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Riparian woody plant diversity and forest structure along an urban-rural gradient

MICHELE L. BURTON* burtoml@auburn.edu
LISA J. SAMUELSON samuelj@auburn.edu
SHUFEN PAN panshuf@auburn.edu
School of Forestry and Wildlife Sciences, Center for Forest Sustainability, 108 White Smith Hall, Auburn University, Auburn, AL 36849, USA

Abstract. Changes in riparian woody plant assemblages are anticipated in the southeastern United States due to increases in urbanization rates. Because riparian forests serve important roles in maintaining water quality and biodiversity, understanding how they respond to urbanization is crucial. The objective of this study was to examine forest structure and woody vegetation diversity indices of riparian communities in response to an urbanization gradient in West Georgia, USA. Measures of forest structure and diversity were compared to measures of urbanization and land cover. Although *Liquidambar styraciflua* and *Quercus nigra* were dominant species in the forest stand and regeneration layer for all riparian communities, the invasive, non-native shrub *Ligustrum sinense* was the most dominant species observed in the regeneration layer for urban, developing, and agriculture communities. The proportion of non-native species in the forest stand and regeneration layer decreased and Shannon diversity of the regeneration layer increased with increasing distance from the urban center. Shifts in diversity indicate that anthropogenic disturbance may subdue the ability of diverse communities to resist non-native plant invasions.

Keywords: urbanization, riparian forests, diversity, land use, invasive species

Introduction

Urbanization is occurring at unprecedented rates in the United States, with over 1.2 million hectares of urban development added annually (Cordell and Macie, 2002). The South ranks high in this respect, consisting of the most states with the greatest total acreage of land developed for urban uses between 1992–1997 (Cordell and Macie, 2002). Forecasts for land use indicate a growth in urban area from about 8.1 million hectares in 1992 to 22.3 million hectares in 2020 and 32.8 million hectares by 2040 (Wear, 2002). The magnitude of this trend is expected to increase as global population continues to climb. Consequently, as urbanization expands into forested areas, biodiversity as well as other important ecosystem functions may be impaired.

Human influences on forest ecosystems in the South have had dramatic impacts on forested ecosystems. Since European settlement, three major time periods have shaped the landscape of the southern United States: (1) the era of agricultural exploitation from the 17th century to the 19th century, (2) the era of timber exploitation during the 20th century

*Author to whom all correspondence should be addressed.

and (3) the era of forest recovery and renewal when in 1964, forestland cover peaked at 60% (Wear, 2002). Today, strong economic growth is shaping the southern landscape. In October 2002, The Southern Forest Resource Assessment identified two major land use trends occurring in the Southeast between 1945–1992: (1) urban and rural transportation tripled from 2.1 to 6.6% of land area, and (2) agricultural uses declined (Wear, 2002). Although the total coverage of forestland in much of the South has not declined due to shifting of agricultural land to forested landscapes, because of the trend towards urban land uses there is increasing concern for the integrity and sustainability of forest ecosystems at the rural-urban interface.

Historically, clearing forests for agriculture in the South was the most notable (Malanson, 1993) but often, transient land use change. For example, hardwood and pine forests again cover lands once cleared for cotton 50 years ago (Conner and Hartsell, 2002), although Hedman *et al.* (2000) reported that forests growing on abandoned agriculture fields in the southeastern Coastal Plain exhibited lower herbaceous species diversity than forests growing on cut-over forest sites. In contrast to agricultural development, urbanization may impose a more permanent type of land use change, due to the nature of impervious surfaces associated with urban development (Jennings and Jarnagin, 2002). Indirectly, urbanization can alter forest systems by modifying hydrologic, nutrient and disturbance cycles, introducing invasive species, and changing microclimate conditions (Zipperer, 2002). In the modern South, of which forests cover 56% relative to 28% in agriculture (cropland + pasture) in 1992 (Wear, 2002), urbanization has now surpassed agriculture as the primary source of lost forestlands (Conner and Hartsell, 2002).

