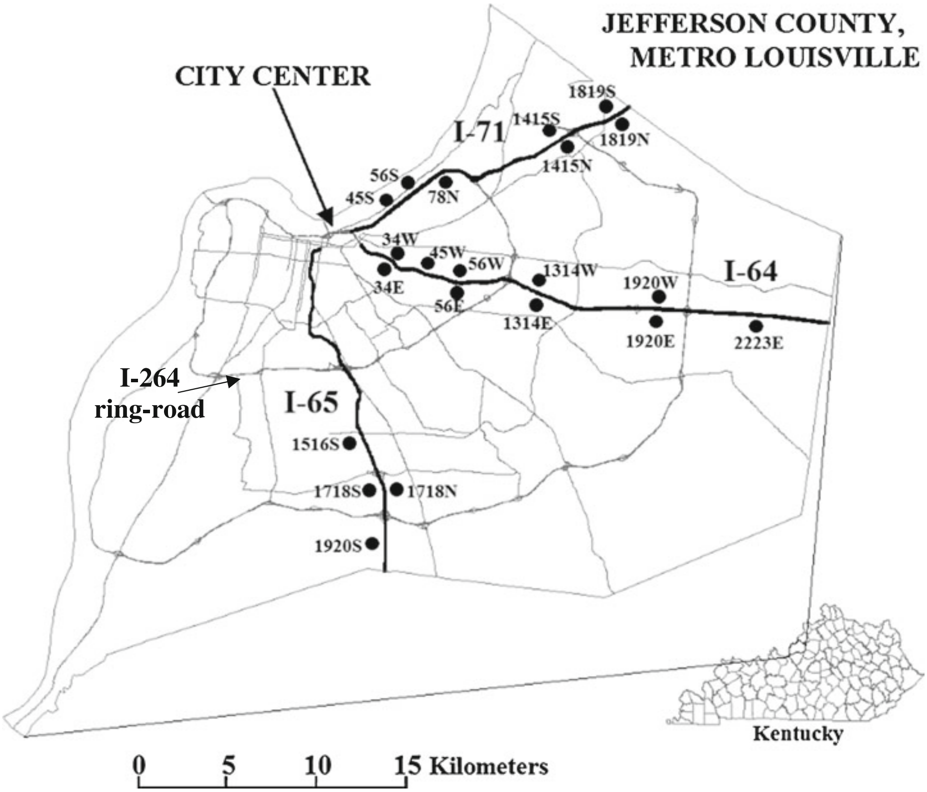


Fig. 1 Map of Jefferson county, metro Louisville, showing location of I-64, I-65, and I-71 forest sites (*black circles*). The I-264 ring-road crosses each interstate approximately 10 km from the city center

of the ring road I-264 11 km from the city center. I-71 has the lowest average traffic density (14,162 vehicles km^{-1} d^{-1}) with a maximum of 69,965 vehicles d^{-1} 2 km from the city center.

Land cover (i.e. impervious surface and vegetation cover) adjacent to each interstate was estimated using Geographic Information Systems (GIS; ArcGIS 9.2, ESRI 2006). A 0.5 km wide transect belt along both sides of the interstate extending from the city center to the county boundary (south I-65; east I-64, and north I-71) was used in GIS to determine impervious and vegetation cover (see below for details on vegetation and impervious surface data layers used). I-65 had the lowest vegetation cover (16.6%) within 0.5 km of the interstate compared to I-64 (23.4%) and I-71 (31.3%), and the highest impervious surface cover (40.8%) compared to I-64 (23.4%) and I-71 (18.4%).

Since these interstates pass through the entire county, soil series change along these interstate corridors (see Trammell 2010 for details). The soil type for the study plots along I-65 consisted almost solely of hydric soils (series names: Zipp, Newark, Melvin, and Lawrence) that occasionally flood due to this area having been the location of an ancient lakebed in the Quarternary period. The main soil series along I-64 developed under mesic hardwood forests (series names: Crider, Caneyville, Hagerstown, Lawrence, Nicholson, and Beasley) that were all formed atop Siluran or Devonian limestone or dolomitic Ordovician bedrock. The soil types varied more along I-71 and consisted of disturbed urban soils (Udorthents), and more natural soil series (series names: Lindside, Newark, and Caneyville) that formed on Silurian limestone bedrock or on Quaternary soils of alluvial origin. Soil characteristics (e.g., pH, bulk density, heavy metals) were measured along with vegetation data in each forest plot. Detailed description of soil data and relationships between soil and vegetation data are described in Trammell et al. (in press). Here we focus on woody vegetation patterns and *aboveground* factors that may be correlated with the observed patterns in the woody vegetation data.

Vegetation composition measurements

At each 100-m^2 plot, composition and size structure were determined for all woody plants (i.e., all adult trees, saplings, seedlings, shrubs, and vines were sampled within each plot). The size structure of adult trees and saplings was determined by measuring diameter-at-breast-height (dbh) and calculating basal area ($BA=\pi r^2$). Species identifications and nomenclature followed Gleason and Cronquist (1991). Adult tree species were those having a dbh ≥2.54 cm, saplings were those with dbh <2.54 cm and height ≥1 m, tree seedlings were those having a dbh <2.54 cm and height <1 m. For some data analyses, the adult tree size class was further divided into a ‘young’ size class (dbh ≥2.54 cm and <10 cm) and the adult size class became those trees having a dbh ≥10 cm. The size structure for shrubs and vines was determined by counting stem density and separating individuals into three height categories: <1 m, ≥1 m and <2 m, and ≥2 m. Importance values (IV) for species were calculated for each plot according to the following equations:

Adult trees or saplings:

$$IV = (RD + RBA)*(100/2)$$

Tree seedlings:

$$IV = RD*100$$

Shrubs or vines:

$$IV = (RD + RD \geq 2m)*(100/2)$$

where RD is the relative density (expressed as a decimal fraction); RBA is the relative basal area. The shrub and vine IV included the relative density of shrubs or vines ≥2 m as a means of weighting large shrubs and vines more heavily in the IV calculation. An exotic species index (ESI) based on the relative densities of exotic trees, shrubs and vines, was calculated for each plot for some analyses according to the following equation:

$$ESI = (\text{exotic tree RD} + \text{exotic shrub RD} + \text{exotic vine RD})*(100/3)$$

In this study, species were defined as exotic if they did not occur in the lower 48 states prior to 1600 CE.

Plot-scale variables

Six plot-scale characteristics (% slope, % canopy openness, sunlight intensity, distance from plot boundary to the forest canopy line, distance from plot boundary to interstate pavement, and traffic density) were measured as possible explanatory variables for the observed patterns in woody vegetation composition. Plot slope (degrees) was measured using a clinometer. Canopy openness and sunlight intensity data were collected 1-m above the ground, resulting in the inclusion of shrub canopy in these measurements. Canopy openness was measured using a densiometer at sixteen evenly spaced points in each study plot. Photosynthetically active radiation (PAR) measurements (μmol s^{-1} m^{-2}) were determined using a LiCor 250 light meter (Lincoln, NE) at 16 points in each plot between the hours of 11 AM and 2 PM in July and August (within 1 to 2 h of true sun peak during daylight savings time). Measurements were taken as 15-second averages and divided by sunlight PAR measurements taken in the open just before and after plot measurements to obtain percent of full sunlight for each plot.

