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Kentucky, USA*

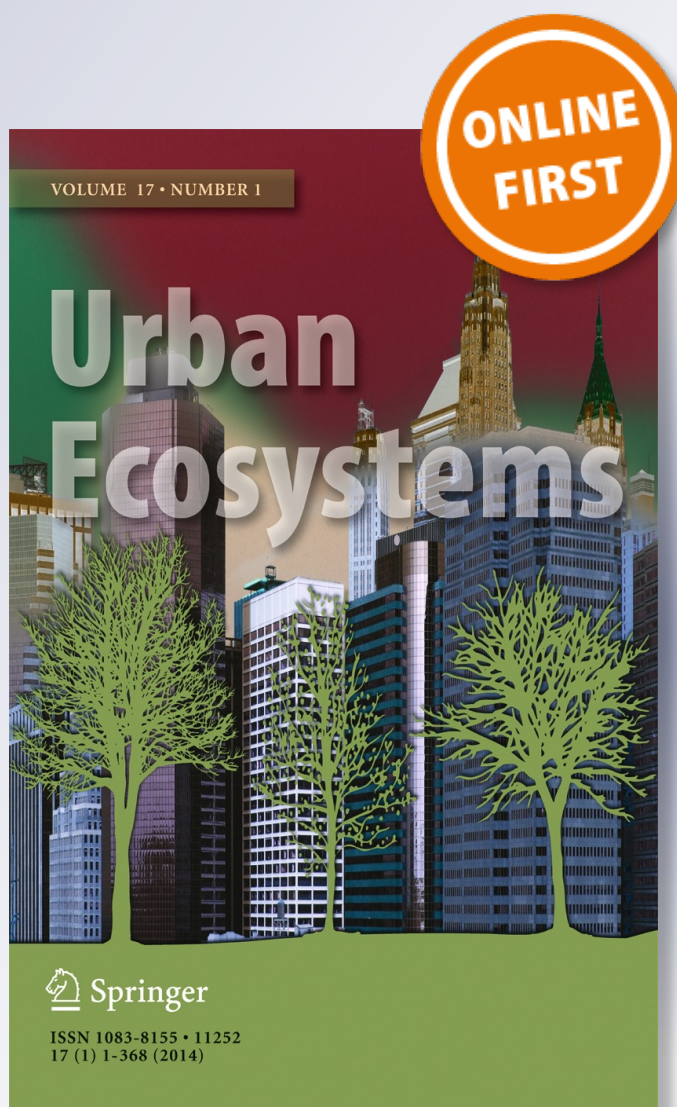
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Woody plant communities along urban, suburban, and rural streams in Louisville, Kentucky, USA

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Abstract Anthropogenic changes in land use and cover (LULC) in stream catchments can alter the composition of riparian plant communities, which can affect ecosystem functions of riparian areas and streams from local to landscape scales. We conducted a study to determine if woody plant species composition and abundance along headwater streams were correlated with categorical and continuous LULC and environmental variables along an urban-to-rural gradient. These variables were calculated at different spatial scales (subcatchment level and within 0.5 and 1 km radii of plots) and used % impervious surface cover (ISC) and finer scale LULC classification levels to determine their ability to explain species composition, diversity, abundance, non-native provenance and wetland indicator status of four plant strata—canopy tree, tree sapling, tree seedling and shrub. At all scales, we found distinct riparian woody communities within land-use categories, with significant differences among shrub species. Fine-scale land-cover variables correlated with species composition of shrub, tree sapling and tree seedling strata, but not the canopy tree stratum. *Celtis occidentalis* and *Acer negundo* were ubiquitous but dominated riparian areas surrounded by development, while *Asimina triloba* was associated with forested rural riparian banks. Non-native shrubs, *Lonicera maackii* and *Euonymus alatus*, were indicative of areas surrounded by development, while the native shrub, *Lindera benzoin*, was associated with deciduous forest. Negative factor-ceiling relationships between canopy tree, sapling and tree seedling densities and % ISC were found, with abrupt declines above approximately 30 % ISC. Facultative wetland shrubs were not found above 30 % ISC. Streambank height, which was strongly negatively correlated with depth to the water table and positively correlated with cumulative catchment area, was negatively correlated with facultative wetland tree and shrub species. In addition, riparian tree sapling and seedling densities declined as the abundance of *Lonicera maackii* increased.

Keywords Urban ecology · Riparian · Urban–rural gradient · Plant communities · *Lonicera maackii*

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Introduction

Riparian zones perform a number of valuable ecosystem services. As ecotones between terrestrial and aquatic systems, riparian areas act as sediment and nutrient filters (Gilliam 1994; Brenner et al. 1991), provide habitat and nutrients to stream and riparian organisms (McNeish et al. 2012; Pennington et al. 2008; Wenger 1999; Naiman and Decamps 1997), and reduce floodwater velocity and erosion potential (Boothroyd et al. 2004; Geyer et al. 2003; Easson and Yarbrough 2002; Wenger 1999). Riparian woody vegetation (trees, shrubs, vines) plays a significant role in providing these services (McNeish et al. 2012; Naiman and Decamps 1997; Gilliam 1994; Brenner et al. 1991). Alterations of riparian vegetation could affect water quality, reducing recreational potential for swimming and fishing, and increasing water treatment costs to towns and cities using streams as drinking water sources. Because urban land reduces water quality, the need to protect water resources from development will increase as cities and suburbs expand (Walsh et al. 2005a). Since riparian woody vegetation provides valuable ecosystem services to aquatic and terrestrial systems (Lowrance et al. 1997), determining how plant community structure and composition changes as the land becomes more developed deserves particular attention. Further, changes in the structure and composition of riparian vegetation may also serve as indicators of broader environmental change (Pennington et al. 2010; Naiman and Decamps 1997).

In addition to direct management and other human activities, such as vandalism, urbanization and accompanying changes in land use and cover (LULC) alters the structure and function of riparian vegetation in several ways (Fig. 1). For instance, LULC directly influences vegetation dynamics (Müller et al. 2013; Brady et al. 2011; Fig. 1, Arrow 1), where vegetation dynamics encompasses species availability, site availability and species performance (Pickett et al. 1987). These in turn interact to determine woody riparian vegetation structure (Fig. 1, Arrow 11). Species availability includes not only species in the riparian zone but also those adjacent to or upstream from it. In fact, the linear nature of riparian communities also would make them more vulnerable to seed capture from the adjacent human-dominated matrix (Borgmann and Rodewald 2005; Cadenasso and Pickett 2001).

Site availability accounts for the creation of germination sites from disturbances (Arrows 8, 9, 10) or death of an individual. LULC interacts with catchment size to change stream hydrology and flooding regimes (Fig. 1, Arrows 2, 3 and 7). Alterations in frequency and intensity of overbank flooding affect riparian vegetation dynamics (Fig. 1, Arrows 8; Naiman and Decamps 1997; Auble et al. 1994) through deposition of propagules and nutrients, and by physical disturbance that may favor species that had not historically occupied riparian zones in a region (Naiman and Decamps 1997; Johnson 1993; Bren 1992).

Species performance encompasses the growth and maturity of a species on the site and is affected by the abiotic and biotic environment. Abiotic factors include incised streams caused by rapid stormwater inputs from pavement and large catchments (Fig. 1, Arrows 2 and 3). Incision creates streambanks perched high above the stream channel and a chronically lowered groundwater table (Walsh et al. 2005b; Paul and Meyer 2001; Fig. 1, Arrows 4 and 5). This results in a condition known as “urban hydrological drought” (Groffman et al. 2003), which may have important consequences for woody riparian vegetation dynamics (Fig. 1, Arrow 6). Biotic influences on plant species performance include competition and herbivory, which are important determinants of vegetation composition and structure (Pickett et al. 1987). For instance, mammalian herbivory, an important factor affecting woody plant recruitment along riparian areas (Liang and Seagle 2002; Naiman and Decamps 1997) may vary in kind and intensity as LULC changes along an urban-to-rural gradient (Fig. 1, Arrow 1).

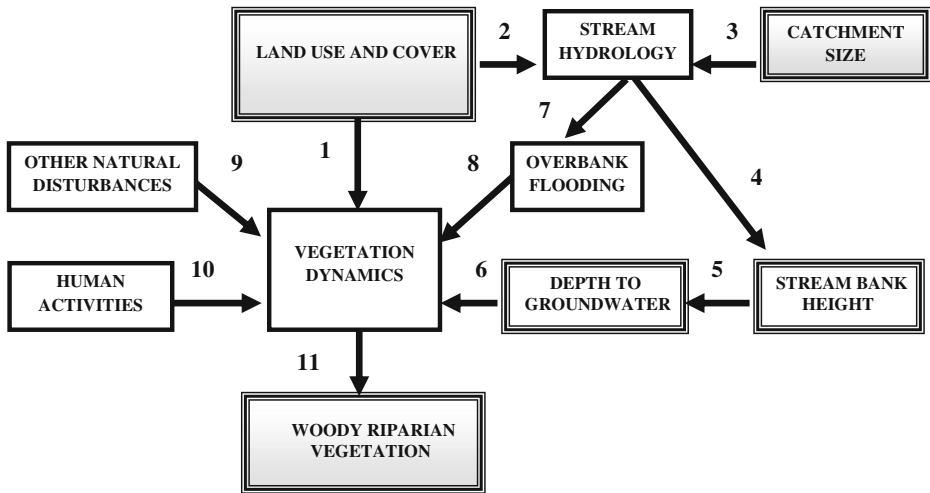


Fig. 1 Conceptual model used for this study to identify intermediate links between variation in land-use and cover (LULC) and catchment size (predictor variables in this study) and community structure of woody riparian vegetation (the focal response variable) along first to third order streams. Overall, LULC, overbank flooding, other natural disturbances, depth to groundwater and human activities in the riparian area directly affect vegetation dynamics (interactions among species availability, site availability, species performance), which ultimately defines the observed community structure of woody riparian vegetation (Arrow 11). Specifically, Arrows 1 and 2 identify LULC direct effects on vegetation dynamics and stream hydrology. Arrow 3 captures the cumulative upstream catchment size effect on stream hydrology. Arrow 4 identifies the influence of stream incisement through stream bank height and resultant depth to groundwater (Arrow 5). Arrow 6 directly links depth to groundwater with vegetation dynamics. Arrows 7, 8 and 9 account for the frequency and intensity of overbank flooding and other natural disturbances. Although we did not select plots where vegetation was directly managed, Arrow 10 accounts for the effects of human activities (e.g., management, vandalism) on vegetation dynamics and subsequently on woody riparian vegetation. Variables measured in this study are denoted by boxes surrounded by triple lines. Variables not measured are in boxes with single lines

Several urban-to-rural gradient studies of riparian plant communities have been completed across a range of habitats and climatic regions. Studies in temperate climates have found both higher (Lyon and Gross 2005) and lower (Burton and Samuelson 2008) woody plant richness associated with urban land. Some studies have found a higher density or proportion of non-native woody species (Burton and Samuelson 2008; Borgmann and Rodewald 2005; Burton et al. 2005; Moffatt et al. 2004) along streambanks in urban land compared to rural counterparts. Conversely, in more arid climates, species composition of urban riparian zones was similar to reference riparian zones (White and Stromberg 2011; Oneal and Rotenberry 2008).

While many of these studies primarily used distance from city centers or coarse-scale impervious surface percentage as correlates of urban conditions and disturbances, recent studies have begun to focus on finer-scale LULC distinctions within uniform distances of study plots to improve the characterization of urban impacts on plant communities (Pennington et al. 2010; Godefroid and Koedam 2007). For example, in Brussels, Belgium, Godefroid & Koedam (2007) assessed the proportion of various built up areas in 1 km² grids and found that different types of built-up areas resulted in different indicator plant species. Pennington et al. (2010) found that riparian areas within 250 m of roads and railroads were characterized by low densities of woody species requiring high soil moisture.

The goal of this study was to examine how LULC variation at coarse- and fine-scales of resolution and measured over different spatial extents may be related to the structure and

species composition of riparian vegetation along an urban-to-rural gradient in Louisville, Kentucky. We had four objectives:

- (1) to describe the woody vegetation assemblages within land-use categories defined using coarse-scale impervious surface cover (ISC) calculated at subcatchment scales;
- (2) to determine the relationships among riparian species abundance and composition, coarse-scale ISC, and finer-scale LULC categories from the National Land Cover Database (NLCD) at two spatial scales (0.5 km and 1 km radii from plot centers);
- (3) to determine whether predictable differences in plant diversity, native vs. non-native species composition and species wetland indicator status existed as ISC and other environmental factors (including streambank height and cumulative upstream catchment area) varied; and
- (4) to determine how well % ISC and cumulative upstream catchment area individually predicted streambank height and how well streambank height predicted depth to groundwater.

Methods

Definitions

The following definitions and abbreviations apply throughout the paper. “LULC” refers to land use and land cover. “LULC scales” refers to coarse- and fine-scale LULC resolution as follows. “ISC” refers to impervious surface cover and is used to define coarse-scale LULC categories (urban, suburban, rural; Table 1). Fine-scale LULC categories were those defined by the National Land Cover Database (NLCD) in mixed Anderson Level categories (e.g., high, medium and low intensity development, deciduous forest cover). “Land-use categories” and “categorical analysis” refers to the categories of urban, suburban, and rural, which were calculated using % ISC within each subcatchment. “Spatial scales” refer to the area within 0.5 km and 1 km radii from plot center, within which the proportions of both coarse- (ISC) and fine-scale (NLCD) LULC types were calculated.