Because of population increases in the United States and around the world, impacts of urbanization on the environment are more pressing today than in the past. Studies have documented significant differences in plant (Porter *et al.*, 2001; Kowarik, 1995), animal (Blair, 1996) and insect (Blair and Launer, 1997) assemblages, soils (Dupouey *et al.*, 2002; Airola and Buchholz, 1984) and water quality (Wang *et al.*, 2001; Wear *et al.*, 1998) along urban gradients. Further investigation of urbanization has revealed that reduction of forest cover and patch size can be correlated with shifts in animal and insect densities and richness (McKinney, 2002) as well as adverse impacts on water quality (Gergel *et al.*, 2002; Tabacchi *et al.*, 1998, 2000).

It is well known that riparian forests serve a unique and vital role in maintaining the quality of our water resources. These forests serve as filters, transformers, sources and sinks for nutrients, sediment and pollutants associated with agriculture and urban runoff (Malanson, 1993; Welsch, 1991) and provide flood control during high rain events (Welsch *et al.*, 2000). Humans, as well as aquatic biota and other animals, depend on these services for well-being and habitat (Naiman *et al.*, 1995). In addition, riparian forests provide aesthetic and recreational values. Studies have also shown that riparian forests serve as corridors for maintaining regional biodiversity (Naiman *et al.*, 1993), providing important links in the landscape for birds and small mammals (Cockle and Richardson, 2003; Rottenborn, 1999; Blair, 1996). Management of riparian buffer zones along streams adjacent to agriculture and managed forests has been implemented in some cases (Platts, 1987). However, where rapid urbanization is occurring at the rural-urban interface, the maintenance of riparian forest buffers is often ignored.

This study is a component of a multidisciplinary research effort designed to examine the multifaceted impacts of urbanization on ecology (biodiversity and water quality), economy, and society of West Georgia by developing an integrated model that aims to forecast environmental changes associated with land use change and urbanization (Lockaby *et al.*, 2005 this issue). Specifically, this study aims to detect trends in riparian forest diversity and structure associated with urbanization by examining the relationships between woody plant diversity, natural regeneration, and forest cover and urbanization indices in riparian communities located along an urban gradient in West Georgia. Urbanization indices include distance to urban center, amount of impervious surface, and land cover parameters such as percent cover of mixed deciduous forest, evergreen forest and agriculture. We will examine the relationships between landscape pattern and riparian forest tree distribution and structure and describe community functional shifts that occur along the gradient. All measures of forest diversity and cover will be tested against measures of urbanization. Here, we present data from six riparian communities along the gradient and discuss important emerging trends.

Methods

Study area and sites

The study was conducted within two counties, Muscogee and Harris, extending northeast of Columbus, GA, USA. The growth pattern of Columbus, Georgia provides a strong gradient of urbanization for ecological study. Population statistics for the bi-county area depict a quickly urbanizing landscape (Table 1). Columbus has a humid, continental climate with mean annual temperature of 18.3°C, and precipitation and snowfall of 129.5 cm and 2.0 cm, respectively.

This study used the watershed as the fundamental unit in which to evaluate the impacts of urbanization on riparian forest diversity and structure. In 2001, watersheds within the Middle Chattahoochee River Basin in West Georgia were selected for a water quality and stream biota study (Schoonover and Lockaby, 2005; Helms and Feminella, 2005 this issue). Low order streams (2nd and 3rd order) were selected for sampling to avoid the complexity found in higher order streams. Woody vegetation sampling sites were coupled with water quality sampling locations to enhance data interpretation and integration. Land ownership consisted of both private and public properties.

Table 1. Population statistics for bi-county study area in western Georgia (US Census Bureau, 2000)

	Muscogee	Harris
No. People	186,291	23,695
% Increase 1990–2000	+4	+33
No. People/km^2	333	20

Table 2. Landscape metrics based on aerial photos (grain size 1-m) for the six riparian communities

Landscape metric	Cooper Creek	Standing Boy Creek	Clines Branch	Ossahatchie Creek	Blanton Creek	Sand Creek
Stream order	2	3	2	3	2	2
Watershed area (ha)	2469	2659	897	1178	330	896
Distance from urban center (km)	8.82	19.79	30.58	31.54	34.28	41.84
Impervious surfaces (%)	28.11	3.34	1.53	3.79	1.36	1.24
Evergreen (%)	25.75	12.39	53.64	24.38	53.29	49.47
Deciduous (%)	12.33	41.07	40.65	4.52	28.15	26.15
Agriculture (% grass)	29.76	39.1	3.80	55.14	15.05	21.35
Land use category	Urban (U)	Developing (D)	Mixed (M)	Agriculture (A)	Pine (P)	Pine (P)
County	Muscogee	Harris	Harris	Harris	Harris	Harris