One initial plot criterion included establishing the plot boundary approximately 5-m from the forest canopy edge along each interstate. However, differences in forest canopy structure, topography, and management regimes, such as variable mowing widths, alongside interstates did not permit this distance to the plot boundary to be consistent across plots. Thus, distance from the plot boundary to the forest canopy edge was measured as a possible predictor for woody vegetation characteristics. The width of the mow zone alongside the interstates was inconsistent; therefore, the edge of the forest occurred at varying distances from the edge of the interstate pavement. This distance was also measured as a possible predictor for vegetation characteristics. Consequently, forest plots were located 4–12 m from the forest canopy edge and 5–31 m from the interstate pavement. Traffic densities adjacent to each plot were obtained using the closest mile-marker for which traffic density is measured (KYTC Traffic Count Program 2007).

Landscape-scale context

It was expected that landscape-scale context (e.g., distance from the city center, land use) surrounding the forest plots could also partially explain the vegetation composition patterns observed. Distance from the city center to each forest plot was measured from a point where all three interstates meet near the Central Business Area. Geographic Information Systems (GIS; ArcGIS 9.2, ESRI 2006) was used to obtain urban metrics (impervious surface, population density, and land use) and woody vegetation cover within semi-circular areas having 500 m, 1 km, and 2 km radii from the center of each plot. Semi-circular, rather than circular, buffer areas were used in order to determine the context around the plot exclusive of the interstate itself. Three spatial scales were chosen (i.e., 500 m, 1 km, and 2 km radii) to determine whether plot variable correlations with landscape context were scale sensitive. Data layers were provided by LOJIC (Louisville and Jefferson County Information Consortium), which maintains spatial maps and aerial photographs of the metropolitan area and digitally drawn data layers to 0.3 m resolution for the county from aerial photographs taken in 2006. Impervious surface cover was determined from the total proportion of land area covered by buildings, roads, miscellaneous transportation (e.g., sidewalks, parking lots), and airports. Population density was determined from the year 2000 census tract data provided by LOJIC. The land-use data provided via LOJIC is a combination of Anderson level I and II land-use types (seven land-use categories: single-family residential, multi-family residential, commercial, industrial, public, parks/cemeteries, and vacant/undeveloped). Woody vegetation cover was calculated from LOJIC data layers showing the total area covered by trees and shrubs. These landscape-scale characteristics were used because it was thought they might provide additional correlates for explaining vegetation composition and distribution patterns along interstate corridors.

Statistical analysis

Indicator species analysis (Dufrêne and Legendre 1997) was used to determine which woody plant species were good indicators for each of the three interstate corridors (I-64, I-65, vs. I-71; PC-ORD v 4.25). Indicator analysis was also used to determine whether plots at different distance categories from the city center could be distinguished from each other (plots close to the city vs. plots further from the city). A good indicator is a species that occurs in one group while not occurring in other groups (McCune et al. 2002). For each species in each group, species indicator values are calculated based on proportional abundance (e.g., the abundance of each species along each highway) and proportional frequency (e.g., proportion of plots along each highway that contain a species) (McCune et al. 2002). Statistical significance was determined by comparing observed indicator values for a species with an expected indicator value obtained by using 1000 Monte Carlo randomizations where species data are randomly reassigned to different groups (e.g., highways).

To determine similarities and differences in patterns in vegetation structure among plots Nonmetric multidimensional scaling (NMDS) analysis was conducted using PC-ORD v 4.25 statistical software (Kruskal 1964; Mather 1976; McCune et al. 2002). Importance values for all tree, shrub, and woody vine species that occurred in more than one plot across all highway plots were used in the NMDS analysis (i.e., rare species were dropped from the analysis). The SØrensen (Bray-Curtis) distance measure and a random starting configuration were used on 40 real data runs. Fifty Monte Carlo runs with randomized data were used for selecting dimensionality. To minimize stress and maximize correlation between variables with ordination configuration, a three-dimensional NMDS ordination solution of 43 species across 21 plots was selected by PC-ORD. The final stress value was found to be satisfactory (final stress = 10.01; instability = 0.00001; 86 iterations). Proportion of variance explained by each dimension is represented by correlations between the distance in ordination space and distance in the original n-dimensional space (dimension 1, r^2=0.670; dimension 2, r^2=0.138; and dimension 3, r^2=0.063). Only dimensions 1 and 2 are shown because they explained most of the variation in the three-dimensional NMDS ordination solution. Correlations between species importance values and dimension scores for each plot were used to assess species contributions to explaining vegetation structural patterns. To assess their ability to explain observed vegetation patterns, six plot-scale and 13 landscape-scale variables (seven land use, four impervious surface, population density, and woody vegetation variables at three buffer distances from plot center) were overlain on the NMDS two-dimensional ordination, thereby creating a biplot (with significant variables graphically represented by vector lines in ordination space). The ability of species (e.g., exotic species index and Amur honeysuckle importance value) and environmental (e.g., distance from the city center) variables to explain patterns in vegetation composition (i.e., NMDS dimension 1 plot scores) was evaluated using bivariate linear regression in Systat 10.2.

To assess whether differences in vegetation characteristics (e.g., tree seedling density) were related to distance from the city center, a single-factor model (ANOVA, Systat 10.2) was used to partition variation across all three highways between plots close to the city center (<10 km) vs. plots far from the city center (>10 km). The 10 km distance was chosen because it approximated the boundary of the city of Louisville before the city-county merger and still encompasses the more densely populated area of the county. In addition, relationships between vegetation data (i.e., tree density, tree basal area, seedling density, sapling density, exotic seedling density, and Amur honeysuckle stem density) and percent light in plots close to the city center versus plots further from the city were evaluated using two sample *t*-tests when data met the assumptions of normality and homoscedasticity after log-transformation. The non-parametric Mann–Whitney test was used when data did not meet the assumptions of normality and homoscedasticity after transformation. All tests for significance are reported at the $\alpha=0.05$ critical value.

Results

Interstate-scale vegetation analysis (I-64, I-65, and I-71)

In the forested verge communities across all three interstates in Louisville, KY, we identified 50 tree species, 22 shrub species, and 18 woody vine species (Appendix Table 5). A relatively small proportion (6%) of the tree species were exotic whereas a larger proportion of the shrub and vine species were exotic (18% and 22%, respectively; Appendix Table 5). Sixty-three percent of the tree species, 39% of shrub species, and 58% of vine species occurred in at least 5% of the plots. The most frequently found adult, sapling, and seedling tree species were native. *Acer saccharum* adults and saplings were the most frequently found and occurred in 62% and 33% of all plots, respectively. The most frequently observed tree seedling species was *Celtis occidentalis*, which occurred in 72% of all plots. In contrast, the most frequently observed shrub species (*Lonicera maackii*, 95% of plots) and vine species (*Lonicera japonica*, 86% of plots) were exotic and invasive.