Study area

The study area consisted of three watersheds—Beargrass Creek (Middle Fork), Goose Creek, and Harrods Creek (South Fork)—located within and adjacent to Louisville, Kentucky, USA (Latitude 38°15'N, Longitude 85°46'W; Fig. 2). Louisville (equivalent to Jefferson County since the city-county governmental merger in 2003) has a population of approximately

Table 1 Name, area, and the number of plots classified as urban, suburban and rural in the three stream catchments. Classification of plots was based on percentage of impervious surface cover determined at the subcatchment scale with ≥ 30 % being urban, between 10 and 30 % being suburban, and ≤ 10 % being rural

Catchment	Area (km ²)	Urban	Suburban	Rural
Beargrass Creek	65	11	3	0
Goose Creek	50	1	9	3
Harrods Creek	60	0	3	11

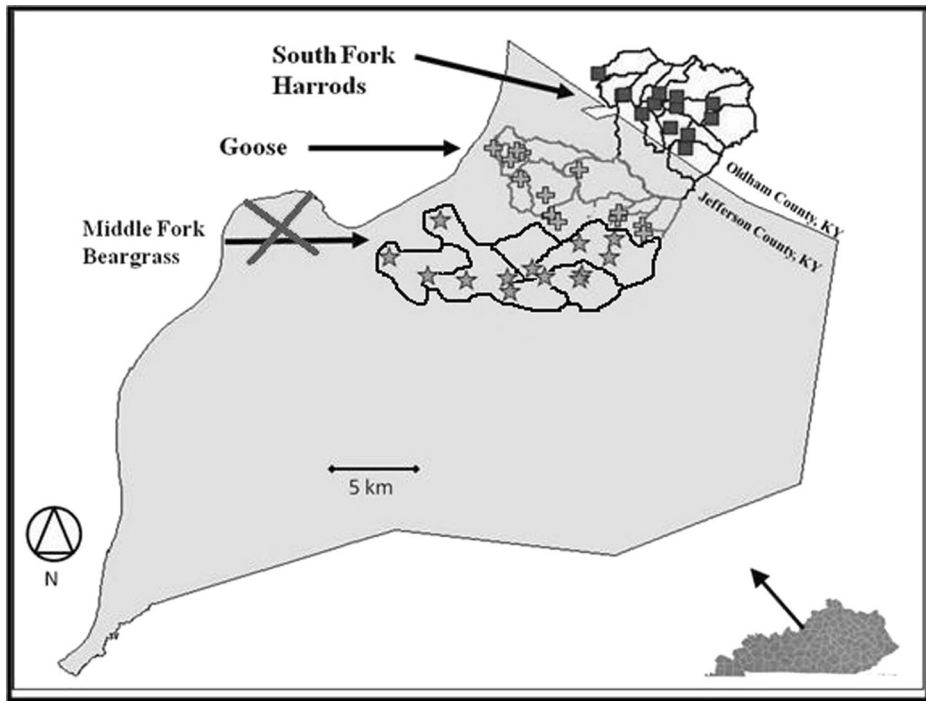


Fig. 2 Map of the three watersheds in Jefferson and Oldham counties in north central Kentucky. Research plots are indicated with markers. Stars denote plots in the Beargrass Creek (urban), crosses the Goose Creek (suburban) and squares the Harrods Creek (rural) watersheds. The X indicates the approximate location of Louisville's central business district. The state map of Kentucky is in the lower right corner with arrow emanating from the location of Jefferson County

741,000 with a mean density of 750 people km^{-2} (U.S. Census Bureau 2010). Beargrass and Goose Creeks occur in Jefferson County, whereas Harrods Creek occurs primarily in Oldham County but also extends into the northeast corner of Jefferson County. The three watersheds are of equivalent sizes (Table 1), but vary by % ISC. Percent ISC for each watershed ranged as follows: Harrods Creek, 10 %; Goose Creek, 20 %; and Beargrass Creek, 33 %. Each of the study streams was listed as impaired on Kentucky's Division of Water 303d list (Kentucky Environmental and Public Protection Cabinet 2011). Sewer overflows were cited as likely impairment sources along Beargrass and Goose Creeks, whereas runoff was the oft-cited source along Harrods Creek.

Watershed classification

Each watershed was divided into subcatchments based on stream order, reach length, and topography using topographic maps and spatial databases from Louisville/Jefferson County Information Consortium (LOJIC). Stream order was based on Strahler (1952), and in this study no streams were above third order. Beargrass Creek watershed contained 13, Goose Creek watershed 12, and Harrods Creek watershed 14 subcatchments, for a total of 39 subcatchments.

Impervious surface cover (ISC) was determined using three data layers (buildings, roads, miscellaneous transportation) from the LOJIC database digitized in 2001. The buildings-layer

included all built structures. The roads-layer included all paved road surfaces, excluding parking lots. The miscellaneous transportation-layer included secondary transportation features such as driveways, parking lots, and sidewalks. Using ArcGIS 9 (ESRI 2010), ISC was determined for each subcatchment and within a 0.5 km and 1 km radius of each vegetation plot center. ISC (km^2) was divided by the total land area (km^2) within the subcatchment or individual areas encompassed by the two radii to determine % ISC at these different spatial scales.

For coarse scale analyses, % ISC in each subcatchment determined the land-use designation for a plot: urban, suburban, or rural (Schueler 1994). Urban subcatchments were defined as containing ≥ 30.0 % ISC; rural ≤ 10.0 %; and suburban were intermediate. Twelve plots were classified as urban, 15 as suburban, and 14 as rural, for a total of 41 plots in 39 subcatchments (Table 1). To explore whether more proximate and finer-scale LULC context may influence vegetation, we used LULC from the National Land Cover Database (2001). The database is composed of pixels from Landsat 5 and 7 images (Homer et al. 2004) with a spatial resolution of 30 meters (m), with each pixel assigned to one of ten Anderson-level classes (deciduous forest, mixed forest, herbaceous forest, crops, pasture, wetland, open-space developed, and high-, medium-, and low-intensity developed). We used these pixels to determine the proportion of ground area covered by each of those Anderson-level classes within a 0.5 km (0.79 km^2 area) and 1 km (3.14 km^2 area) radius of each plot center. Those proportions were included as potential explanatory variables in ordination analyses for plant species composition at each plot.

Plot location and establishment

Riparian plot locations were chosen using ArcGIS 9.0 software and a digital map of the watersheds. A riparian zone was defined as level ground from the edge of the stream bank to either an upland slope (defined as beginning of the terrace), a structural barrier (roads, parking lots, buildings), or other obstruction (grazed pasture, ditch, ephemeral stream channel). Locations were used if they were at least partially covered with unmanaged vegetation (not mown, grazed, or cultivated) and were at least 100 m from the nearest stream fork to avoid sampling riparian zones from different subcatchments. The final plot location was chosen randomly onsite. Only one side of the stream was sampled at each plot location. Riparian zones less than 12 m wide were sampled with a partial plot.

To establish the plots, after a random starting point along the bank edge was determined, a transect was laid perpendicular to and away from the stream channel for the width of the riparian zone. Plot centers for circular plots (plot radius = 5.64 m, plot area = 100 m^2) were placed at the 6 m mark along the transect. For the canopy tree stratum, species and diameter at breast height (DBH) were recorded for live woody stems $\geq 2.54 \text{ cm}$ DBH within the 100 m^2 plot. Tree saplings (live woody stems $\geq 1 \text{ m}$ high but $< 2.54 \text{ cm}$ DBH) and shrub stems ($\geq 1 \text{ m}$ high) were recorded by species in three plots, each $10 \text{ m} \times 2 \text{ m}$, nested mostly within the circular plots. To measure tree seedling density (stems $< 1 \text{ m}$ high), four 1 m^2 quadrats were established within each of the $10 \times 2 \text{ m}$ plots. Trees, saplings and shrubs were measured in 2005 (June to August) and 2006 (May to October), and tree seedlings from May to October in 2006 (White 2011).

Plant identification and classification

Plant identification followed Wharton and Barbour (1973) and Jones (2005). However, life form (i.e., tree or shrub) and all species names and codes use the U.S. Department of

Agriculture (USDA) PLANTS Database as the authority (2012). Native and non-native designation, at the continental level, was determined using Jones (2005) and the U. S. Department of Agriculture, Natural Resources Conservation Service (2009). Wetland indicator status (WIS) was based on the USDA PLANTS database's National Wetland Plant List (2012). The five major WIS categories are obligate wetland (OBL), facultative wetland (FACW), facultative (FAC), facultative upland (FACU), and upland (UPL).

Species importance value and diversity

Species importance values (IV) were calculated for each plot and for each land-use category for each woody stratum (trees, saplings, tree seedlings and shrubs). Plot IV's were also calculated for each WIS and provenance designation (native or non-native) by stratum. Tree stratum relative density (stems ha^{-1} basis) and relative basal area ($\text{m}^2 \text{ha}^{-1}$ basis) were used to compute the IV at the plot level according to the following equation: $((\text{relative density} + \text{relative basal area}) * 100)/2$. The species IV for each land-use category was derived as above, but with relative frequency of occurrence in plots included according to the equation: $((\text{relative density} + \text{relative basal area} + \text{relative frequency}) * 100)/3$. Relative density and relative frequency were used to calculate the IV for tree saplings and tree seedlings for each plot and land-use category according to the following equation: $((\text{relative density} + \text{relative frequency}) * 100)/2$.

Four diversity measures—species richness, Shannon's index (Magurran 2004; Shannon 1948), Simpson's reciprocal index (Magurran 2004; Simpson 1949), and Shannon's equitability index—were computed for each plot to assess variation with % ISC and other variables. Species richness was computed for each woody stratum. Because of different plot sizes, richness was calculated as the number of species in a plot divided by the log of the area sampled (Nilsson et al. 1997; Conner and McCoy 1979). However, untransformed values are reported for easier communication. The other measures of species diversity were computed using EstimateS (Colwell 2009). Densities of woody species (trees, tree saplings, tree seedlings, and shrubs) were used to compute Simpson's reciprocal and Shannon's indexes. Tree, tree sapling, and tree seedling information were collected at different spatial scales, so densities were computed separately for each woody stratum and added together where shared species existed. In EstimateS, diversity index estimators were not used, so the observed species order within the input files was used to compute the indices.

Other potential explanatory variables

Percent ISC (within 0.5 and 1 km radii of each plot center), canopy openness, bank height, plot size, stream order, cumulative upstream catchment area, and monetary value of residential property were included to determine whether they might explain variation in plant species composition among plots. Percent ISC was determined as previously described. Percent canopy openness was measured using a spherical densiometer (Lemmon 1957, 1956) held over the middle of each 1 m^2 tree seedling quadrat and averaged for each 100 m^2 plot. Because catchment size can affect stream hydrology, and therefore riparian plant composition, cumulative catchment area was calculated in GIS by adding subcatchment areas upstream of the plot to the area of the subcatchment in which the plot was located. Streambank height was measured in one location adjacent to each plot and relative to the middle of the stream channel. Where the center of the channel was not reachable from the bank or by wading, bank height was measured at arm's reach from the edge of the bank. These measurements were used as a proxy for depth to groundwater (explained below) in correlations with plot species

composition. Additional bank height measurements were taken 50 m to either side of the plot midline at 13 of the 41 plots. These 13 additional measurements were averaged with the 41 plot measurements to assess differences in bank height between land-use categories.

Property values were determined from information at the Property Valuation Administrator offices in Jefferson and Oldham counties. Land value in which the plot occurred defined its property value. Plots on the edge of a park abutting residential housing or businesses were assigned the average value of surrounding privately owned parcels. Plots located within public parks or natural areas were assigned a value of \$1 to indicate no private monetary value.

Groundwater wells

For two years, nearstream water table depth was determined at a subset of plots (12 plots in the first year and 13 in the second) to establish correlations with bank height. At each plot, one piezometer well was installed within 0.5 to 1 m of the stream bank edge. The shafts of the piezometer wells were constructed of poly-vinyl chloride (PVC) pipe with a 1.25-inch inner diameter to allow insertion of a measuring tape for determining groundwater depth from the soil surface. Shaft lengths varied depending on depth to the water table (White and Stromberg 2011). Depth to groundwater measurements in the well were made approximately every two weeks from November 2006 to October 2008 (excluding October and December 2007) using a tape measure coated with Keson® ultra-fine marking chalk. Wells were located at 12 plots (3 urban, 5 suburban, 4 rural) until September 2007, with 8 on private property. In October 2007, 4 wells were removed and 5 new wells were installed at different locations to better capture the variation in bank height across the LULC gradient. This brought the total number of sampled wells to 13 for the remainder of the sampling period (6 urban, 3 suburban, 4 rural), with 6 on private property. An even plot replication by land-use type was constrained by permissions from private landowners to install wells on their property.

Data analysis

To determine if plant communities varied by subcatchment-scale LULC (objective 1), a descriptive categorical analysis was conducted involving species importance values and measures of abundance for woody strata. Plots were grouped into urban, suburban, and rural land-use categories using % ISC at the subcatchment scale. For each land-use category, species importance values were calculated separately by stratum as previously described. Other relationships explored at this spatial scale and resolution included frequency, mean density, and species richness (transformed as described previously) for all woody strata, mean basal area and diameter distribution for trees, and diversity indices (Shannon's, Simpson's, and Shannon's Equitability). The non-parametric Kruskal-Wallis test (Kruskal and Wallis 1952) was used to test for significance, since the data did not meet the assumptions of ANOVA.

A multi-response permutation procedure (MRPP) (McCune and Grace 2002) was used to determine if species composition within urban, suburban, and rural land-use categories differed sufficiently to justify such a classification (Mielke and Berry 2007). A separate MRPP was conducted for trees, tree saplings, tree seedlings, and shrubs. If the MRPP analysis indicated distinct groups based on the assigned land-use categories (urban, suburban, and rural), then indicator species analysis (ISA) (Dufrene and Legendre 1997) was used to identify the defining species for each land-use group.

To determine how well % ISC and fine-scale LULC within 0.5 km and 1 km of plot centers explained plot species composition (objective 2), we used ordination analysis. Using non-metric multidimensional scaling (NMS) in PC-Ord v. 4.41 (McCune and Mefford 1999),

research plots were ordinated by species composition and their relationship with fine-scale LULC and other environmental variables assessed. The biplot feature in PC-Ord was used to generate a vector for each environmental variable with an $r^2 \geq 0.2$ for one or more axes. The direction of the vector corresponds to the direction of positive correlation, and the length of the vector indicates the relative strength of the correlation. For each axis, coefficients of determination were listed for each environmental variable with a visible vector. The top two species with the greatest correlation with the axes are noted in the plot.

To address objective 3, measures of species diversity, abundance, wetland indicator status, and provenance were plotted against environmental variables (e.g., cumulative catchment area, stream bank height) and % ISC within 0.5 km and/or 1 km radii of plot center using a mix of scatterplots and regressions. Additionally, these relationships were explored using only plots along first order streams to eliminate sources of variation in species diversity that could be due to large differences in catchment area. We also used scatterplots to explore the relationship between species diversity and *L. maackii* density.

We used least-squares regression analysis to determine how tightly depth to groundwater and streambank height were related, and how well cumulative upstream catchment area and % ISC explained variation in stream bank height (objective 4). Measurements for depth to groundwater were averaged separately for each well from November 2006 to September 2007 and from November 2007 to October 2008.