The average density of trees >2.54 cm dbh across all three highways was 1,587 stems ha^{-1} (range = 500 to 3,200 stems ha^{-1}) and the mean basal area was 52.4 m^2 ha^{-1} (range = 9.3 to 113.4 m^2 ha^{-1}). The stands along the most heavily traveled interstate, I-65, had the highest average stem density (1,775 stems ha^{-1}) and the highest basal area (70.5 m^2 ha^{-1}) compared to the stem density in stands along I-64 and I-71 (1,600 and 1,386 stems ha^{-1}, respectively) and to their basal areas of 42.1 and 44.7 m^2 ha^{-1}, respectively. A large proportion of the tree stem density (> 2.54 cm dbh) in forested verges along I-65, I-64, and I-71 consisted of native species (Table 1). The dominant tree species contributing to stem density and basal area differed along each interstate. I-65 and I-71 each contained one native species that contributed at least 26% to their respective

Table 1 Tree species distributions in forested verges of three interstate corridors in Louisville, KY, the mean stem densities (stems ha^{-1}) and basal areas ($m^2\ ha^{-1}$) of individuals with >2.54 cm dbh. Interstates arranged left to right in decreasing order of traffic density. Bold values represent the species that contributed the most to stem density (two species) and basal area (one species) for each highway. N=4 plots for I-65, 10 plots for I-64, and 7 plots for I-71; all plots 100 m^2

Species	Density (stems ha^{-1})			Basal area ($m^2\ ha^{-1}$)		
	I-65	I-64	I-71	I-65	I-64	I-71
Carya ovata	–	**1,100**	–	–	12.3	–
Prunus serotina	–	**1,100**	100	–	1.6	1.9
Sassafras albidum	*	800	–	*	2.3	–
Carya sp	300	–	**800**	7.9	–	19.4
Acer saccharum	150	343	**750**	24.0	10.8	4.3
Cercis canadensis	–	233	–	–	2.3	–
Platanus occidentalis	–	100	200	–	32.1	14.2
Acer negundo	*	200	167	*	1.6	5.8
Quercus rubra	*	200	100	*	24.6	18.1
Ailanthus altissima	–	550	–	–	7.8	–
Juglans sp	–	133	–	–	4.6	–
Albizia julibrissin	–	100	–	–	**57.7**	–
Fraxinus sp	–	100	–	–	22.1	–
Juglans cinerea	–	100	–	–	1.9	–
Ostrya virginiana	–	100	–	–	1.6	–
Populus deltoids	–	–	200	–	–	7.2
Ulmus thomasii	–	–	200	–	–	1.1
Morus rubra	–	*	100	–	*	3.0
Quercus palustris	100	–	–	8.0	–	–
Liriodendron tulipifera	133	–	–	9.2	–	–
Acer sp.	150	–	100	20.7	–	4.4
Acer rubrum	150	–	–	**41.0**	–	–
Celtis occidentalis	200	275	225	1.2	6.4	2.4
Robinia pseudoacacia	200	150	375	8.5	18.5	**34.7**
Juniperus virginiana	200	*	*	1.7	*	*
Carya tomentosa	250	180	375	1.5	12.3	14.5
Diospyros virginiana	350	150	–	9.0	3.3	–
Nyssa sylvatica	**400**	–	–	11.6	–	–
Ulmus rubra	**525**	–	200	5.0	–	1.9

* = less than 1.0 $m^2\ ha^{-1}$; – = absent

Data are not shown for species with stems larger than 2.54 cm dbh, but that did not comprise more than 1.0 $m^2\ ha^{-1}$ basal area along an individual interstate. For I-65 these were *Acer negundo*, *Acer pseudoplatanus*, *Prunus sp*, *Quercus rubra*, and *Sassafras albidum*; for I-64 *Acer pseudoplatanus*, *Aesculus glabra*, *Aralia spinosa*, *Asimina triloba*, *Cornus florida*, *Cornus sp*, *Prunus hortulana*, and *Quercus sp.*; for I-71 *Juglans nigra* and *Quercus muehlenbergii* mean basal areas (*Acer rubrum* and *Robinia pseudoacacia*, respectively), with these species occurring in at least half of the plots on each interstate. The dominant species contributing to mean basal area along I-64 was an exotic species (*Albizia julibrissin*), but it only occurred in one plot. Two other species contributing substantially to basal area along I-64 were the natives, *Quercus rubra* and *Platanus occidentalis*.

Differences in tree community diversity in each tree size class category are revealed by examining rank-abundance curves for each interstate highway (Fig. 2). Species richness, species composition, and community evenness (as revealed by the slope of the curves) differed among the tree size classes and the three interstates (Fig. 2). Community evenness across the adult and young tree size classes along I-65, I-64, and I-71 (Fig. 2a,b,e,f,i,j) was high among species, with no single species dominating the communities. However, while sapling evenness was also high along I-64 (Fig. 2g), saplings along I-65 and I-71 as well as seedlings across all three interstates were dominated by only a few species (e.g., Fig. 2k). All of the tree species along I-65 and I-71 were native, with the exception of *Acer*

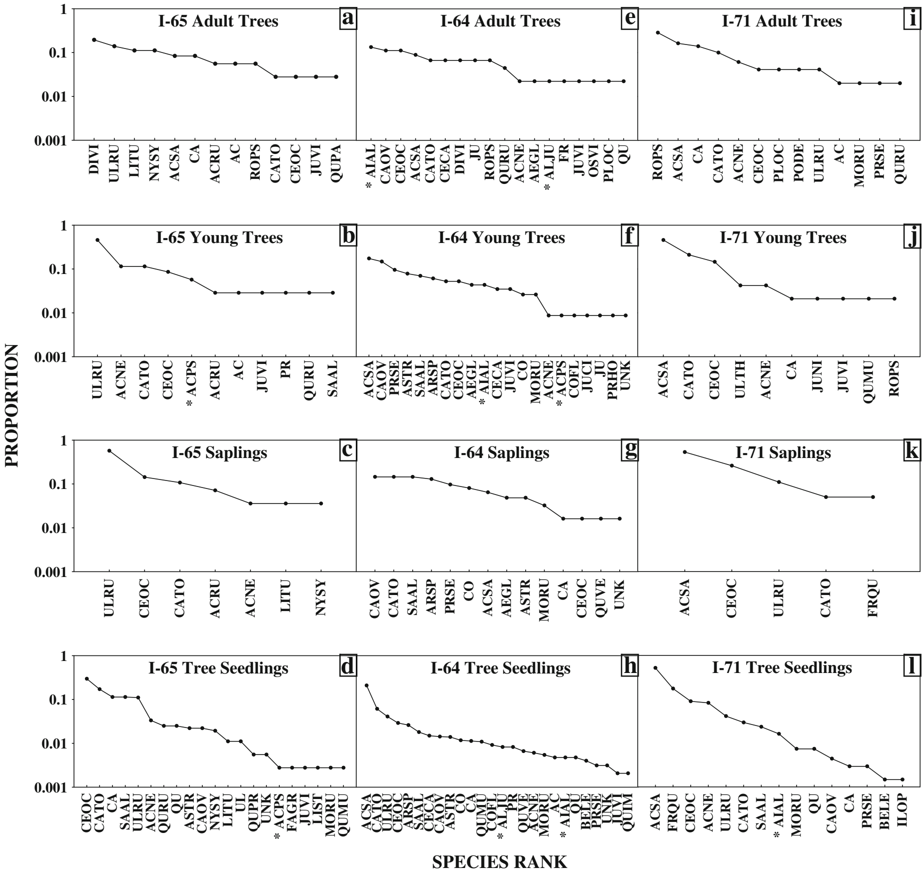


Fig. 2 Rank abundance of tree species along three interstates, I-65, I-64, and I-71, in Louisville, KY. Interstates are arranged according to traffic density (i.e., I-65 highest traffic density, I-71 lowest traffic density). Tree species are separated based on size classes: adult trees (dbh: >10 cm), young trees (dbh: 2.55–10 cm), and saplings (dbh: 1.0–2.54 cm and >1 m height). Exotic species are denoted by an asterisk next to species codes. See Appendix Table 6 for species codes

pseudoplatanus along I-65 (Fig. 2b, ACPS). The exotic species, *Ailanthus altissima*, was the most abundant in the adult size class along I-64; however, the second most abundant adult tree was the native *Carya ovata* (Fig. 2e).

The Shannon diversity index for all tree species across the three interstates (H'=3.64) was close to the maximum diversity (H' max=3.71) and tree species were equally abundant across the interstates (J=0.98). The Shannon diversity index was similar across all three interstates (I-65: H'=2.50, I-64: H'=2.91, I-71: H'=2.17) and relatively close to the maximum diversity possible for each interstate (I-65: H' max=2.89, I-64: H' max=3.37, I-71: H' max=2.83). The tree species were almost equally abundant for all three interstates (I-65: J=0.87, I-64: J=0.86, I-71: J=0.77).

The indicator species analysis identified the species that were the best indicators of each forest community along I-64, I-65, and I-71. I-65 was found to have eight species, all native, that were significant indicators of the forested communities along its verge within the county (Table 2). It is not surprising that *Ulmus rubra* had the highest indicator value (IV=92.3) using this analysis considering its position on the rank-abundance diagrams across all tree size classes (Fig. 2a–c). The high indicator value for *Liriodendron tulipifera* alongside I-65 (IV=75.0) was due to its complete absence in plots sampled along I-64 and I-71. The only woody shrub and vine species that were selected as indicators of the highway verge communities along I-64 and I-71 were the exotic invasives, *Lonicera maackii* and *Euonymus fortunei*, respectively (Table 2).

Landscape-scale vegetation analysis

The NMDS ordination explained 87.1% of the total variation in adult tree, shrub, and vine species composition along these three interstates in Louisville, KY. Dimension 1 explained 67.0% of the variation in the NMDS ordination and thus is the most important in determining patterns among species and plot distributions. Dimension 2 explained less variation (13.8%) in species distribution. The distribution of woody plant communities displayed a pattern across NMDS dimension 1 based on the relative densities of exotic tree, shrub, and vine species (exotic species index; Fig. 3), and exotic species relative abundance was significantly and negatively correlated with dimension 1 (r=−0.82, p<0.001). The forest plots with greater exotic species abundance (left side of dimension 1; Fig. 3) were closer to the city center (positive vector in Fig. 3), surrounded by more parks/cemeteries (negative vectors in Fig. 3), and had greater slope

Table 2 Indicator species based on interstate groupings: I-65 (n=4 plots), I-64 (n=10 plots), and I-71 (n=7 plots). Species listed in groups (I-65, I-64, vs. I-71) based on the location of the maximum observed indicator value (IV) for that species. Observed IV for each species determined significant using a Monte Carlo test based on 1,000 randomizations

Species	Group	IV	*p* value
Ulmus rubra	I-65	92.3	0.002
Liriodendron tulipifera		75.0	0.008
Toxicodendron radicans		68.0	0.010
Acer rubrum		50.0	0.040
Cornus oblique		50.0	0.033
Smilax rotundifolia		50.0	0.033
Lindera benzoin		44.3	0.049
Acer sp.		42.9	0.037
Lonicera maackii	I-64	48.3	0.012
Euonymus fortunei	I-71	64.1	0.023

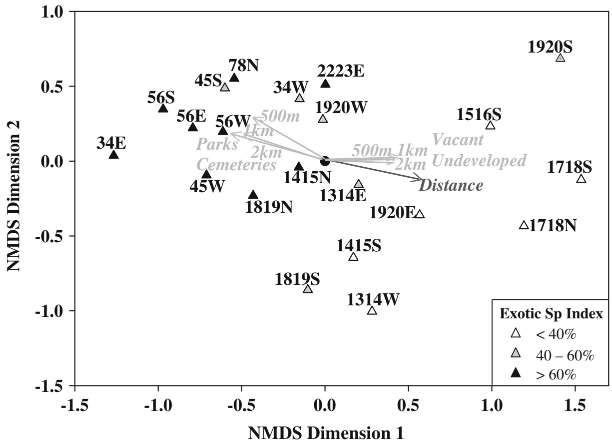


Fig. 3 Woody plant communities located on I-64, I-65, and I-71 are shown in NMDS dimension 1 vs. dimension 2 ordination space. Relative densities of exotic tree, shrub, and vine species are shown for each site (Exotic Species Index = (exotic tree relative density + exotic shrub relative density + exotic vine relative density)*(100/3)). Landscape-scale variables most strongly correlated with dimension 1 are distance from the city center (r=0.60, p<0.01; *dark gray vector*), vacant and undeveloped land-use cover at 500 m, 1 km, and 2 km around plots (r=0.54, r=0.54, and r=0.53, respectively; p<0.02), and park/cemetery land-use cover at 500 m, 1 km, and 2 km (r=−0.45, r=−0.52 and r=−0.55, respectively; p<0.05)

(negative vector in Fig. 4). Not surprisingly, the forest plots with fewer exotic species (right side of dimension 1; Fig. 3) were further from interstate pavement (positive vector Fig. 4) and surrounded by more vacant/undeveloped land cover and woody vegetation cover (positive vectors in Figs. 3 and 4, respectively). However, unexpectedly these forest plots were adjacent to greater traffic density (positive vector in Fig. 4). Seven exotic species were found in our forest plots (Fig. 4); however, most of these species were only found in a few plots (e.g., *Acer pseudoplatanus*, *Ailanthus altissima*, and *Rosa multiflora* present in two plots) and all of the exotic species except one (*Lonicera maackii*) exhibited weak correlations with dimension 1.