Results

Relationships with urban, suburban, rural land use at the subcatchment-scale

Plant communities and diversity

A total of 35 tree (identified to species level; Tables 2, 3, and 4) and 16 shrub species (Table 5) were found across all plots in this study, with two tree and six shrub species classified as non-native. No trees were classified as obligate wetland species, but three were classified as facultative wetland species (*Acer saccharinum*, *Fraxinus pennsylvanica*, *Platanus occidentalis*). One obligate wetland shrub species (*Rosa palustris*) was found in one urban plot, and one facultative wetland shrub (*Lindera benzoin*) was observed in plots across all land uses. Across all land-use categories, only four of the 41 plots (one urban, one rural, two suburban) contained FACW tree seedlings. Of those four, the urban and rural plots also contained FACW trees, and one of the suburban plots contained FACW saplings as well as trees. A total of 24 species occurred in the tree stratum, 19 species in the sapling layer, and 21 species in the tree seedling layer. Nine species found in the regenerative layer (saplings and tree seedlings combined that were identified to species level) were absent in the tree stratum. On the other hand, for 10 canopy tree species no individuals in the regenerative layer were found, suggesting recruitment bottlenecks for these species.

Species richness and diversity indices did not significantly differ for any stratum by land-use (Table 6). Mean richness values for all strata were less than 3 species per plot. Mean tree sapling richness was the lowest of all strata in all land-use categories. Although not statistically significant, suburban riparian areas contained the highest mean species richness for all strata with the exception of shrubs, which was highest in rural plots. Suburban riparian zones also exhibited the highest diversity and equitability index values (Table 6).

The existence of each stratum varied among plots in the three land-use categories. Five rural and two suburban plots contained no trees ≥ 2.54 cm DBH, whereas all urban plots contained

Table 2 Species frequency, mean density ($\pm$ S.E.), mean basal area ($\pm$ S.E.) and % importance value (IV) in the canopy tree stratum (≥ 2.5 cm dbh) by land use categories determined at the subcatchment scale in Jefferson and Oldham Counties, Kentucky. Species are organized alphabetically by those occurring in urban, then suburban, then rural plots

Species	Urban				Suburban				Rural			
	Freq.	Density (stems ha ⁻¹)	Basal Area (m ² ha ⁻¹)	IV	Freq.	Density (stems ha ⁻¹)	Basal Area (m ² ha ⁻¹)	IV	Freq.	Density (stems ha ⁻¹)	Basal Area (m ² ha ⁻¹)	IV
<i>Acer negundo</i> (FAC) ¹	0.33	233 (132)	2 (1)	18	0.53	196 (75)	4 (2)	28	0.29	43 (20)	1 (0.8)	12
<i>Acer saccharum</i> (FACU)	0.17	42 (24)	0.72 (0.66)	7	0.27	86 (39)	1.4 (0.8)	9	0.21	56 (33)	2 (1.9)	15
<i>Aesculus glabra</i> (FACU)	0.08	8 (8)	0.51 (0.51)	2	0.07	7 (7)	0.01 (0.01)	1	0.07	36 (36)	2 (1.9)	4
<i>Carya cordiformis</i> (FACU)	0.08	25 (25)	2 (2)	4	0	0	0	0	0	0	0	0
<i>Celtis occidentalis</i> (FACU)	0.25	108 (58)	6 (3)	14	0.33	61 (29)	0.09 (0.06)	8	0.07	14 (14)	03 (0.25)	3
<i>Fraxinus americana</i> (FACU)	0.08	17 (17)	1 (0.9)	3	0.2	47 (27)	1.9 (0.13)	10	0.14	50 (43)	1 (0.6)	8
<i>Fraxinus pennsylvanica</i> (FACW)	0.08	43 (43)	0.1 (0.1)	3	0.07	18 (18)	0.02 (0.02)	2	0	0	0	0
<i>Juglans nigra</i> (FACU)	0.25	33 (19)	2 (1)	7	0.07	13 (9)	0.1 (0.1)	3	0.14	21 (15)	3 (2.5)	13
<i>Morus alba</i> * (UPL)	0.17	205 (155)	3 (2)	13	0.07	20 (20)	0.54 (0.54)	3	0	0	0	0
<i>Morus rubra</i> (FACU)	0.08	8 (8)	0.3 (0.3)	2	0	0	0	0	0	0	0	0
<i>Picea pungens</i> (NI)	0.08	8 (8)	0.3 (0.3)	2	0	0	0	0	0	0	0	0
<i>Platanus occidentalis</i> (FACW)	0.25	38 (23)	10.8 (6)	17	0.07	7 (7)	0.03 (0.03)	1	0.07	7 (7)	1 (1)	5
<i>Prunus cerasifera</i> * (NI)	0.08	21 (21)	0.3 (0.3)	2	0	0	0	0	0	0	0	0
<i>Ulmus rubra</i> (FAC)	0.17	30 (22)	1 (1)	5	0.4	118 (67)	15 (1.3)	15	0.07	7 (7)	0.02 (0.02)	2
<i>Acer saccharinum</i> (FACW)	0	0	0	0	0.07	27 (27)	0.8 (0.8)	9	0	0	0	0
<i>Asimina triloba</i> (FACU)	0	0	0	0	0.13	20 (14)	0.06 (0.05)	3	0.14	94 (86)	0.01	0
<i>Cornus alternifolia</i> (NI)	0	0	0	0	0.07	35 (35)	0.2 (0.2)	3	0	0	0	0
<i>Staphylea trifolia</i> (FAC)	0	0	0	0	0.07	48 (48)	0.03 (0.03)	3	0	0	0	0
<i>Tilia americana</i> (FACU)	0	0	0	0	0.13	40 (34)	0.7 (0.7)	6	0	0	0	0
<i>Carpinus caroliniana</i> (FAC)	0	0	0	0	0	0	0	0	0.07	12 (12)	0.03 (0.03)	2
<i>Cercis canadensis</i> (FACU)	0	0	0	0	0	0	0	0	0.07	14 (14)	0.1 (0.1)	3
<i>Cornus florida</i> (FACU)	0	0	0	0	0	0	0	0	0.14	22 (15)	0.02 (0.01)	5

Table 2 (continued)

Species	Urban				Suburban				Rural			
	Freq.	Density (stems ha ⁻¹)	Basal Area (m ² ha ⁻¹)	IV	Freq.	Density (stems ha ⁻¹)	Basal Area (m ² ha ⁻¹)	IV	Freq.	Density (stems ha ⁻¹)	Basal Area (m ² ha ⁻¹)	IV
<i>Juniperus virginiana</i> (FACU)	0	0	0	0	0	0	0	0	0.07	71 (71)	3 (3)	14
<i>Quercus alba</i> (FACU)	0	0	0	0	0	0	0	0	0.07	7 (7)	0.4 (0.4)	3
SUM	820 (242)	29 (9)	100	100	742 (125)	11 (3)	100	100	455 (131)	12 (4)	100	100

¹ Wetland indicator status—See text for categories

* Non-native species

Classification of subcatchment based on %ISC: Urban > 30 % (*n* = 12 plots), Suburban between 10 and 30 % (*n* = 15 plots), Rural < 10 % (*n* = 14 plots)

Table 3 Species frequency, mean density ($\pm$ S.E.) and % importance value (IV) in the tree sapling stratum (>1 m tall and <2.5 cm DBH) by land use categories determined at the subcatchment scale in Jefferson and Oldham Counties, Kentucky. Species are organized alphabetically by those occurring in urban, then suburban, then rural plots

Species	Urban			Suburban			Rural		
	Freq	Density (stems ha^{-1})	IV	Freq	Density (stems ha^{-1})	IV	Freq	Density (stems ha^{-1})	IV
<i>Acer negundo</i> (FAC) ¹	0.17	162 (139)	18	0.13	167 (155)	8	0.21	46 (27)	12
<i>Acer saccharum</i> (FACU)	0.08	83 (83)	9	0.07	78 (78)	4	0	0	0
<i>Carya cordiformis</i> (FACU)	0.08	14 (14)	5	0.13	49 (38)	5	0	0	0
<i>Celtis occidentalis</i> (FACU)	0.25	514 (343)	43	0.20	45 (26)	7	0.14	68 (49)	13
<i>Fraxinus americana</i> (FACU)	0.08	28 (28)	6	0.20	59 (39)	7	0.14	29 (20)	8
<i>Fraxinus quadrangulata</i> (NI)	0.08	35 (35)	7	0.07	23 (23)	3	0	0	0
<i>Maclura pomifera</i> (FACU)	0.08	14 (14)	5	0	0	0	0	0	0
<i>Morus rubra</i> (FACU)	0.08	14 (14)	5	0	0	0	0	0	0
<i>Aesculus glabra</i> (FACU)	0	0	0	0.07	11 (11)	2	0.14	83 (72)	12
<i>Asimina triloba</i> (FACU)	0	0	0	0.20	606 (324)	20	0.43	322 (175)	42
<i>Cercis canadensis</i> (FACU)	0	0	0	0.07	12 (12)	2	0	0	0
<i>Cornus spp.</i>	0	0	0	0.07	111 (111)	5	0	0	0
<i>Fraxinus pennsylvanica</i> (FACW)	0	0	0	0.07	139 (139)	5	0	0	0
<i>Prunus serotina</i> (FACU)	0	0	0	0.07	11 (11)	2	0	0	0
<i>Quercus rubra</i> (FACU)	0	0	0	0.07	12 (12)	2	0	0	0
<i>Staphylea trifolia</i> (FAC)	0	0	0	0.07	667 (667)	18	0	0	0
<i>Tilia americana</i> (FACU)	0	0	0	0.07	12 (12)	2	0	0	0
<i>Ulmus rubra</i> (FAC)	0	0	0	0.13	92 (72)	6	0.14	24 (16)	7
<i>Robinia pseudoacacia</i> (FAC)	0	0	0	0	0	0	0.07	60 (60)	7
SUM		863(427)	100		2,093(868)	100		632(189)	100

¹ Wetland indicator status—See text for categories

Classification of subcatchment based on %ISC: Urban >30 % ($n=12$ plots), Suburban between 10 and 30 % ($n=15$ plots), Rural <10 % ($n=14$ plots)

trees in this stratum. Four rural, six suburban and four urban plots contained no tree saplings. Two rural, two suburban and two urban plots contained no tree seedlings. All but three plots (all suburban) contained shrubs. Average tree basal area was largest ($29.2 \pm 9.0 \text{ m}^2 \text{ ha}^{-1}$) in urban ($n=12$ plots), intermediate in suburban ($18.9 \pm 3.1 \text{ m}^2 \text{ ha}^{-1}$) ($n=13$ plots), and smallest ($13.1 \pm 5.7 \text{ m}^2 \text{ ha}^{-1}$) in rural riparian areas ($n=9$ plots; $p=0.57$). Plots without trees were not included in calculating these means. Mean basal area values in Table 2 differ from those above because all plots were used to compute basal area to provide an average of tree coverage by land use. Although no statistically significant differences for stem densities were observed across land-use categories for any of the strata, urban riparian areas had the highest canopy tree ($820 \pm 242 \text{ stems ha}^{-1}$) and shrub ($11,370 \pm 3,639 \text{ stems ha}^{-1}$) densities (Tables 2 and 5, respectively), and suburban riparian areas had the highest sapling ($2,093 \pm 868 \text{ stems ha}^{-1}$) and tree seedling ($9,768 \pm 2,732 \text{ stems ha}^{-1}$) densities (Tables 3 and 4, respectively).

Table 4 Species frequency, mean density ($\pm$ S.E.) and % importance value (IV) in the tree seedling stratum (<1 m tall) by land use categories determined at the subcatchment scale in Jefferson and Oldham Counties, Kentucky. Species are organized alphabetically by those occurring in urban, then suburban, then rural plots

Species	Urban			Suburban			Rural		
	Freq	Density (stems ha ⁻¹)	IV	Freq	Density (stems ha ⁻¹)	IV	Freq	Density (stems ha ⁻¹)	IV
<i>Acer negundo</i> (FAC) ¹	0.42	3,785 (2,812)	45	0.60	1,167 (362)	16	0.29	1,012 (567)	16
<i>Aesculus glabra</i> (FACU)	0.08	139 (139)	4	0.20	222 (128)	5	0.14	119 (81)	5
<i>Celtis occidentalis</i> (FACU)	0.33	1,736 (817)	26	0.60	2,556 (1,520)	24	0.36	992 (499)	17
<i>Fraxinus americana</i> (FACU)	0.25	278 (157)	11	0.20	283 (157)	5	0.21	1,647 (1,098)	19
<i>Fraxinus</i> spp.	0.08	69 (69)	3	0	0	0	0	0	0
<i>Gleditsia triacanthos</i> (FAC)	0.08	139 (139)	4	0	0	0	0	0	0
<i>Morus rubra</i> (FACU)	0.08	69 (69)	3	0	0	0	0	0	0
<i>Platanus occidentalis</i> (FACW)	0.08	69 (69)	3	0.07	111 (111)	2	0.07	79 (79)	2
<i>Acer saccharum</i> (FACU)	0	0	0	0.27	833 (467)	9	0.21	1,012 (653)	14
<i>Asimina triloba</i> (FACU)	0	0	0	0.20	1,444 (977)	11	0.29	387 (198)	10
<i>Carya cordiformis</i> (FACU)	0	0	0	0.07	222 (222)	2	0.07	60 (60)	2
<i>Cercis canadensis</i> (FACU)	0	0	0	0.07	111 (111)	2	0	0	0
<i>Cornus drummondii</i> (FAC)	0	0	0	0.07	222 (222)	2	0	0	0
<i>Fraxinus pennsylvanica</i> (FACW)	0	0	0	0.07	1,222 (1,222)	7	0	0	0
<i>Fraxinus quadrangulata</i> (NI)	0	0	0	0.07	242 (242)	2	0.07	159 (159)	3
<i>Liriodendron tulipifera</i> (FACU)	0	0	0	0.13	167 (121)	3	0	0	0
<i>Prunus serotina</i> (FACU)	0	0	4	0.20	222 (128)	5	0.14	119 (81)	5
<i>Ulmus rubra</i> (FAC)	0	0	0	0.07	424 (424)	3	0.07	119 (119)	3
<i>Acer</i> spp.	0	0	0	0	0	0	0.07	119 (119)	3
<i>Juglans cinerea</i> (FACU)	0	0	0	0	0	0	0.07	89 (89)	3
<i>Quercus rubra</i> (FACU)	0	0	0	0	0	0	0.07	159 (159)	3
SUM		6,284(2,716)	100		9,768(2,732)	100		5,952(2,063)	100

¹ Wetland indicator status—See text for categories.