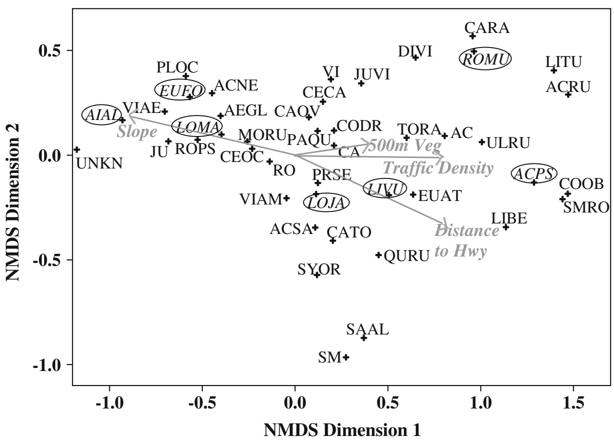


Fig. 4 Tree, shrub, and vine species in all forest plots along I-64, I-65, and I-71 are shown in NMDS dimension 1 vs. dimension 2 ordination space. The species codes for exotic species are shown in italics and circled. Plot-scale (slope, distance to highway, and traffic density; r=−0.75, r=0.73, and r=0.69, respectively; p<0.001) and landscape-scale (% woody vegetation cover within 500 m of plot center; r=0.45, p<0.05) variables most strongly correlated with dimension 1 are shown (*gray vectors*). See Appendix Table 6 for species

The species that explained the most variation in dimension 1 (83.9%) was an exotic, invasive species, Amur honeysuckle (*Lonicera maackii*, $r=-0.92$, $p<0.001$). In addition, two native tree species, slippery elm (*Ulmus rubra*) and red maple (*Acer rubrum*), respectively explained 46.1% and 39.3% of the variation in the species distribution across dimension 1 ($r=0.68$ and $r=0.63$, respectively; $p<0.01$). However, both tree species were present in relatively few plots (*Ulmus rubra* = 5 plots, and *Acer rubrum* = 2 plots) and should not be considered strong determinants of plot distribution across dimension 1. One vine species was also correlated positively with dimension 1, a native species (*Toxicodendron radicans*, $r=0.66$, $p<0.01$). The number of species ha^{-1} in plots across all three interstates was also positively correlated with dimension 1 ($r=0.68$, $p<0.001$), and was significantly and positively correlated with distance from the city center ($r=0.84$, $p<0.001$).

The landscape-scale variable that most strongly correlated with plots along dimension 1 was distance from the city center ($r=0.60$, $p<0.01$; Fig. 3). Since the former city of Louisville boundary occurred near a ring road expressway about 10 km from the city center (I-264, Fig. 1), we chose to conduct additional analyses comparing plots that were <10 km and >10 km from the city center. Indicator species analysis showed that *Lonicera maackii*, the species most strongly explaining variation in the NMDS ordination, was the strongest indicator of plots located <10 km from the city center (Table 3). We found significantly more *Lonicera maackii* stems in plots located <10 km from the city center (18,388 live stems ha^{-1}) compared with plots between 10 and 26 km from the city (3,462 stems ha^{-1}, $p<0.001$).

Plots located within 10 km of the city center had lower mean tree stem density and basal area than plots further from the city center (1,037 vs. 1,885 stems ha^{-1}, 43.7 vs. 51.3 m^2 ha^{-1}, respectively); however, these differences were not significant ($p>0.05$). The four most abundant tree species in plots further from the city were natives whereas the most abundant tree species in plots closer to the city center was an exotic invasive species (*Ailanthus altissima*; Table 4). In plots further from the city, the natives *Acer saccharum*, *Carya ovata*, *Carya tomentosa*, and *Ulmus rubra* were represented by many individuals in the 2.55–11.4 dbh size class and all four species were present in the 11.5–19.9 dbh size class (Fig. 5). In plots close to the city center, the most abundant species in the 2.55–11.4 dbh size class (*Acer saccharum*) was not present in larger tree size classes (Fig. 5), indicating that establishment of this species in intermediate size classes has not

Table 3 Indicator species based on distance from city center groupings. Species listed for the two groups, plots close to city ($n=8$) and plots further from city ($n=13$), are based on the location of the maximum observed indicator value (IV) for that species. Observed IV for each species determined significant at two levels ($p<0.1$ and $p<0.05$) according to Monte Carlo test based on 1,000 randomizations

Species	Group	IV	*p* value
Acer negundo	Close to city	**46.3**	**0.028****
Juglans sp.	(<10 km)	37.5	0.049*
Lonicera maackii		**69.2**	**0.006****
Euonymus fortunei		54.9	0.091*
Acer saccharum	Further from city	57.1	0.065*
Carya tomentosa	(>10 km)	**68.6**	**0.011****
Lindera benzoin		38.5	0.103*
Lonicera japonica		**74.3**	**0.004****
Toxicodendron radicans		63.3	0.076*
Vitis sp.		46.2	0.071*

*$p<0.10$

**$p<0.05$

Table 4 Mean stem density (stems ha^{-1}) and basal area (m^2 ha^{-1}) of trees (stems >2.54 cm dbh) in plots close to the city center (n=8) and plots further from the city center (n=13). Bold values represent the species that contributed the most to density (four species), basal area (one species), and importance value (two species). Importance Value = (relative density + relative basal area + relative frequency)*(100/3)

Species	Density (stems ha^{-1})		Basal area (m^2 ha^{-1})		Importance value	
	Close (<10 km)	Far (>10 km)	Close (<10 km)	Far (>10 km)	Close (<10 km)	Far (>10 km)
Ailanthus altissima	**550**	–	7.8	–	14.4	–
Acer saccharum	**467**	430	2.2	13.4	16.9	**29.4**
Robinia pseudoacacia	**367**	225	38.6	17.1	**22.3**	13.9
Celtis occidentalis	**325**	183	6.5	1.9	**20.6**	16.4
Ulmus rubra	200	**525**	1.9	5.0	6.2	13.0
Populus deltoids	200	–	7.2	–	7.1	–
Ulmus thomasii	200	–	1.1	–	6.1	–
Acer negundo	175	*	4.8	*	19.0	*
Platanus occidentalis	150	–	23.1	–	13.6	–
Juglans sp.	133	–	4.6	–	14.5	–
Acer sp.	100	150	4.4	20.7	5.8	9.1
Carya tomentosa	100	280	3.7	11.9	5.7	**28.6**
Albizia julibrissin	100	–	**57.7**	–	15.0	–
Fraxinus sp	100	–	22.1	–	8.8	–
Juglans cinerea	100	–	1.9	–	5.4	–
Morus rubra	100	*	3.0	*	5.5	*
Quercus palustris	–	100	–	8.0	–	4.3
Ostrya virginiana	–	100	–	1.6	–	3.2
Liriodendron tulipifera	–	133	–	9.2	–	9.7
Quercus rubra	–	133	–	14.3	–	10.6
Acer rubrum	–	150	–	**41.0**	–	12.5
Cercis Canadensis	–	233	–	2.3	–	8.9
Diospyros virginiana	–	250	–	6.2	–	12.2
Nyssa sylvatica	–	400	–	11.6	–	5.9
Sassafras albidum	–	450	–	1.3	–	7.0
Carya sp.	–	**550**	–	13.6	–	9.4
Prunus serotina	–	**600**	–	1.8	–	7.6
Carya ovata	–	**1,100**	–	12.3	–	11.1

* = less than 1.0 m^2 ha^{-1}; –= absent

Data are not shown for species with stems larger than 2.54 cm dbh, but that did not comprise more than 1.0 m^2 ha^{-1} basal area in the plots close to the city or far from the city. For plots close to the city center these were *Aesculus glabra* and *Prunus hortulana*; for plots far from the city center *Acer pseudoplatanus*, *Aralia spinosa, Asimina triloba*, *Cornus florida*, *Cornus sp*, *Juglans nigra*, *Juniperus virginiana*, *Prunus sp*, *Quercus muehlenbergii*, and *Quercus sp*.

been successful in recent decades. The exotic invasive species, *Ailanthus altissima*, was found only in the smaller size classes in plots close to the city center (Fig. 5).