Classification of subcatchment based on %ISC: Urban >30 % ($n=12$ plots), Suburban between 10 and 30 % ($n=15$ plots), Rural <10 % ($n=14$ plots).

Based on importance values, the dominant woody species changed across each land-use category (Tables 2–5). In addition, the most dominant species within land-use categories shifted among woody strata. *Acer negundo*, *Celtis occidentalis* and *Fraxinus americana* were ubiquitous across all land-use categories and strata. In urban riparian zones, *A. negundo*, and *C. occidentalis* were important in the canopy (IV=18 % and 14 %, respectively), sapling (IV=18 % and 43 %, respectively) and seedling (IV=45 % and 26 %, respectively) strata (Tables 2, 3, and 4). *P. occidentalis*, a native riparian species, had the second highest IV in the urban tree stratum (IV=17 %), but its IV was much lower in the tree strata of suburban (IV=1 %) and rural plots (IV=5 %).

Table 5 Species frequency, mean density ($\pm$ S.E.) and % importance value (IV) in the shrub stratum by land-use categories determined at the subcatchment scale in Jefferson and Oldham Counties, Kentucky. Species are organized alphabetically by those occurring in urban, then suburban, then rural plots

Species	Urban			Suburban			Rural		
	Freq	Density (stems ha ⁻¹)	IV	Freq	Density (stems ha ⁻¹)	IV	Freq	Density (stems ha ⁻¹)	IV
<i>Cornus</i> spp.	0.08	799 (799)	5	0	0	0	0	0	0
<i>Euonymus alatus</i> * (NI) ¹	0.17	69 (48)	5	0.33	389 (226)	12	0.07	48 (48)	2
<i>Hibiscus syriacus</i> * (NI)	0.08	660 (660)	5	0.07	111 (111)	3	0	0	0
<i>Hypericum prolificum</i> (FACU)	0.08	14 (14)	2	0	0	0	0	0	0
<i>Lagerstroemia indica</i> * (NI)	0.08	417 (417)	4	0	0	0	0	0	0
<i>Ligustrum sinense</i> * (FACU)	0.08	389 (389)	4	0.40	2,456 (1,484)	28	0.29	1,631 (1,170)	14
<i>Lindera benzoin</i> (FACW)	0.25	458 (309)	9	0.27	728 (418)	12	0.57	1,551 (645)	20
<i>Lonicera maackii</i> * (NI)	1.00	8,370 (2,111)	63	0.60	2,767 (1,401)	31	0.86	2,265 (971)	22
<i>Rosa palustris</i> (OBL)	0.08	194 (194)	3	0	0	0	0	0	0
<i>Amelanchier arborea</i> (FAC)	0	0	0	0.07	56 (56)	2	0	0	0
<i>Cornus racemosa</i> (NI)	0	0	0	0.07	89 (89)	2	0.07	83 (83)	2
<i>Rosa multiflora</i> * (FACU)	0	0	0	0.13	489 (394)	7	0.36	631 (362)	10
<i>Rubus</i> spp.	0	0	0	0.07	222 (222)	3	0	0	0
<i>Hydrangea arborescens</i> (FACU)	0	0	0	0	0	0	0.07	119 (119)	2
<i>Symphoricarpos orbiculatus</i> (UPL)	0	0	0	0	0	0	0.21	4,536 (4,273)	26
<i>Viburnum acerifolium</i> (UPL)	0	0	0	0	0	0	0.07	60 (60)	2
SUM		11,370(3,639)	100		7,307(1,983)	100		10,924(4,034)	100

¹ Wetland indicator status—See text for categories.

* Non-native species

Classification of subcatchment based on %ISC: Urban>30 % ($n=12$ plots), Suburban between 10 and 30 % ($n=15$ plots), Rural<10 % ($n=14$ plots).

While no saplings of *P. occidentalis* were observed in any plots, seedlings with similarly low densities and importance values were found across plots in all land-use categories (Tables 3 and 4). *C. occidentalis* and *A. negundo* saplings dominated urban riparian zones. *Staphylea trifolia* and *Asimina triloba* dominated suburban zones; and *A. triloba* saplings dominated rural ones (Table 3). *A. triloba* was absent in urban riparian zones. The tree seedling species with the highest IV's in urban and suburban plots were *A. negundo* (IV=45 % and 16 %, respectively) and *C. occidentalis* (IV=26 % and 24 %, respectively). In rural zones, *Fraxinus americana* (IV=19 %), *C. occidentalis* (IV=17 %) and *A. negundo* (IV=16 %) seedlings were most important (Table 4).

Tree diameter distributions also varied across land-use categories (Table 7). Regardless of land-use category, highest stem densities occurred in the 2.5–10 cm diameter class. In addition, suburban and urban riparian zones had two to four times greater stem

Table 6 Mean species richness ($\pm$ SE) by stratum and mean diversity ($\pm$ SE) by land-use category determined at the subcatchment scale

Land Use ¹	Stratum	Richness ²	Shannon's index	Simpson's index	Shannon's equitability index
Rural	Trees	1.6 ($\pm$ 0.2)	1.12 ($\pm$ 0.16)	2.90 ($\pm$ 0.42)	0.68 ($\pm$ 0.06)
	Tree saplings	1.3 ($\pm$ 0.2)			
	Tree seedlings	2.0 ($\pm$ 0.4)			
	Shrubs	2.2 ($\pm$ 0.2)			
Suburban	Trees	2.5 ($\pm$ 0.2)	1.23 ($\pm$ 0.17)	3.25 ($\pm$ 0.43)	0.77 ($\pm$ 0.04)
	Tree saplings	1.7 ($\pm$ 0.3)			
	Tree seedlings	2.9 ($\pm$ 0.6)			
	Shrubs	1.9 ($\pm$ 0.2)			
Urban	Trees	2.3 ($\pm$ 0.3)	0.96 ($\pm$ 0.18)	2.59 ($\pm$ 0.39)	0.54 ($\pm$ 0.09)
	Tree saplings	0.9 ($\pm$ 0.2)			
	Tree seedlings	1.4 ($\pm$ 0.3)			
	Shrubs	1.9 ($\pm$ 0.2)			

¹ Classification of subcatchment based on % ISC: Urban > 30 % ($n=12$ plots), Suburban between 10 and 30 % ($n=15$ plots), Rural < 10 % ($n=14$ plots).

² Richness was transformed as ($\#$ species/log(area sampled)). Untransformed richness values are reported, however, SE was calculated from transformed values.

densities in the 10–20 cm (218 and 168 stems ha^{-1} , respectively) and 20–30 cm (81 and 84 stems ha^{-1} , respectively) classes than rural riparian zones (48 and 32 stems ha^{-1} , respectively). Large diameter trees (>40 cm DBH) were more numerous in the urban subcatchments (38 stems ha^{-1}), as opposed to 8 stems each in suburban and rural ones. *P. occidentalis* (FACW) and *C. occidentalis* (FACU) dominated the large diameter class in urban riparian areas, whereas *Fraxinus americana* (FACU) and *Juglans nigra* (FACU) dominated the large diameter class in suburban and rural areas, respectively (Table 8). Regardless of land-use category, *P. occidentalis*, a native riparian species, was absent in the smaller diameter classes.

Urban, suburban, and rural plots exhibited distinct patterns of woody species composition. However, MRPP analysis of trees, tree saplings, and tree seedlings yielded no distinct groupings. Instead, the distinction among land-use categories was based upon variation in the shrub layer, with a chance-corrected within-group agreement (A) of 0.03 and a p -value=0.02. Although A was relatively small (max=1), values in community ecology rarely exceed 0.1, with values approaching 0.3 considered high (McCune and Grace 2002). Subsequent ISA confirmed that *Lonicera maackii*, a non-native invasive shrub from Asia, was a significant indicator species within urban riparian zones (IV=59 %, $p=0.005$; Table 8). This was not surprising since the shrub occurred in over half of all plots and in all urban plots (Table 5), and its mean density in urban plots (8,370 stems ha^{-1}) was three times greater than in suburban (2,767 stems ha^{-1}) or rural areas (2,265 stems ha^{-1}). The defining species for suburban shrub assemblages was *Euonymus alatus* (IV=34 %, $p=0.033$), another Asian invasive (Table 8). Rural riparian shrub assemblages did not contain a significant indicator species; however, the native facultative wetland shrub, *L. benzoin* (IV=30 %, $p=0.18$; Table 8) occurred with the highest frequency (0.57) and abundance (1,551 stems ha^{-1}) in rural riparian areas (Table 5). The only obligate wetland shrub species, *R. palustris*, occurred in a single urban plot (Table 5).

Table 7 Diameter distribution of dominant tree species ($>5\%$ IV) in riparian zones by land-use category determined at the subcatchment scale. Values are stems ha^{-1}

Land use ¹	Species	Diameter class (cm)				
		2.5–10	10–20	20–30	30–40	$>40^{\#}$
Rural	<i>Acer negundo</i>	16	8	8	8	
	<i>Acer saccharum</i>	8	16			
	<i>Asimina triloba</i>	63				
	<i>Fraxinus americana</i>	32	16	8		
	<i>Juglans nigra</i>				16	8 (55)
	<i>Juniperus virginiana</i>	8	8	16	8	
Total		127	48	32	32	8
Suburban	<i>Acer negundo</i>	105	65	41	16	
	<i>Acer saccharum</i>	32	32	24	24	
	<i>Celtis occidentalis</i>	32	8			
	<i>Fraxinus americana</i>	16	24	8		8 (46)
	<i>Tilia americana</i>	8	32	8		
	<i>Ulmus rubra</i>	65	57		8	
Total		258	218	81	48	8
Urban	<i>Acer negundo</i>	196	47	28		
	<i>Acer saccharum</i>	37	19			
	<i>Celtis occidentalis</i>	37	28	19	9	19 (53)
	<i>Juglans nigra</i>		9	28		
	<i>Morus alba</i> *	28	65	9		
	<i>Platanus occidentalis</i>				9	19 (93)
Total		298	168	84	18	38

¹ Classification of subcatchment based on % ISC: Urban $>30\%$ ($n=12$ plots), Suburban between 10 and 30 % ($n=15$ plots), Rural $<10\%$ ($n=14$ plots).

* Non-native species

[#] Number in parentheses is the largest diameter tree within the size class.

Riparian bank height and groundwater table

At the subcatchment scale, mean bank height did not statistically differ among the three land-use categories ($p=0.10$). Urban subcatchments had a mean (± 1 S.E.) height of $1.22\text{ m} \pm 0.13$,

Table 8 Indicator values for shrub species in urban, suburban and rural riparian zones. Indicator values were calculated using indicator species analysis, where a value of 0 means the species is never present in the group and a value of 1 means the species is always present and exclusive to the group. Probabilities for the indicator values were determined using a Monte Carlo randomization technique (1,000 permutations)

Land Use ¹	Species	Common name	Indicator value	Probability
Urban	<i>Lonicera maackii</i> *	Amur honeysuckle	0.59	0.005
Suburban	<i>Euonymus alatus</i> *	Burning bush	0.34	0.033
Rural	<i>Lindera benzoin</i>	Spicebush	0.30	0.18

¹ Land-use classification based on % ISC determined at the subcatchment scale: Urban $>30\%$ ($n=12$ plots), Suburban between 10 and 30 % ($n=15$ plots), Rural $<10\%$ ($n=14$ plots). *Non-native species

followed by rural ($0.96 \text{ m} \pm 0.10$), and then suburban ($0.90 \text{ m} \pm 0.10$). However, the highest streambanks occurred along urban streams (maximum stream bank height: urban=2.50 m, suburban=1.90 m, rural=1.80 m).

Cumulative upstream catchment area and depth to the water table were both correlated with streambank height (Figs. 3 and 4). Depth to the water table showed a strong negative relationship with bank height in 2007 (Fig. 3a; adj. $r^2=0.87$, $p<0.0001$) and 2008 (Fig. 3b; adj. $r^2=0.89$, $p<0.0001$). Cumulative upstream catchment area explained variation in bank height when all subcatchments across the three watersheds were pooled (Fig. 4; adj. $r^2=0.40$, $p<0.0001$) and when subcatchments within each watershed were analyzed separately (Beargrass—adj. $r^2=0.43$, $p=0.006$; Goose – adj. $r^2=0.28$, $p=0.036$; Harrods – adj. $r^2=0.30$, $p=0.025$). However, the relationship showed some irregularities when subcatchment

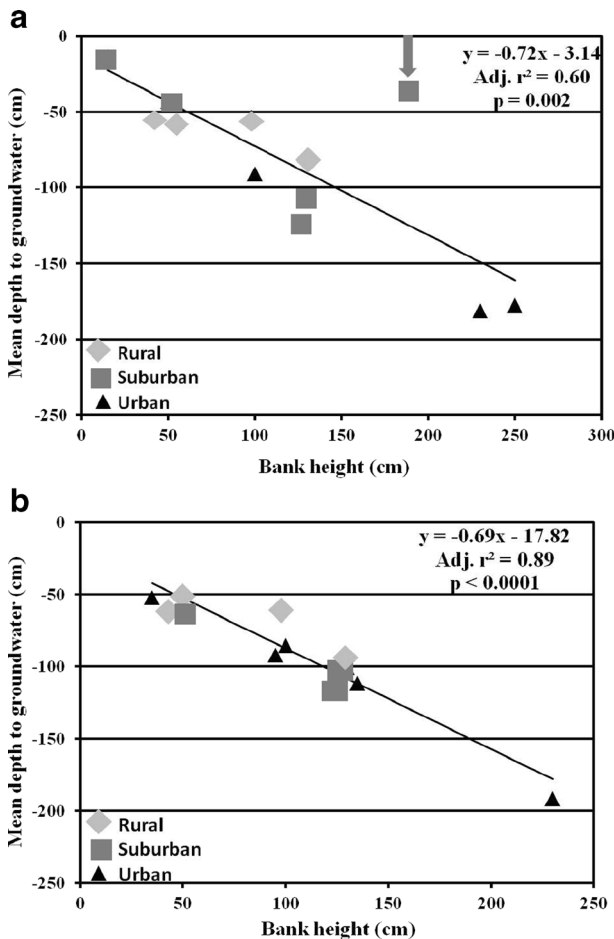


Fig. 3 Nearstream mean depth to groundwater (water table) in relation to bank height in years 2007 (a) and 2008 (b). Depth to groundwater was measured twice per month in riparian groundwater wells in urban, suburban, and rural plots from November 2006 to October 2007 (a) ($n=12$ plots) and from November 2007 to October 2008 (b) ($n=13$ plots). Urban subcatchments contain $\geq 30\%$ impervious surface cover, rural subcatchments contain $\leq 10\%$ impervious surface cover, and suburban subcatchments contain values in between 10 and 30 % impervious surface cover. The plot marked with an arrow in (a) was within 200 m of the Ohio River and was influenced to a greater extent by hydrologic dynamics of the Ohio than the other plots, and was not used in the second year

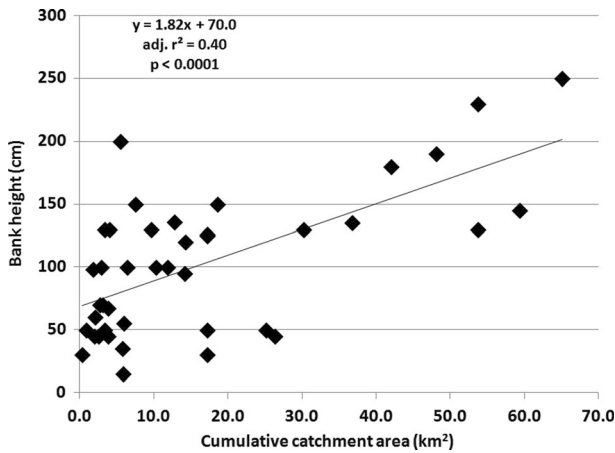


Fig. 4 Regression of bank height with upstream cumulative catchment area of 41 plots in three watersheds encompassing an urban-to-rural land-use gradient

areas above and below 20 km² were evaluated separately. Cumulative upstream catchment areas below 20 km² could not explain differences in bank height (adj. $r^2=0.08$, $p=0.068$). The streams within those subcatchments were primarily first order, with a few second order streams. Cumulative upstream catchment areas above 20 km² showed a stronger relationship with bank height (adj. $r^2=0.52$, $p=0.011$). Streams within those subcatchments were second and third order. Relationships between these factors and their ability to explain plant species diversity and WIS are reported in a subsequent section.

Relationships with finer scale LULC and %ISC at smaller spatial scales

Ordinations revealed that %ISC and LULC within 1 km of research plots were related to, but were not exclusive determinants of, woody species composition. Canopy tree species composition was not visibly influenced by % ISC or LULC within a 0.5 km or 1 km radius from a plot (Fig. 5a). However, coefficients of variation with % ISC were slightly higher for the 1 km as opposed to 0.5 km radius for tree saplings, tree seedlings, and shrubs (Fig. 5b–d; Table 9). No other environmental metric explained species composition of any stratum.

Since % ISC within a 1 km radius was a better predictor of species composition than within a 0.5 km radius (Table 9), we next used NLCD (Anderson) LULC variables calculated within a 1 km radius of each plot to assess their ability to predict species composition (Fig. 5). The influence of the Anderson LULC types differed by woody stratum, but with some common trends throughout. The influence of low-intensity urban development, open-space developed, and/or deciduous forest cover on woody species composition were the most commonly detected, since vectors for each of those variables were present in ordinations of tree saplings, tree seedlings, and shrubs (Table 9, Fig. 5b–d). High-intensity developed and medium-intensity developed LULC were also correlated with species assemblages of saplings and shrubs, respectively (Fig. 5b–d). However, high-intensity developed land cover displayed the shortest vector length, indicating a small influence on species composition. This may be explained by the fact that high-intensity developed land cover usually comprised less than 7 % of surrounding LULC within a 1 km radius of plots.

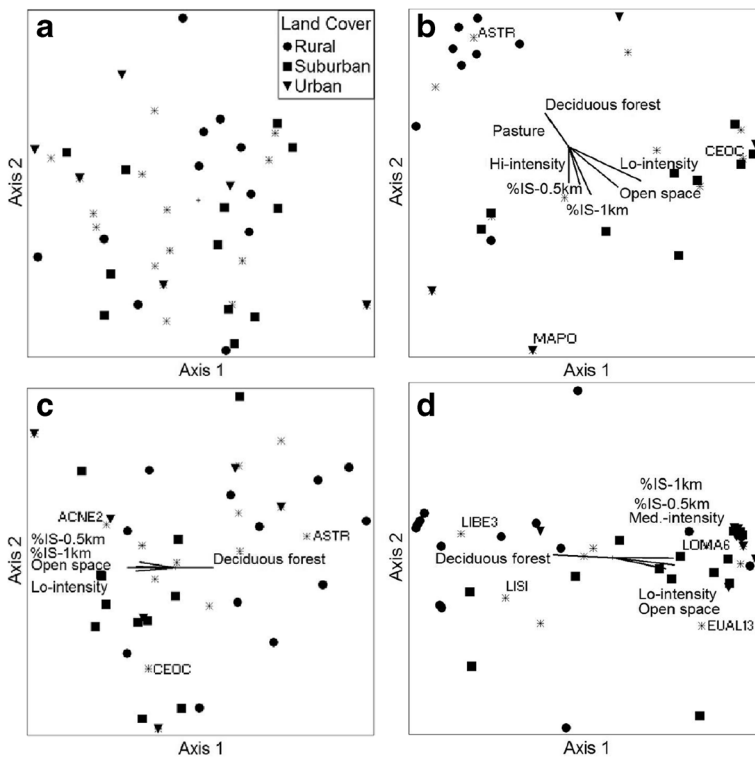


Fig. 5 Non-metric multidimensional scaling of research plots arranged according to similarities in species composition of tree (a), tree sapling (b), tree seedling (c), and shrub (d) strata. Species are shown as asterisks, with key species labeled with their species code (see Table 10 for species names). Environmental metrics shown are % impervious surface cover (%IS) surrounding each plot at 2 scales (1 km and 0.5 km radius), as well as finer scale Anderson (NLCD) land-cover categories within a 1 km radius. NLCD land-cover categories shown include low- (Lo-intensity), medium- (Med.-intensity), and high-intensity (Hi-intensity) developed, open-space developed, and deciduous forest. Definitions are shown in Appendix Table 12. Vectors representing plot environmental metrics are pointing in the direction of increasing proportions, with the length of each vector representing the strength of correlation. Vectors are shown only if they had an $r^2 \geq 0.2$ along at least one axis. Table 9 contains the variance explained (r^2) along each axis and for vectors. Triangles denote urban (≥ 30 % ISC; $n=8$ plots), squares suburban (10–30 % ISC; $n=16$ plots) and circles rural (≤ 10 % ISC; $n=17$ plots) plots using % ISC calculated within a 1 km radius of plot centers. Individual graphs do not contain a total of 41 plots since certain strata were absent in some plots. Some plots are also hidden from view if overlapping

A moderate to high degree of collinearity was observed among the NLCD variables in the ordinations (Appendix Table 13). Deciduous forest cover was negatively correlated with all of the “developed” categories (high-, medium-, low-intensity, open-space), with correlation coefficients ranging from -0.56 to -0.76 . Among “developed” categories, high- and medium-intensity ($r=0.84$), and low-intensity and open-space developed ($r=0.79$), were most strongly correlated.

Comparison of species composition between the ordination conducted at small spatial scales and the categorical analyses at the subcatchment scale revealed similar patterns. The ordinations generally resulted in plot separation by % ISC and developed LULC vs. deciduous forest cover. Some of the key species that contributed to this separation are shown in Table 10 and Fig. 5 b–d. For tree saplings, *C. occidentalis* and *A. triloba* were key species resulting in

Table 9 Coefficients of determination (r^2) for % ISC and National Land Cover Database (NLCD) variables (determined within at 0.5 and 1.0 km radii of plot centers) along ordination axes shown in Fig. 5b–d. Only the top three NLCD variables—low intensity developed, open space developed, and deciduous forest—are shown for each ordination. Negative vs. positive values indicate directionality along the axes relative to other variables along the same axis. The highest r^2 along each axis are bolded

Woody strata	Axis	Axis r^2	%ISC 0.5 km	%ISC 1 km	NLCD Variable		
					Low intensity developed	Open space developed	Deciduous forest
Tree saplings	1	0.26	0.06	0.13	0.42	0.29	(–) 0.14
	2	0.30	(–) 0.22	(–) 0.29	(–) 0.20	(–) 0.24	0.20
Tree seedlings	1	0.35	(–) 0.21	(–) 0.23	(–) 0.24	(–) 0.29	0.23
	2	0.20	0.04	0.01	(–) 0.02	0	0
Shrubs	1	0.49	0.32	0.35	0.36	0.31	(–) 0.35
	2	0.28	0	0	(–) 0.04	(–) 0.06	0.02

separation of plots surrounded by low-intensity LULC and deciduous forest, respectively (Fig. 5b). *A. triloba* and *Maclura pomifera* also contributed to plot separation along axis 2 (Fig. 5b); however, *M. pomifera* was only present in a single urban plot. In the categorical analysis, *C. occidentalis* (IV=43 %) and *A. triloba* (IV=42 %) were also found to be important urban and rural sapling species, respectively (Table 3). In the tree seedling ordination (Fig. 5c), the separation of deciduous forest plots from developed plots was partially due to the presence of *A. triloba* and *A. negundo*, respectively. This coincided with the categorical analysis, where *A. negundo* seedlings were important in urban plots (IV=45 %), and *A. triloba* was of mid-level importance in suburban (IV=11 %) and rural plots (IV=10 %), but absent from urban plots (Table 4). Among shrubs, the non-natives *L. maackii* and *E. alatus* were indicative of plots surrounded by development, and *Ligustrum sinense* (non-native) and *L. benzoin* (native) were of primary importance in the deciduous forest group in the ordination (Table 10; Fig. 5d). In the subcatchment-scale categorical analysis, *L. maackii* and *E. alatus* were significant

Table 10 Coefficients of determination (r^2) for species along ordination axes shown in Fig. 5b–d. The two species with the highest r^2 were chosen for each axis (in bold). Negative and positive signs indicate directionality along the axis relative to other species on that axis. Species codes are provided adjacent to the species name for reference with Fig. 5

Stratum	Species	Axis	
		1	2
Tree saplings	<i>C. occidentalis</i> (CEOC)	0.63	(–) 0.005
	<i>A. triloba</i> (ASTR)	(–) 0.27	0.58
	<i>M. pomifera</i> (MAPO)	0.004	(–) 0.18
Tree seedlings	<i>A. triloba</i>	0.42	0.02
	<i>A. negundo</i> (ACNE2)	(–) 0.40	0.12
	<i>C. occidentalis</i>	(–) 0.07	(–) 0.75
Shrubs	<i>L. maackii</i> (LOMA6)	0.69	0.05
	<i>L. benzoin</i> (LIBE3)	(–) 0.62	0.08
	<i>E. alatus</i> (EUAL13)	0.07	(–) 0.21
	<i>L. sinense</i> (LISE)	(–) 0.18	(–) 0.13

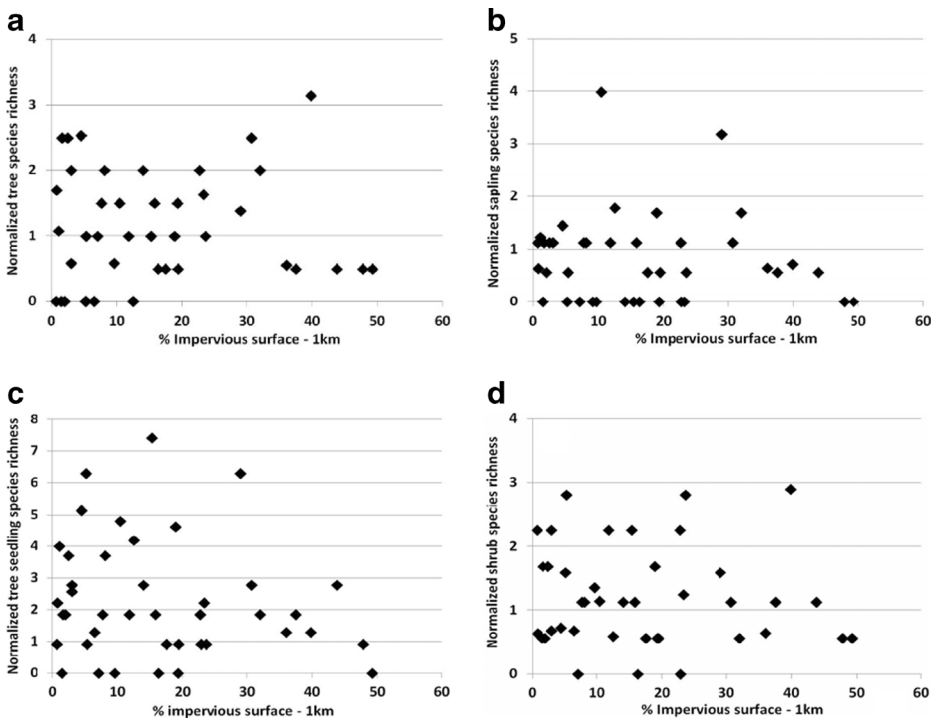


Fig. 6 Factor-ceiling distributions of species richness of tree (a), tree sapling (b), tree seedling (c), and shrub (d) strata in relation to % impervious surface within a 1 km radius of plots. Species richness was normalized as $S/\log(\text{area sampled})$ due to varying plot sizes constrained by varying riparian widths. 71 % of plots were 100 m². $N=41$ plots

indicator species in urban (IV=63 %) and suburban (IV=12 %) plots, respectively (Tables 5 and 8), while *L. sinense* and *L. benzoin* were important suburban (IV=28 %) and rural (IV=20 %) species, respectively (Table 5).

Species diversity and abundance relative to %ISC (1 km radius) and environmental variables

Since % ISC within 1 km (as opposed to 0.5 km) of plot centers correlated best with species composition, we used that scale to assess the relationship between % ISC and species diversity. We found a negative factor-ceiling relationship between them, with abrupt species richness declines for all strata occurring approximately between 30 and 40 % ISC (Fig. 6a–d). These relationships, as described by Thomson et al. (1996), occur when the explanatory variable can predict a minimum or maximum value of the response variable, but no mathematical relationship is evident among areas of central tendency.

We also found similar factor-ceiling relationships between % ISC and densities of tree seedlings and tree saplings (Fig. 7a–b). Tree seedling density declined from 34,000 to 10,000 stems ha⁻¹ in plots surrounded by greater than 20 % ISC (1 km scale). Sapling densities were reduced from approximately 5,000 stems ha⁻¹ to near zero beyond 32 % ISC. A single urban plot had a sapling stem density of greater than 12,000 stems ha⁻¹, but this was most likely due to the unusually low stem density there of the invasive shrub, *L. maackii*, which was otherwise very dense in urban plots.