Based on sapling and seedling stem density data, it appears that tree regeneration in plots further from the city center was significantly greater than in plots closer to the

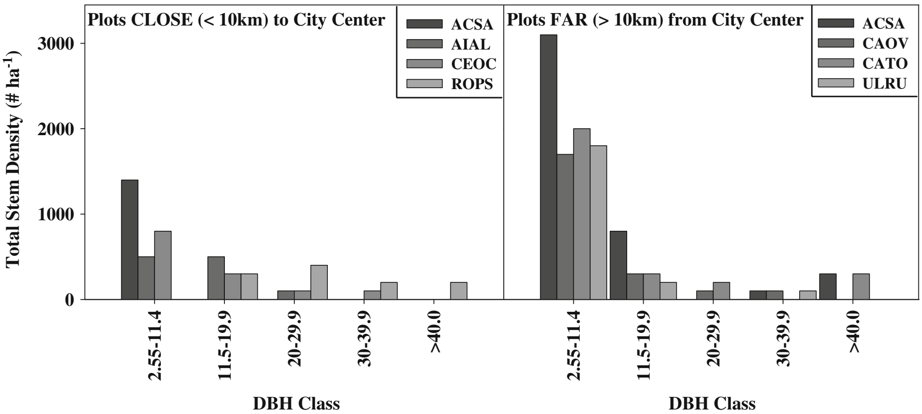


Fig. 5 Total stem density (# ha^{-1}) by dbh class in plots close (<10 km) and far (>10 km) from the city center (±1 SE). Total stem density of the four most dominant species shown, representing 59% of total density in plots close to the city center and 46.5% of total density in plots far from the city center. Species codes: ACSA—*Acer saccharum*, AIAL—*Ailanthus altissima*, CAOV—*Carya ovata*, CATO—*Carya tomentosa*, CEOC—*Celtis occidentalis*, ROPS—*Robinia pseudoacacia*, ULRU—*Ulmus rubra*

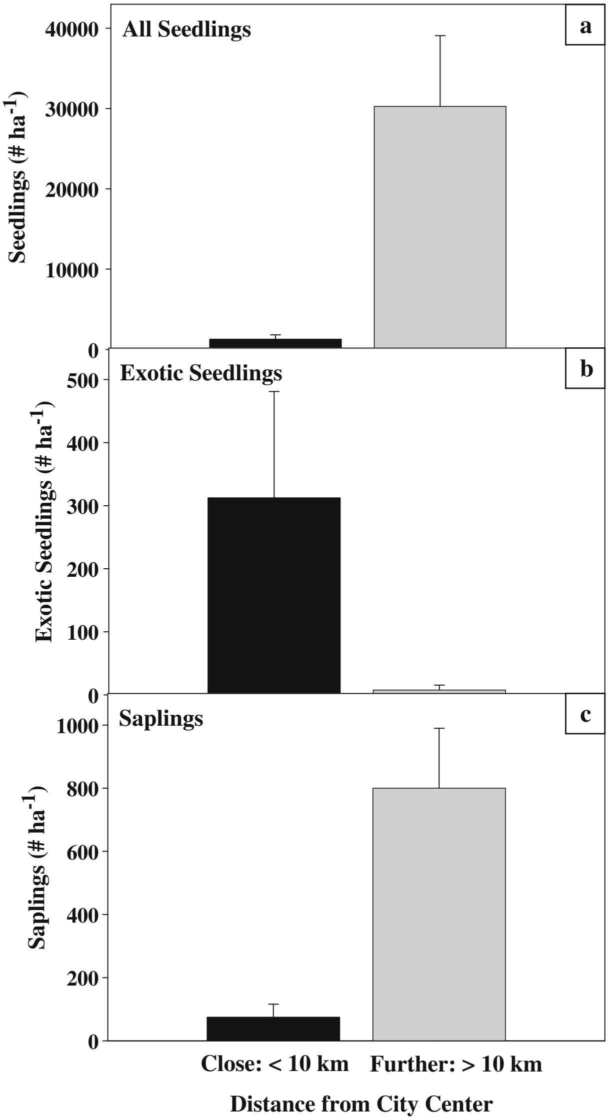
city (saplings = 800 vs. 75 stems ha^{-1}, seedlings = 30,262 vs. 1,275 stems ha^{-1}, $p<0.001$; Fig. 6a,c). However, exotic tree species appear to be more successful in establishing populations in plots closer to the city center than in plots further from the city (313 vs. 8 stems ha^{-1}, $p=0.07$; Fig. 6b). Seedling stem density was significantly and positively related with % light ($r^2=0.55$, $p<0.001$), and plots further from the city center had significantly greater % light than plots close to the city (4.75% vs. 1.39%, $p<0.01$). The % light reaching the forest floor decreased exponentially as honeysuckle stem density increased ($y=3.5\ e^{-0.0095}$; $r^2=0.50$).

Discussion

We investigated the abundance and distribution of native and exotic woody vegetation and tree regeneration in forests along three interstate corridors in Louisville, KY, and discovered several factors that are correlated with the observed patterns in this woody vegetation community. Since understory exotic species potentially threaten the ability of native trees to regenerate in these highway verge forests, we examined the patterns in vegetation composition with respect to native and exotic species at both the interstate-scale (I-64, I-65, and I-71) and at the landscape-scale (urban-scale gradient). Finally, we determined where native woody species are regenerating along these interstates and what factors (e.g., distance to the city center) may explain the observed patterns.

The tree community across all three interstates combined was comprised predominantly (94%) of native tree species, and the most abundant tree, sapling, and seedling species were natives. In contrast, the most abundant shrub and vine species across all interstates were exotic invasive species. The forest communities along the three urban interstates in Louisville, KY are also quite diverse with respect to the adult tree community. Not only was tree species richness high (50 species), but the Shannon diversity index for all tree species pooled across the three interstates ($H'=3.64$) was also close to the maximum

Fig. 6 Mean tree seedling, exotic tree seedling, and sapling density (stems ha^{-1}) in plots located close to the city center (<10 km from city center) and further from the city center (>10 km from city center) (±1 SE)



diversity (H' max=3.71), indicating that the tree species were equally abundant across the interstates (J=0.98). The tree diversity found along these interstates is slightly higher than the tree diversity found in upland (H'=2.5) and old-growth forests (H'=2.80) in Kentucky. This may be partly attributed to higher mean tree density along these interstates (1,587 stems ha^{-1}) compared to the upland (1,468 stems ha^{-1}) and the old-growth forest (1,397 stems ha^{-1}; Muller 1982; Muller and McComb 1986). Therefore, highly diverse native tree communities have been maintained along these metropolitan interstates via natural recruitment processes over the last four decades, despite exposure to potentially high cumulative pollutant loads emanating from the highways and the city at large. However, our study showed that exotic plant invasions may be compromising the continued regeneration of many native tree species along highways. Forest plots closer to the city center had greater exotic species abundance (a pattern primarily driven by Amur honeysuckle) and lower tree seedling regeneration. Since abiotic factors from the interstate (e.g., traffic density) or the surrounding city (e.g., industrial land use) did not explain the reduced tree seedling density observed in our forest plots, it appears that the biotic pressure from exotic species, particularly Amur honeysuckle, poses more of a threat to native species regeneration in these forests. Therefore, understanding patterns in exotic species presence and spread in forests adjacent to urban interstates will be important for predicting the composition and density of the future forest.