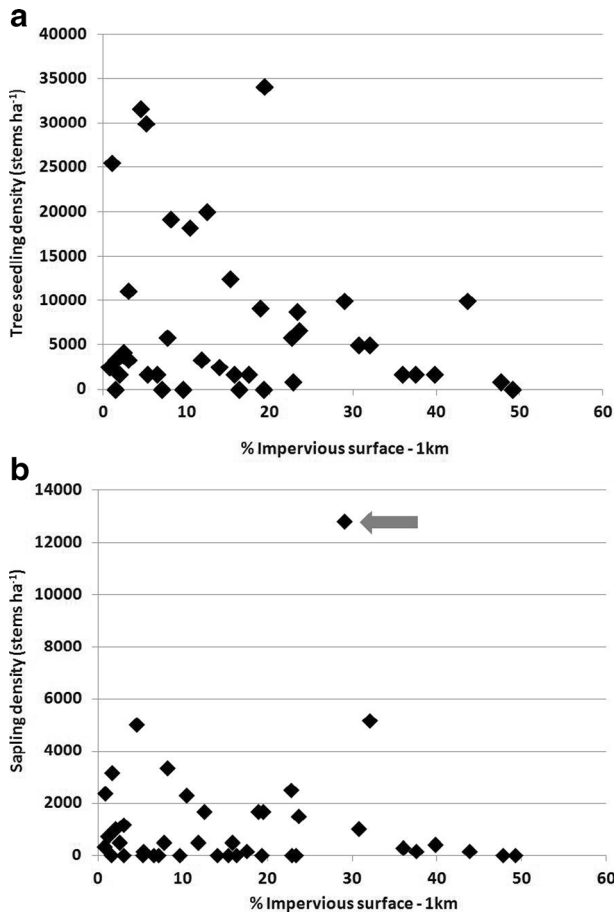


Fig. 7 Factor-ceiling distributions of density (stems ha⁻¹) of tree seedlings (**a**) and tree saplings (**b**) in relation to % impervious surface within a 1 km radius of plots. $N=41$ plots. The plot marked with an arrow was urban with a low density of the non-native shrub *L. maackii*

Since bank height and cumulative catchment area were strongly correlated (Fig. 4), we only present relationships found between species diversity and cumulative upstream catchment area as an environmental metric, because the hydrological and plant species differences between headwaters and downstream distances is well studied (Gomi et al. 2002; Nilsson et al. 1994; Nilsson et al. 1989). An inverse relationship was found between cumulative upstream catchment area and richness of all strata (Fig. 8a–d). Species richness of canopy tree, tree sapling, and shrub strata, as well as variation in species richness, was reduced with increasing catchment area upstream of the plot. Maximum richness (normalized to area sampled) for trees and shrubs decreased 5-fold from the smallest to the largest cumulative catchment areas. Maximum richness decreased 7- to 8-fold for tree saplings (Fig. 8). No new relationships were found when plots along first order streams were analyzed separately to control for cumulative catchment area.

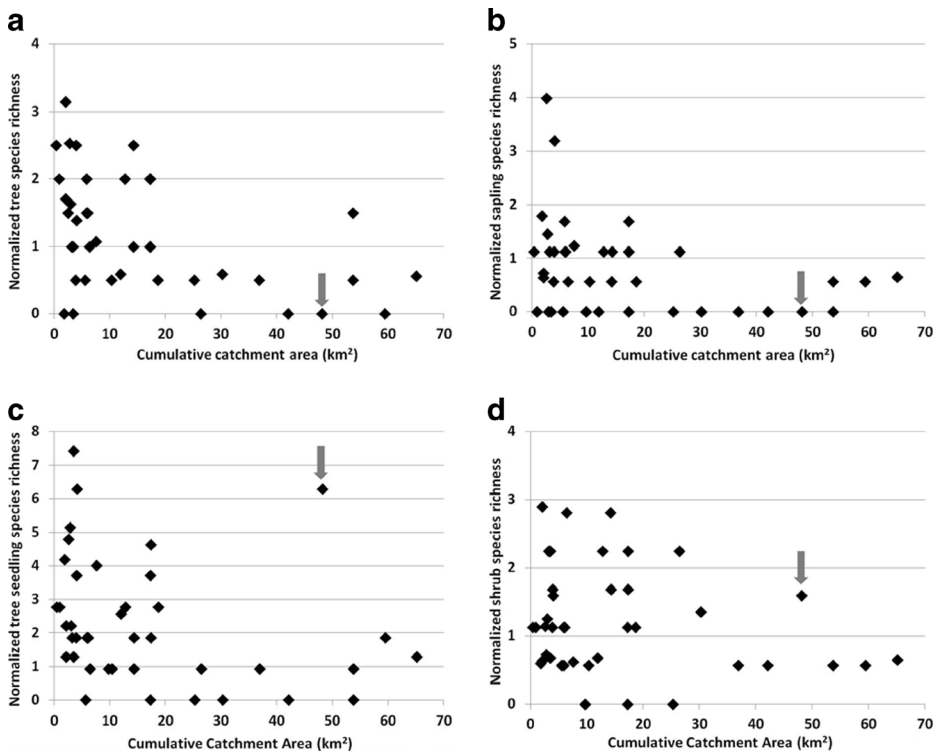


Fig. 8 Factor-ceiling distributions of cumulative catchment area (km²) and species richness of tree (a), tree sapling (b), tree seedling (c), and shrub (d) strata. Species richness was normalized as $S/\log(\text{area sampled})$ due to varying plot sizes constrained by varying riparian widths. 71 % of plots were 100 m². $N=41$ plots. The plot marked with an arrow (also in Fig. 3a) was within 200 m of the Ohio River and was influenced to a greater extent by the hydrologic dynamics of this 8th order river than the other plots

Wetland and Non-native species relative to %ISC (1 km radius) and environmental variables

Trees classified as FACW were not found along stream banks higher than 100 cm and where the cumulative upstream catchment area was above 15 km² (White 2011). Conversely, facultative (FAC), facultative upland (FACU), and upland (UPL) species occurred adjacent to streambanks across the range of bank heights measured (up to 250 cm high). In the two plots adjacent to the highest banks, FAC and UPL trees were the sole inhabitants. No relationships were found between bank height and the WIS of saplings and tree seedlings (White 2011).

The importance value of shrubs classified as FACW and NI (no wetland classification) exhibited factor-ceiling distributions in relation to % ISC within 1 km of the plot. FACW shrubs occurred only in plots with less than 30 % ISC (Fig. 9a). Plots with >30 % ISC were dominated almost exclusively by NI shrubs, principally *L. maackii* and *E. alatus* (Fig. 9b). Only shrub species classified as NI and UPL were found in the five plots where streambank height exceeded 150 cm (not shown).

Most of the non-native species in this study were shrub species (Table 5). Each land-use category (urban, suburban, and rural) contained approximately the same non-native shrub

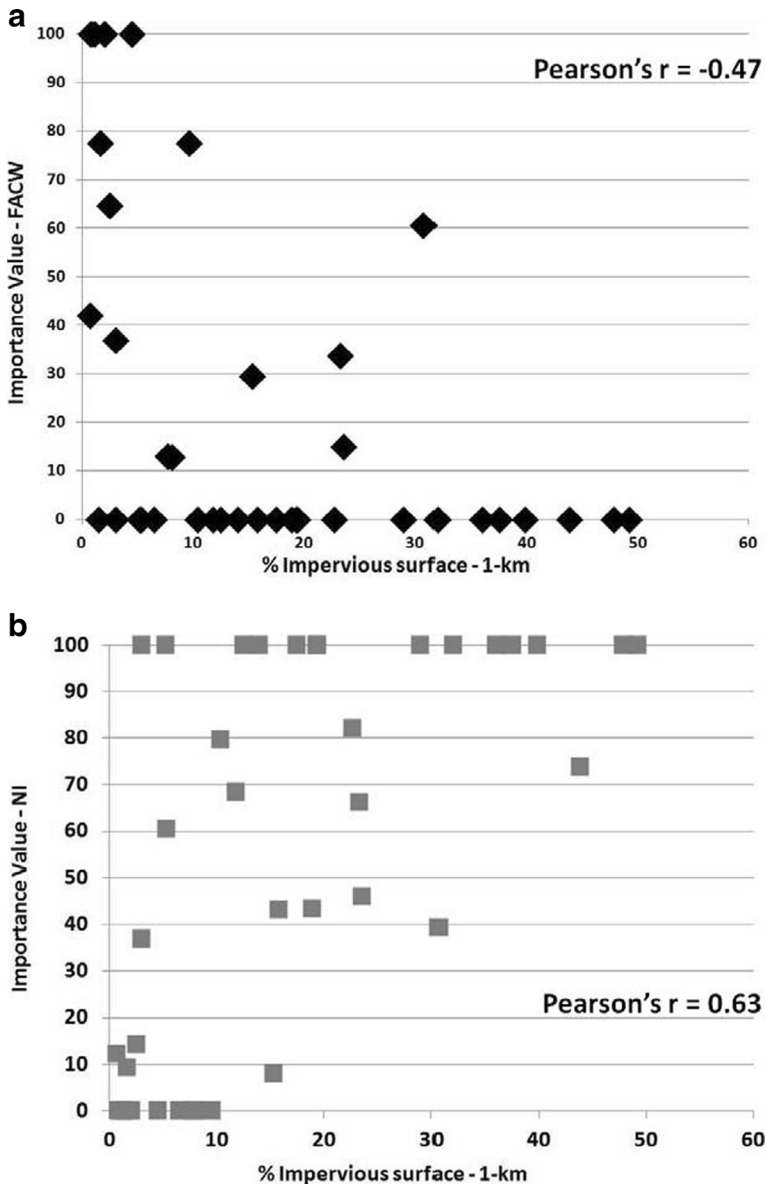


Fig. 9 Shrub importance values based on two categories of wetland indicator status (facultative wetland (FACW) **(a)** and “not otherwise indicated” (NI) **(b)**) in relation to increasing proportions of impervious surface cover (within a 1 km plot radius) exhibiting **(a)** negative and **(b)** positive factor-ceiling distributions. Shrub species classified as NI were primarily non-native invasive shrubs, with *L. maackii* making up the bulk of the category and *E. alatus* of lesser importance

species richness, with urban and suburban areas containing five non-native shrub species, and rural riparian areas containing four (Table 5). However, scatterplots revealed positive “floor” distributions, with non-native shrub importance values increasing as % ISC within a 1 km radius increased ($r=0.54$, not shown; White 2011). Although most plots

contained some non-native shrubs, the majority of plots with greater than 30 % ISC within 1 km were dominated by them (not shown).

The relative importance of *L. maackii*, an indicator species for urban areas and a nearly ubiquitous shrub species in all plots, increased with increasing % ISC within 1 km of plot centers ($r=0.55$; not shown). In addition, tree seedling densities and, to a lesser extent, tree sapling densities showed a marked decrease (negative “ceiling” distributions) with increasing *L. maackii* densities (White 2011). The highest tree seedling and sapling densities occurred at the lowest *L. maackii* densities (<5,000 to 12,000 stems ha^{-1}), and approached zero at high *L. maackii* stem densities (>12,000 stems ha^{-1}). While a single plot with the highest sapling density was urban (Fig. 7b), the unusually low density of *L. maackii* in this plot may have contributed to the establishment of these saplings. These results show *L. maackii* to be an urban species with likely negative impacts on the regeneration layer for other woody plants in riparian areas.

Discussion

Species composition

At the subcatchment scale we found the most prominent differences in species composition among land-use categories in the shrub stratum. This stratum distinguished urban, suburban, and rural land-use categories, with non-native shrub species defining urban (*L. maackii*) and suburban (*E. alatus*) riparian sites, and a native FACW shrub species (*L. benzoin*) being most prominent in rural riparian zones.

Eight tree species occurred in all land-use categories, but only *A. negundo*, *C. occidentalis* and *Fraxinus americana* were found in all three tree strata across all land uses, indicating successful recruitment over the past several decades. *A. negundo* and *C. occidentalis* were especially prominent in urban and suburban areas, and were the most frequently occurring tree seedling species across all land-use categories. As noted in Burns and Honkala (1990), both species are able to propagate under a variety of conditions, which would contribute to their success across the broad range of hydrological and terrestrial disturbances found in urban to rural riparian areas. Although ubiquitous, *Fraxinus americana* was less abundant and is regionally threatened by the Emerald Ash Borer (Kovacs et al. 2010; MacFarlane and Meyer 2005). This species was also one of the more important species in the rural tree seedling community (Table 4). As individuals succumb to this invasive pest and create canopy gaps, opportunistic species may occupy their niche, thereby changing the species composition of these communities. Other species have not exhibited successful recruitment. *Platanus occidentalis*, a FACW and regionally important riparian tree, was not present in the sapling stratum, and occurred in the seedling stratum in only one urban, suburban, and rural plot each.

In this study, LULC within a 1 km radius of plots was a slightly better predictor of species composition than LULC within a 0.5 km radius. Low-intensity developed LULC correlated best with woody species composition for the sapling, tree seedling, and shrub strata. Low-intensity developed LULC covered a greater areal percentage of the study area (mean=13 %) than the other developed categories (High intensity developed mean=3 %, Medium intensity mean=5 %), which potentially contributed to its stronger correlation with vegetation. Neither coarse- nor fine-scale LULC was associated with variation in species composition of canopy trees. Other studies have found that land uses and covers closer to the focal plant community offer greater capacity for predicting plant community structure. For instance, Fernandes et al. (2011) found that variation in woody (canopy trees and shrubs) species structure along the

River Tagus in Portugal was better explained by LULC within 30 m of the riparian zone as opposed to 200 m. However, in that study landscape metrics and species patterns also exhibited a high degree of spatial auto-correlation, so that vegetation patches closer together were more similar, which likely contributed to the greater influence of LULC at the smaller 30 m scale. Increasing ISC and finer scale LULC (buildings, roads and railroads) within a 250 m radius was correlated with a decrease in woody species with high moisture requirements (Pennington et al. 2010). However, being the only spatial scale considered, no assessments can be made regarding the abilities of LULC at that scale to explain variation in plant communities compared to others. Taken together, these studies so far indicate that no single spatial scale of influence of % ISC and LULC categories on the riparian plant community can be recommended for cross-system comparisons.

Species abundance and diversity

Many of the patterns of plant species richness and abundance exhibited factor-ceiling distributions in relation to several variables. Species richness of all strata, and tree sapling and seedling densities declined substantially as % ISC within a 1 km radius increased. In this study, thresholds of tolerance occurred between 30 % and 50 % ISC. Such thresholds have been shown in studies relating degree of urban development to in-stream processes and organisms, where increases in impervious area resulted in declines in measures of stream health, including macroinvertebrate communities, biotic integrity indexes, and algal indexes (King et al. 2005; Walsh et al. 2005a; Walsh et al. 2005b; Booth et al. 2004). This suggests the possibility of a relationship between, or common factors contributing to, the declining richness and abundance of riparian vegetation and declining streamwater habitat and quality. One possibility could include the increasing abundance of invasive, non-native shrubs in urban and suburban riparian areas and declining stream habitat quality for stream organisms (McNeish et al. 2012).

The decline in species richness of all strata, but particularly saplings and tree seedlings, with increasing % ISC was reported in other studies. Burton and Samuelson (2008) and Pennington et al. (2010) found tree species richness declined in both the forest stand layer and the regeneration layer as % ISC (at 30 m and 250 m plot radii, respectively) increased. Furthermore, Pennington et al. (2010) found the species diversity response to urbanization was greater in the understory than the canopy layer, indicating that the understory was responding more synchronously to current urban conditions than the canopy stratum. Another study by Dallimer et al. (2012) found no pattern concerning overall plant species richness (woody plants and forbs) with changing land-use in Sheffield, England. However, that particular study used a coarser spatial measure of land-use change (distance from the city center) and may have missed more subtle differences that were detected in our study as well as others. We speculate that the lower plant richness in urban riparian areas may be attributed to a combination of a) fewer available propagules in urban areas (seed limitation) (Porter et al. 2001); b) abiotic conditions that reduce species' ability to reproduce, germinate and grow (Brown and Peet 2003); and/or c) biotic factors, such as greater competition (see *L. maackii* discussion below) and selective herbivory, favoring establishment of fewer species (Liang and Seagle 2002).

Tree, tree sapling, and shrub species richness also decreased with increasing cumulative upstream catchment area. The relationships showed both a decline in species richness as well as a decline in the range of possible richness values. This was unexpected since greater cumulative area could result in greater diversity of propagules being deposited on

streambanks during flood events. The relationship was found even when first order streams were analyzed separately. In contrast to our findings, Nilsson et al. (1994) found higher species richness of vascular plants in the Vindel River system in Sweden along the main channel, and lower species richness along the tributaries. Also, Nilsson et al. (1989) found that, along the Torne River in Sweden, species richness of ruderal species increased with downstream distance, but richness of native species peaked along the middle reaches of the system. However, those river systems are much larger (12,654 km² and 17,950 km² catchments, respectively) than the ones presented in our study (between 50 and 65 km²), and large river systems exhibit wider floodplains and different hydrological dynamics than smaller systems.

One possibility for the unexpected decline in woody plant species richness as cumulative upstream catchment area increased may involve the flooding frequency of upstream and downstream locations, given that bank height also increased with cumulative catchment area. Brown and Peet (2003) showed species richness of both native and non-native species were positively correlated with flooding frequency in mountainous riparian areas. This was attributed to immigration-driven selection pressures due to propagule deposition and frequent disturbance. Since we had higher banks adjacent to downstream plots, flooding frequency may have been reduced due to the increased bankfull height of the downstream reaches. However, since we did not measure flooding intensity or frequency in our watersheds, this remains speculative.

The relative importance of non-native shrubs, which was positively correlated with % ISC, was due primarily to the high prevalence and density of *L. maackii*, the Amur honeysuckle. Boyce (2010) reported its occurrence in a majority of the counties in Kentucky, USA, noting its increased abundance in counties with larger populations. This shrub has also been positively correlated with % ISC and urban land use in other studies (Pennington et al. 2010; Borgmann and Rodewald 2005; Hutchinson and Vankat 1997; Luken and Thieret 1996). For example, Borgmann and Rodewald (2005) found a positive relationship between the degree of urban LULC (pavement and buildings) within a 1 km radius of riparian plots and percent cover of *L. maackii*. The importance of this finding relates to the well-known negative effects this introduced species has on the surrounding plant community, particularly the woody regenerative layer (Loewenstein and Loewenstein 2005; Collier et al. 2002; Luken and Thieret 1996).

In this study, % ISC is positively correlated with *L. maackii* abundance. Therefore, we cannot distinguish whether the declines in abundance of saplings and tree seedlings with increasing % ISC (1 km radius; Fig. 7b) is due to urban conditions and disturbances alone or to the suppressive effects of *L. maackii* on tree recruitment, or both. A single plot with a relatively high % ISC (Fig. 7b) and a relatively low density of *L. maackii* exhibited a high sapling density, suggesting that competitive release of saplings when *L. maackii* was low was a more direct determinant of sapling density in our study than other urban conditions. This possibility is supported by the many studies showing negative relationships between this exotic shrub and tree seedling and sapling richness and abundance (Trammell and Carreiro 2011; Burton et al. 2005; Loewenstein and Loewenstein 2005; Collier et al. 2002; Merriam and Feil 2002; Luken and Thieret 1996).

These findings indicate that as areas become more urbanized, non-native and generalist shrubs, such as *L. maackii*, may spread along riparian zones negatively affecting the performance of other species. Therefore, in addition to abiotic conditions and disturbances created by increasing impervious surface (e.g. more intense heat island, drier soils, greater surface runoff), non-native invasive shrubs are promoting declines in tree seedlings and saplings and thereby threatening overstory species regeneration in riparian as well as in other urban forest remnants in the region.

Patterns of wetland indicator status

One premise at the start of this study was that streambank height would be positively correlated with urban LULC and with groundwater depth and, therefore, could be used as a surrogate for urban hydrologic drought (Groffman et al. 2003). We could then explore the potential for bank height to explain riparian species composition and species attributes. However, the link between bank height and LULC categories was not statistically significant in this study, although the highest bank heights were found next to some of the urban plots. We established a strong link between bank height and groundwater depth, but also discovered a positive correlation between bank height and cumulative upstream catchment area, which was not linked to LULC. Nonetheless, our findings regarding the WIS of trees shows that wetland tree survivorship has been reduced adjacent to higher stream banks, since FACW tree species did not occur adjacent to banks higher than 100 cm (Fig. 9a), and non-wetland species persisted next to stream banks up to 150 cm (Fig. 9b). Ehrenfeld (2005) found similar results in wetlands (riparian and non-riparian) of New Jersey, where the absence of obligate (OBL) wetland species was associated with lowered water tables in urban environments. However, FACW species persisted in urban wetlands in New Jersey. Although we found no relationship between the relative importance of FACW trees (>2.54 cm DBH) and % ISC, Pennington et al. (2010), who conducted a study in Cincinnati, Ohio about 160 km from Louisville, found a negative correlation between % ISC within a 250 m plot radius and stem density of canopy species (>10 cm DBH) with high moisture requirements. The Gwynns Falls watershed in Baltimore, Maryland, USA exhibited an absence of wetland (FACW and OBL) species in the tree stratum and an abundance of upland species in the urban portions of the watershed, even though saplings and tree seedlings of wetland species persisted (Groffman et al. 2003).

FACW shrubs were conspicuously absent in urban riparian zones in Louisville. *L. benzoin*, a native shrub, was the most prominent FACW species, and it occurred primarily in rural riparian habitats. Furthermore, the decreasing proportion of wetland shrub species as impervious surface increased (Fig. 9a), independent of bank height, indicates that factors other than riparian water table depth are contributing to their loss of dominance. Pennington et al. (2010) found a similar negative correlation between understory species (shrubs and tree stems <10 cm DBH) with mesic moisture requirements and % ISC. We found an absence of FACW saplings and a low frequency of occurrence of FACW tree seedlings as % ISC increased. Our results indicate FACW species of the various woody strata are being influenced by more than local hydrology, with the success of wetland shrubs linked positively to relatively low % ISC (<30 %).

The relative importance of bank height and groundwater depth on wetland species establishment in urban and suburban riparian areas remains unclear. Because FACW tree species, such as *P. occidentalis*, occurred primarily in the canopy layer and were relatively absent from the regeneration layer suggests that selection pressures, from a wetland species perspective, have changed since the now larger trees became established, and that wetland tree species are not propagating and/or surviving regardless of stream bank height or land-use category. Only generalist (NI) and UPL shrub species occurred adjacent to streambanks higher than 150 cm. Below that limit, however, no patterns were evident. FACW shrubs may be influenced by other conditions created by or correlated with increasing impervious surface, including

potentially greater competition from increasing riparian colonization by non-native shrub species like *L. maackii* (McEwan et al. 2010).

Conclusions

We found that both coarse scale (% ISC at the subcatchment spatial scale) and finer, local scale LULC variables were useful for explaining differences in riparian plant community composition, abundance, and diversity across woody plant strata (Fig. 1). Low-intensity developed and deciduous forest cover types within 1 km of the plots were highly correlated with woody plant community composition, with the exception of the canopy tree stratum. The most distinct differences among land-use categories were explained by variation in the shrub layer, with the non-natives, *L. maackii* and *E. alatus*, defining urban and suburban communities, respectively. More detailed studies aimed at determining the specific effects of urban LULC on riparian plant communities should use fine-scale measures of urbanization, and a broader range of radial distances from plots to explore thresholds of LULC influence on their structure and functions. However, at this time use of any particular set of LULC variables or spatial scale cannot be recommended for cross-system comparisons.

Many of the differences in woody plant communities that were related to LULC varied by stratum. Canopy trees did not strongly correlate with LULC at any scale, suggesting that their composition and diversity reflects past land cover and usage. Changes in the shrub layer tracked current LULC most closely, as did variation in sapling and tree seedling strata. However, saplings and tree seedlings were also negatively correlated with non-native shrub density. Since several studies have shown the non-native shrub, *L. maackii*, can have large inhibitory or competitive effects on the performance of other species (McEwan et al. 2010; Dorning and Cipollini 2006; Luken and Thieret 1996), we believe the increase in importance of *L. maackii* with % ISC likely contributed strongly to the urban effects observed on species richness and densities of saplings and tree seedlings (Fig. 1, Arrows 1 and 11).

FACW shrub species are also being reduced with increasing % ISC. These shrub species were almost entirely absent from urban plots as generalist species (*L. maackii* and *E. alatus*) became dominant. FACW saplings and tree seedlings were conspicuously reduced within the landscape compared to larger FACW trees, indicating that environmental conditions and selection pressures have likely changed since earlier establishment of these canopy trees. FACW tree species were absent along relatively high streambanks (>1 m) with low water tables, regardless of LULC. While streambank height along these low order streams did predict groundwater depth (Fig. 1, Arrow 5), we found that cumulative upstream catchment area was a stronger predictor of streambank height (Fig. 1, Arrows 3 and 4) than % ISC at the subcatchment scale. This was due to the fact that streams in some rural and suburban subcatchments were also incised wherever cumulative upstream catchment area was large. Nonetheless, the highest streambanks were still found along urban streams, suggesting that together % ISC and cumulative catchment area may affect riparian vegetation dynamics by changing regimes of overbank flooding (Fig. 1, Arrows 7 and 8) and by their combined effects on bank height and depth to groundwater (Fig 1, Arrows 4, 5 and 6).

Riparian zones, a transition zone between land and water, exist in a state of perpetual flux. The direction of change in the Louisville region, especially in urban areas, seems to be towards a less diverse suite of woody plant species, a reduction in native and wetland species abundance, and an

increase in non-native shrubs. Land managers and riparian restoration teams should consider these findings when deciding whether invasive species eradication is needed before planting trees and in deciding which woody species to plant in riparian areas. For example, woody species survivorship in different LULC contexts will vary, and managers need to be informed that species chosen for plantings should match not only local conditions but disturbance regimes determined by upstream catchments where land use may be rapidly changing.

Due to their linear nature and exceptional openness to inputs of species, matter and energy from the stream and their upland matrix, riparian plant communities in many regions face numerous threats to their native diversity. In the Mid-West region of the USA, these communities are currently threatened by non-native shrubs and insect pests like the Emerald Ash Borer. Unless it is managed, *L. maackii*, already widespread throughout Kentucky (Boyce 2010), will continue to suppress both woody and herbaceous species in urban and suburban riparian areas. This shrub will become more common in rural forested areas as urban sprawl spreads, perhaps using riparian areas themselves as corridors. Also, by creating numerous canopy gaps due to the death of an important riparian and floodplain tree genus (*Fraxinus*), the emerald ash borer may facilitate the spread of exotic shrubs, vines and trees, and opportunistic natives. The collective impacts of these disturbances on the structural integrity of native riparian communities, their faunal diversity, and stream quality make informed and timely management imperative.

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Appendix

Table 11 Wetland indicator status and species provenance codes used in this study and their definitions. (U. S. Department of Agriculture PLANTS Database 2012; U. S. Department of Agriculture, Natural Resources Conservation Service (2009))

Code	Term	Meaning
OBL	Obligate	Almost always a hydrophyte, rarely in uplands
FACW	Facultative wetland	Usually a hydrophyte but occasionally found in uplands
FAC	Facultative	Commonly occurs as either a hydrophyte or non-hydrophyte
FACU	Facultative upland	Occasionally is a hydrophyte but usually occurs in uplands
UPL	Upland	Rarely is a hydrophyte, almost always in uplands
NI	No indicator	Insufficient information available to determine an indicator status
N	Native	Plants that have developed over hundreds of years in an area—pre-European settlement
E	Exotic/Non-native	Plants that have been introduced with human assistance into an area in which it was not found pre-European-settlement
Z	Naturalized	Non-native species that do not need human assistance to reproduce, thereby maintaining themselves over an unspecified period of time

Table 12 National Land Cover Database (2001) land-cover classification categories, definitions, and examples

Classification	Definition
Developed, open space	Includes areas with a mixture of some built structures, but mostly vegetation in the form of lawn grasses. Impervious surfaces account for less than 20 % of total cover (e. g. park, golf course).
Developed, low intensity	Includes areas with a mixture of built structures and vegetation. Impervious surfaces account for 20–49 % of total cover (e. g. single family housing).
Developed, medium intensity	Includes areas with a mixture of built structures and vegetation. Impervious surfaces account for 50–79 % of the total cover (e. g. single family housing)
Developed, high intensity	Includes highly developed areas where people reside or work in high numbers. Impervious surfaces account for 80–100 percent of the total cover (Apartments, Commercial/Industrial).
Deciduous forest	Areas dominated by trees generally greater than 5 meters tall, and greater than 20 % of total vegetation cover. More than 75 % of the tree species shed foliage simultaneously in response to seasonal change.
Mixed forest	Areas dominated by trees generally greater than 5 meters tall, and greater than 20 % of total vegetation cover. Neither deciduous nor evergreen species are greater than 75 % of total tree cover.
Herbaceous	Areas dominated by graminoid or herbaceous vegetation, generally greater than 80 % of total vegetation. These areas are not subject to intensive management such as tilling, but can be utilized for grazing.
Pasture	Areas of grasses, legumes, or grass-legume mixtures planted for livestock grazing or the production of seed or hay crops, typically on a perennial cycle. Pasture/hay vegetation accounts for greater than 20 % of total vegetation.
Cultivated crops	Areas used for the production of annual and perennial woody crops. Crop vegetation accounts for greater than 20 % of total vegetation (e. g. corn, orchard)
Wetlands	Areas where soil or substrate is periodically saturated with or covered with water.