Since several studies have shown that exotic species can spread rapidly via road corridors (e.g., Rentch et al. 2005), we expected exotic species would be more abundant in forests adjacent to highway sectors with the highest traffic density, but this is not what was observed in this study. The forest communities next to highway stretches with the highest traffic density (right side of NMDS) had the lowest exotic species index (Figs. 3 and 4). While the exotic shrub, Amur honeysuckle (*Lonicera maackii*), was the most important species explaining variation in vegetation composition across forested verges for all three interstates, its presence was minimal (range = 0 to 40 stems plot^{-1}) along the most heavily traveled highway, I-65. The soil types in these forests (hydric, occasionally flooded soils) may have constrained growth and widespread colonization of Amur honeysuckle along I-65. Even though Amur honeysuckle has been shown to reach substantial densities in intact forests close to stream corridors in Ohio (Medley 1997), it is unknown whether this species can spread very far into swamps or urban wetlands. An alternative explanation for the lack of Amur honeysuckle along the I-65 corridor in Louisville may be that the forest patches along this interstate are more isolated by large areas of impervious cover (including the international airport) from dense populations of Amur honeysuckle that exist along highways, parks, and residential areas elsewhere across the city, and their seeds have not yet been dispersed there by birds (Bartuszevige and Gorchov 2006).

We also expected exotic species would be more abundant closer to the city center. This expectation was met since plots closest to the city center (positioned on the left side of the NMDS in Fig. 3) contained the highest relative density of exotic trees, shrubs, and vines. Amur honeysuckle was the strongest indicator species for plots close to the city center (Table 3) and had much higher stem densities closer to the city. This finding was not surprising since Amur honeysuckle has been known to attain high densities in many different urban environments, including open areas, forest edges, riparian corridors, and even intact forests within urban areas (Borgmann and Rodewald 2005; Luken and Thieret 1996). The importance of exotic species distribution in explaining the separation of plots in the NMDS analysis was influenced by Amur honeysuckle abundance in plots close to the city center where it was most likely introduced by urban residents, local parks, and the Department of Transportation after interstate construction. Amur honeysuckle was an important determinant of other plant community patterns and may affect future forest composition by affecting seedling recruitment and other plant processes.

The forests along highway verges are habitats that are not actively managed by people, so they maintain natural ecosystem processes (i.e., tree regeneration, community succession). Therefore, current species composition (i.e., exotic species) and landscape-scale factors, rather than direct human management, may be determinants of forest community succession and tree regeneration in these interstate forests. This study showed that the ability of adult trees to regenerate in the plots closer to the city center appears to be negatively affected. There is at least an order of magnitude fewer tree seedlings and saplings in plots closer to the city center. While the number of exotic seedlings comprises a small proportion of total seedlings, the number of exotic tree seedlings was 98% higher in plots closer to the city as well (Fig. 6). One potential cause for this is the presence of very high Amur honeysuckle densities in plots closer to the city. Several studies have shown that tree regeneration is negatively correlated with the presence of Amur honeysuckle (Collier et al. 2002; Hutchinson and Vankat 1997), and several mechanisms for explaining this relationship have been explored. Using lab bioassays, Dorning and Cipollini (2006) showed that alleopathic compounds produced by Amur honeysuckle leaves and roots reduced germination of native herbaceous species while not interfering with self-germination. However, this effect has not been demonstrated to be an important factor in explaining reduced woody species densities in the presence of Amur honeysuckle in field experiments. Aboveground changes in resources (i.e., light levels) may provide an alternative explanation for reduced tree seedling regeneration under Amur honeysuckle. This shrub forms dense thickets with maximum light levels that are typically only 1% of full sunlight (Luken et al. 1997). In our forest plots, the mean maximum light level at 1-m height in plots closer to the city center was 1.4% of full sun where honeysuckle stem densities averaged 18,388 stems ha^{-1}. In fact, only one plot with high honeysuckle stem density exhibited mean light levels greater than 1% of full sun. In contrast, light levels at 1-m height in plots further from the city were 4.7% of full sun, and these averaged much lower honeysuckle stem densities (3,462 stems ha^{-1}) and higher tree saplings and seedling densities (Fig. 6). Across all forested highway plots, total seedling densities increased with increasing light levels, suggesting that the dense canopy of Amur honeysuckle may best explain the reduced tree regeneration in plots close to the city center.

Tree regeneration is an important determinant of future forest community composition, and reduced tree seedlings in plots close to the city may translate into altered tree composition compared to plots further from the city. The four most abundant adult tree species in plots further from the city were all native species that were represented across all dbh size classes (Fig. 5). However, an exotic species, *Ailanthus altissima*, had the highest mean stem density in forest communities close to the city (Table 4) where the most abundant tree species (*Acer saccharum*) was only present in the smallest size class (Fig. 5). Even though large reproductive *Acer saccharum* trees were not found in our plots, they must have been nearby since *Acer saccharum* appears to be reproducing and establishing successfully in these plots. However, *Acer saccharum* does not appear to be transitioning into larger size classes in the plots closer to the city, which may be a result of reduced light in these plots. Differences in the adult tree composition between plots close to the city versus those further from the city may continue to diverge in species composition in the future due to light reduction, if dense Amur honeysuckle populations are maintained closer to the city.

By providing redundancy in ecosystem function (e.g., primary production) and services (e.g., carbon storage and sequestration), the high biodiversity of these forested verges along Louisville's urban interstates is likely an important determinant of its resilience to future stressors and disturbances (Hooper et al. 2005). However, total species richness across the interstate forest communities was shown to decrease closer to the city where the average species richness (all trees, shrubs, and vines) for plots close to the city center was half the species richness of plots further from the city (10 vs. 20 species plot^{-1}), indicating that factors associated with increasing urbanization have reduced woody plant diversity. Our study suggests that those factors may be biotic rather than abiotic. The relative density of exotic trees, shrubs, and vines in plots close to the city was 1.5 times higher than in plots further from the city. The prevalence of exotic woody species, especially Amur honeysuckle, in forest plots close to the city may potentially contribute to lower species richness in these forests. Other studies have shown species richness of tree seedlings and herbaceous plants to be reduced in Ohio forests invaded by Amur honeysuckle (Collier et al. 2002; Hutchinson and Vankat 1997). Therefore, exotic species invasions may impose a greater threat to the future resiliency of these highway verge forests in urban areas than pollution from the highway and other emission sources, such as coal-powered power plants. Further study of edaphic factors, some of which have been reported in Trammell et al. (in press), may also contribute to our understanding of how this shrub and other exotic species may be affecting the current and future forest by reducing woody plant species richness and recruitment.

Conclusion

We found that the most important determinants of vegetation composition across the metropolitan area were the distance from the city center and the presence of an exotic invasive shrub, Amur honeysuckle (*Lonicera maackii*). As opposed to plots 10 km or greater from the city center, plots closer to the city had much higher Amur honeysuckle density, higher exotic adult tree species (*Ailanthus altissima* and *Albizia julibrissin*) presence, lower tree seedling and sapling recruitment, and lower species richness. The presence of exotic invasive species, the decreased tree regeneration, and the altered adult tree composition in plots closer to the city suggests that the currently high native tree composition of these forests may decline in the future.

A surprising finding was that verges along the most heavily traveled interstate, I-65, were almost entirely composed of native tree, shrub, and vine species. Thus, the potential for current abiotic factors along interstates to have a negative effect on woody plant growth and survivorship may not be as important as the direct impact of exotic species introductions by urban residents, local parks, or highway verge management (Dept. of Transportation). This provides optimism that naturally regenerating forests can persist in the urban environment along interstate corridors and continue to provide ecosystem services (e.g. pollutant filtration, noise reduction, carbon sequestration, habitat and corridor functions for wildlife) as long as the introduction and spread of invasive exotic plants can be controlled. To promote the ability of native woody species in maintaining their populations along forested highway verges, management needs to reduce exotic invasive species and to plant native species. These "forgotten forests" contribute many ecological services to our urban residents. They deserve recognition for their value and should be managed to maximize their benefits to society and their utility as conservation corridors and habitat.

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Appendix

Table 5 Total tree, shrub, and vine species across all three highways in Louisville, KY. Total area sampled = 2,100 m^2 (Species according to Gleason and Cronquist (1991)). Exotic species demarcated with an **E**

Tree species	Shrub species	Vine species
Acer negundo L.	*Cornus amomum* Miller.	*Ampelopsis cordata* Michx. **E**
Acer pseudoplatanus L. **E**	*Cornus drummondi* C.A.Meyer.	*Ampelopsis* sp.
Acer saccharum Marshall.	*Cornus obliqua* C.A.Meyer.	*Celastrus orbiculatus*Thunb. **E**
Acer rubrum L.	*Cornus sp.*	*Euonymus fortunei* **E**
Acer sp.	*Crataegus crus-galli* L.	(Turez.) Hand-Mazz
Aesculus glabra Willd.	*Euonymus americanus* L.	*Lonicera japonica* Thunb. **E**
Ailanthus altissima (Miller) Swingle. **E**	*Euonymus atropurpureus* Jacq. **E**	*Parthenocissus quinquefolia*
Albizia julibrissin Durazz. **E**	*Euonymus* sp.	(L.) Planchon.
Aralia spinosa L.	*Ligustrum vulgare* L. **E**	*Smilax glauca* Walter.
Asimina triloba (L.) Dunal	*Lindera benzoin* L.Blume.	*Smilax hispida* Muhl.
Betula lenta L.	*Lonicera maackii* Maxim. **E**	*Smilax rotundifolia* L.
Betula sp.	*Prunus* sp.	*Smilax* sp.
Carya ovata (Miller) K. Koch.	*Rhamus lanceolata* Pursh.	*Sicyos angulatus* L.
Carya tomentosa (Poiret) Nutt.	*Rhamus* sp.	*Toxicodendron radicans*
Carya sp.	*Rosa multiflora* Thumb. **E**	(L.) Kuntze.
Celtis occidentalis L.	*Rosa setigera* Michx.	*Campsis radicans*
Cercis canadensis L.	*Rosaceae* sp.	(L.) Seemann.
Cornus florida L.	*Rubus allegheniensis* T.C.Porter.	*Vitis aestivalis* Michx.
Cornus sp.	*Rubus occidentalis* L.	*Vitis riparia* Michx.
Diospyros virginiana L.	*Rubus* sp.	*Vitis vulpine* L.
Fagus grandifolia Ehrh.	*Symphoricarpos orbiculatus*	*Vitis/ampelopsis* hybrid[a]
Fraxinus quadrangulata Michx.	Moench.	*Vitis* sp.
Fraxinus sp.	*Viburnum* sp.	
Ilex opaca Aiton.		
Juglans cinerea L.		
Juglans nigra L.		
Juglans sp.		
Juniperus virginiana L.		
Liquidambar styraciflua L.		
Liriodendron tulipifera L.		
Morus rubra L.		
Nyssa sylvatica Marshall.		
Ostrya virginiana (Miller) K. Koch.		
Platanus occidentalis L.		
Populus deltoides Marshall.		
Prunus hortulana L.H. Bailey.		
Prunus serotina Ehrh.		
Prunus sp.		
Quercus imbricaria Michx.		
Quercus muehlenbergii Engelm.		

Table 5 (continued)

Tree species	Shrub species	Vine species
Quercus palustris Muenchh.		
Quercus prinus L.		
Quercus rubra L.		
Quercus velutina Lam.		
Quercus sp.		
Robinia pseudoacacia L.		
Sassafras albidum (Nutt.) Nees.		
Ulmus rubra Muhl.		
Ulmus thomasii Sarg.		
Ulmus sp.		

[a] Pat Haragan (personal communication)

Table 6 Tree, shrub, and vine species codes

Species name	Code	Species name	Code
Acer negundo	ACNE	*Liriodendron tulipifera*	LITU
Acer pseudoplatanus	ACPS	*Lonicera maackii*	LOMA
Acer rubrum	ACRU	*Lonicera japonica*	LOJA
Acer saccharum	ACSA	*Morus rubra*	MORU
Acer sp.	AC	*Nyssa sylvatica*	NYSY
Aesculus glabra	AEGL	*Ostrya virginiana*	OSVI
Ailanthus altissima	AIAL	*Parthenocissus quinquefolia*	PAQU
Albizia julibrissin	ALJU	*Platanus occidentalis*	PLOC
Aralia spinosa	ARSP	*Populus deltoides*	PODE
Asimina triloba	ASTR	*Prunus hortulana*	PRHO
Betula lenta	BELE	*Prunus serotina*	PRSE
Campsis radicans	CARA	*Prunus sp.*	PR
Carya ovata	CAOV	*Quercus imbricaria*	QUIM
Carya tomentosa	CATO	*Quercus muehlenbergii*	QUMU
Carya sp.	CA	*Quercus palustris*	QUPA
Celtis occidentalis	CEOC	*Quercus prinus*	QUPR
Cercis canadensis	CECA	*Quercus rubra*	QURU
Cornus drummondi	CODR	*Quercus velutina*	QUVE
Cornus florida	COFL	*Quercus sp.*	QU
Cornus oblique	COOB	*Robinia pseudoacacia*	ROPS
Cornus sp.	CO	*Rosa multiflora*	ROMU
Diospyros virginiana	DIVI	*Rosaceae sp.*	RO
Euonymus atropurpureus	EUAT	*Sassafras albidum*	SAAL
Euonymus fortunei	EUFO	*Smilax rotundifolia*	SMRO
Fagus grandifolia	FAGR	*Smilax sp.*	SM
Fraxinus quadrangulata	FRQU	*Symphoricarpos orbiculatus*	SYOR
Fraxinus sp.	FR	*Toxicodendron radicans*	TORA

Table 6 (continued)

Species name	Code	Species name	Code
Ilex opaca	ILOP	*Ulmus rubra*	ULRU
Juglans cinerea	JUCI	*Ulmus thomasii*	ULTH
Juglans nigra	JUNI	*Ulmus sp.*	UL
Juglans sp.	JU	*Unknown*	UNK
Juniperus virginiana	JUVI	*Vitis aestivalis*	VIAE
Ligustrum vulgare	LIVU	*Vitis/ampelopsis hybrid*	VIAM
Lindera benzoin	LIBE	*Vitis sp.*	VI
Liquidambar styraciflua	LIST		

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