Table 13 Collinearity matrix for National Land Cover Database (NLCD) variables within a 1 km buffer of research plots

	High intensity	Medium intensity	Low intensity	Open space	Deciduous
High intensity	1				
Medium intensity	0.84	1			
Low intensity	0.35	0.63	1		
Open space	0.11	0.39	0.79	1	
Deciduous	−0.62	−0.76	−0.69	−0.56	1

References

- Auble GT, Friedman JM, Scott ML (1994) Relating riparian vegetation to present and future streamflows. *Ecol Appl* 4:544–554
- Booth DB, Karr JR, Schauman S, Konrad CP, Morley SA, Larson MG, Burges SJ (2004) Reviving urban streams: land use, hydrology, and human behavior. *J Am Water Resour Assoc* 40:1351–1364
- Boothroyd IKG, Quinn JM, Langer ERL, Costley KJ, Steward G (2004) Riparian buffers mitigate effects of pine plantation logging on New Zealand streams 1. riparian vegetation structure, stream geomorphology and periphyton. *For Ecol Manag* 194:199–213
- Borgmann KL, Rodewald AD (2005) Forest restoration in urbanizing landscapes: interactions between land uses and exotic shrubs. *Restor Ecol* 13:334–340
- Boyce RL (2010) Invasive shrubs in Kentucky. *Northeast Nat* 17:1–32
- Brady MJ, McAlpine CA, Miller CJ, Possingham HP, Baxter GS (2011) Mammal responses to matrix development intensity. *Aust Ecol* 36:35–45
- Bren LJ (1992) Tree invasion of an intermittent wetland in relation to changes in the flooding frequency of the River Murray. *Aust J Ecol* 17:395–408
- Brenner FJ, Mondok JJ, McDonald RJ Sr (1991) Impact of riparian areas and land use on four non-point source pollution parameters in Pennsylvania. *J Pennsylvania Acad Sci* 65:65–70
- Brown RL, Peet RK (2003) Diversity and invasibility of southern Appalachian plant communities. *Ecology* 84: 32–39
- Burns RM, Honkala BH (1990) *Hardwoods*. Agriculture Handbook 654. vol 2. Washington, DC, USA
- Burton ML, Samuelson LJ (2008) Influence of urbanization on riparian forest diversity and structure in the Georgia Piedmont, US. *Plant Ecol* 195:99–115
- Burton ML, Samuelson LJ, Pan S (2005) Riparian woody plant diversity and forest structure along an urban–rural gradient. *Urban Ecosyst* 8:93–106
- Cadenasso ML, Pickett STA (2001) Effect of edge structure on the flux of species into forest interiors. *Conserv Biol* 15:91–97
- Collier MH, Vankat JL, Hughes MR (2002) Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. *Am Midl Nat* 147:60–71
- Colwell RK (2009) EstimateS: statistical estimation of species richness and shared species from samples. 8.2 edn
- Conner EF, McCoy ED (1979) The statistics and biology of the species-area relationship. *Am Nat* 113:791–833
- Dallimer M, Rouquette JR, Skinner AMJ, Armsworth PR, Maltby LM, Warren PH, Gaston KJ (2012) Contrasting patterns in species richness of birds, butterflies and plants along riparian corridors in an urban landscape. *Divers Distrib* 18:742–753
- Dorning M, Cipollini D (2006) Leaf and root extracts of the invasive shrub, *Lonicera maackii*, inhibit seed germination of three herbs with no autotoxic effects. *Plant Ecol* 184:287–296
- Dufrene M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67:345–366
- Easson G, Yarbrough LD (2002) The effects of riparian vegetation on bank stability. *Environ Eng Geosci* 8:247–260
- Ehrenfeld JG (2005) Vegetation of forested wetlands in urban and suburban landscapes in New Jersey. *J Torrey Bot Soc* 132:262–279
- Fernandes MR, Aguiar FC, Ferreira MT (2011) Assessing riparian vegetation structure and the influence of land use using landscape metrics and geostatistical tools. *Landsc Urban Plan* 99:166–177
- Geyer W, Brooks K, Nepl T (2003) Stream bank stability of two Kansas river systems during the 1993 flood in Kansas, USA. *Trans Kans Acad Sci* 106:48–53
- Gilliam JW (1994) Riparian wetlands and water quality. *J Environ Qual* 23:896–900
- Godefroid S, Koedam N (2007) Urban plant species patterns are highly driven by density and function of built-up areas. *Landsc Ecol* 22:1227–1239
- Gomi T, Sidle RC, Richardson JS (2002) Understanding Processes and Downstream Linkages of Headwater Systems. *Bioscience* 5:905–916
- Groffman PM, Bain DJ, Band LE, Belt KT, Brush GS, Grove JM, Pouyat RV, Yesilonis IC, Zipperer WC (2003) Down by the riverside: urban riparian ecology. *Frontiers in Ecol and Environ* 1:315–321
- Homer C, Huang C, Yang L, Wylie B, Coan M (2004) Development of a 2001 national landcover database for the United States. *Photogramm Eng Remote Sens* 70:829–840
- Hutchinson TF, Vankat JL (1997) Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. *Conserv Biol* 11:1117–1124

- Johnson WC (ed) (1993) Divergent responses of riparian vegetation to flow regulation on the Missouri and Platted rivers. Proceedings of the Symposium on the Restoration Planning for the Rivers of the Mississippi River Ecosystem. U. S. Department of the Interior, Washington D. C.
- Jones RL (2005) Plant life of Kentucky : an illustrated guide to the vascular flora. University Press of Kentucky, Lexington, KY, USA
- Kentucky Environmental and Public Protection Cabinet (2011) Final 2010 Integrated Report to Congress on the Condition of Water Resources in Kentucky. vol II
- King RS, Baker ME, Whigham DF, Weller DE, Jordan TE, Kazyak PF, Hurd MK (2005) Spatial considerations for linking watershed land cover to ecological indicators in streams. *Ecol Appl* 15:137–153
- Kovacs KF, Haight RG, McCullough DG, Mercader RJ, Siegert NW, Liebhold AM (2010) Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. *Ecol Econ* 69:569–578
- Kruskal WH, Wallis WA (1952) Use of ranks in one-criterion variance analysis. *J Am Stat Assoc* 47:583–621
- Lemmon PE (1956) A spherical densiometer for estimating forest overstory density. *For Sci* 2(4):314–320
- Lemmon PE (1957) A new instrument for measuring forest overstory density. *J For* 55:667–668
- Liang SY, Seagle SW (2002) Browsing and microhabitat effects on riparian forest woody seedling demography. *Ecology* 83:212–227
- Loewenstein NJ, Loewenstein EF (2005) Non-native plants in the understory of riparian forests across a land use gradient in the Southeast. *Urban ecosyst* 8:79–91
- Lowrance R, Altier LS, Newbold JD, Schnabel RR, Groffman PM, Denver JM, Correll DL, Gilliam JW, Robinson JL, Brinsfield RB, Staver KW, Lucas W, Todd AH (1997) Water quality functions of riparian forest buffers in Chesapeake Bay watersheds. *Environ Manag* 21:687–712
- Luken JO, Thieret JW (1996) Amur honeysuckle, its fall from grace. *Bioscience* 46:18–24
- Lyon J, Gross NM (2005) Patterns of plant diversity and plant-environmental relationships across three riparian corridors. *For Ecol Manag* 204:267–278
- MacFarlane DW, Meyer SP (2005) Characteristics and distribution of potential ash tree hosts for emerald ash borer. *For Ecol Manag* 213:15–24
- Magurran AE (2004) Measuring Biological Diversity. Blackwell, Malden, MA, USA
- McCune B, Grace JB (2002) Analysis of Ecological Communities, 2nd edn. MjM Software Design, Gleneden Beach, OR, USA
- McCune B, Mefford MJ (1999) PC-Ord. Multivariate Analysis of Ecological Data, 441st edn. MjM Software, Gleneden Beach, Oregon
- McEwan RW, Arthur-Paratley LG, Rieske LK, Arthur MA (2010) A multi-assay comparison of seed germination inhibition by *Lonicera maackii* and co-occurring native shrubs. *Flora - Morphol, Distrib, Funct Ecol Plants* 205:475–483
- McNeish R, Benbow M, McEwan R (2012) Riparian forest invasion by a terrestrial shrub (*Lonicera maackii*) impacts aquatic biota and organic matter processing in headwater streams. *Biological Invasions*:1–13.
- Merriam RW, Feil E (2002) The potential impact of an introduced shrub and on native plant diversity and forest regeneration. *Biol Invasions* 4:369–373
- Mielke PW, Berry KJ (2007) Permutation Methods: A Distance Function Approach. Springer, New York
- Moffatt SF, McLachlan SM, Kenkel NC (2004) Impacts of land use on riparian forest along an urban – rural gradient in southern Manitoba. *Plant Ecol* 174:119–135
- Müller N, Ignatieva M, Nilon CH, Werner P, Zipperer WC (2013) Patterns and trends in urban biodiversity and landscape design. In: Elmqvist T, Goodness J, Güneralp B, Marcotullio PJ, McDonald RI, Parnell S, Hasse D, Sendstad M, Seto KC, Wilkinson C (eds) Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities: A Global Assessment. Springer-Verlag, New York, pp 123–174
- Naiman RJ, Decamps H (1997) The ecology of interfaces: riparian zones. *Ann Rev Ecol Syst* 28:621–658
- National Land Cover Database (2001) http://www.mrlc.gov/nlcd01_leg.php
- Nilsson C, Ekblad A, Dynesius M, Backe S, Gardfjell M, Carlberg B, Hellqvist S, Jansson R (1994) A comparison of species richness and traits of riparian plants between a main river channel and its tributaries. *J Ecol* 82:281–295
- Nilsson C, Grelsson G, Johansson M, Sperens U (1989) Patterns of plant species richness along riverbanks. *Ecology* 70:77–84
- Nilsson C, Jansson R, Zinko U (1997) Long-term responses of river-margin vegetation to water-level regulation. *Science* 276:798–800
- Oneal AS, Rotenberry JT (2008) Riparian plant composition in an urbanizing landscape in southern California, U.S.A. *Landsc Ecol* 23:553–567
- Paul MJ, Meyer JL (2001) Streams in the urban landscape. *Ann Rev Ecol Syst* 32:333–365
- Pennington DN, Hansel J, Blair RB (2008) The conservation value of urban riparian areas for landbirds during spring migration: Land cover, scale, and vegetation effects. *Biol Conserv* 141:1235–1248

- Pennington DN, Hansel JR, Gorchov DL (2010) Urbanization and riparian forest woody communities: Diversity, composition, and structure within a metropolitan landscape. *Biol Conserv* 143:182–194
- Pickett STA, Collins SC, Armesto JJ (1987) Models, mechanisms, and pathways of succession. *Bot Rev* 53:335–371
- Porter E, Forschner B, Blair R (2001) Woody vegetation and canopy fragmentation along a forest-to-urban gradient. *Urban Ecosyst* 5:131–151
- Schueler TR (1994) The importance of imperviousness. *Watershed Protect Tech* 1:100–111
- Shannon CE (1948) A mathematical theory of communication. *Bell Syst Tech J* 27:379–423
- Simpson EH (1949) Measurement of diversity. *Nature* 163:688
- Strahler AN (1952) Hypsometric (area-altitude) analysis of erosional topography. *Geol Soc Am Bull* 63:1117–1142
- Thomson JD, Weiblen G, Thomson BA, Alfaro S, Legendre P (1996) Untangling Multiple Factors in Spatial Distributions: Lilies, Gophers, and Rocks. *Ecology* 77:1698–1715
- Trammell TE, Carreiro MM (2011) Vegetation composition and structure of woody plant communities along urban interstate corridors in Louisville, KY, U.S.A. *Urban Ecosyst* 14:501–524
- U. S. Census Bureau (2010) <http://quickfacts.census.gov/qfd/states/21/21111.html>
- U. S. Department of Agriculture, Natural Resources Conservation Service (2009) Native, Invasive, and Other Plant Related Definitions. http://www.nrcs.usda.gov/wps/portal/nrcs/detail/ct/technical/ecoscience/invasive/?cid=nrcs142p2_011124.
- U. S. Department of Agriculture PLANTS Database (2012) National Plant Data Center, Baton Rouge, La 70874–4490 USA. <http://plants.usda.gov>.
- Walsh CJ, Fletcher TD, Ladson AR (2005a) Stream restoration in urban catchments through redesigning stormwater systems: looking to the catchment to save the stream. *J N Am Benthol Soc* 24:690–705
- Walsh CJ, Roy AH, Feminella JW, Cottingham PD, Groffman PM, Morgan RP II (2005b) The urban stream syndrome: current knowledge and the search for a cure. *J N Am Benthol Soc* 24:706–723
- Wenger S (1999) A review of the scientific literature on riparian buffer width, extent and vegetation. Office of Public Service and Outreach, Institute of Ecology, University of Georgia, Athens
- Wharton ME, Barbour RW (1973) *Trees and Shrubs of Kentucky*. University Press of Kentucky, Lexington
- White JM, Stromberg JC (2011) Resilience, Restoration, and Riparian Ecosystems: Case Study of a Dryland, Urban River. *Restor Ecol* 19:101–111
- White RJ (2011) Riparian corridor vegetation structure and soil function along urban, suburban, and rural streams in Louisville, KY, USA. Ph.D. Dissertation. University of Louisville, Louisville, KY. 284 pp.