Spatial analysis and GIS

Aerial photographs (grain size 1-m) taken of the study area in March 2003 were used to quantify land cover (Lockaby *et al.*, 2005 this issue). Specific independent variables obtained from GIS analyses that were used in riparian vegetation analyses include: distance to urban center, percent impervious surfaces, and proportion of watershed in deciduous forest, evergreen forest, and agriculture (pasture). Each watershed exhibits a dominant land cover type including: mixed forests (M), evergreen forests-pine plantations (P), rural-agriculture (A), developing-suburban (D), and urbanized (U) that reflects a gradient of increasing urban influences (Table 2). Refer to Lockaby *et al*. (2005 this issue) for greater detail of the study area and GIS methods.

Sampling procedures

At each riparian community, a total of 24, 0.01-ha plots were sampled on six transects. The 35-m long transects were 100-m apart and ran perpendicular to and across the stream. On each transect, four, 100-m^2 plots were placed 15-m apart (two on each side of the stream). The first plot was placed next to the stream (depending on incision and vegetation of streambank). Within each plot, the forest stand was characterized by all woody plants $\geq$2.5-cm DBH (diameter at 1.6-m height). The woody plant regeneration layer was sampled within five 1-m^2 randomly chosen subplots in each 100-m^2 plot. All woody stems $<$2.5-cm DBH within the sub-sample were identified and counted. As a measure of forest cover, leaf area index (LAI) was sampled one meter from the ground using a plant canopy analyzer (LiCor LAI 2000, Lincoln NE) along each of the six transects during peak growing season (late June through early August). Twenty LAI measurements were taken along each transect and averaged by transect and then by site. Nomenclature followed Godfrey (1988).

Statistical analysis

Woody vegetation diversity indices including importance values, total number of species (S), Shannon diversity index (H') and evenness index (J') (Pielou, 1977) were calculated for the forest stand and regeneration layer at each site.

1. Shannon Index (1949) $H' = -\sum_{i=1}^{S^*} (p_i \ln p_i)$
2. Evenness $J' = \frac{H'}{H_{\max}}$

Where H' is the average uncertainty per species in an infinite community made up of S^* species and p_i is the proportion of the total sample belonging to the ith category (Shannon and Weaver, 1949). $H_{\max}$ was calculated as the natural log of the total number of species sampled in each community (Ludwig and Reynolds, 1988). All species were classified as either native or non-native and the proportion of woody non-native species was determined as a percent for both the forest stand and regeneration layer. Non-native species were species that were not known to have occurred within the region prior to European settlement according to Godfrey (1988).

As measures of forest structure, density (# stems ha^{-1}), basal area, and average DBH were calculated for each site. Relative density (species density/total density) $*$ 100, relative frequency (species frequency/total frequency) $*$ 100, and relative basal area (species basal area/total basal area) $*$ 100 were calculated for the forest stand and species importance values (IV_{300}) were calculated as relative density + relative frequency + relative basal area. Importance values (IV_{200}) were also calculated for the regeneration layer as relative frequency + relative density. Linear regression analyses were used to detect significant ($\alpha = 0.05$) relationships in forest structure and diversity in response to landscape metrics (Table 2) and non-native plant distribution. Tests of heterogeneity of variance assumptions indicated no need for transformed data.

Results

Across all communities sampled, a total of 61 species (five non-native) were observed in the forest stand and 52 species (five non-native) were observed in the regeneration layer (Appendix 1). Thirty-eight species were common to both the forest stand and regeneration layer. The non-native shrub, *Ligustrum sinense* Lour. was the most dominant woody plant in the forest stand and regeneration layer for the riparian communities located closest to the urban center (Cooper Creek and Standing Boy Creek) with importance values of 64.2 and 71.6 for the forest stand, and 83.6 and 94.8 for the regeneration layer, respectively (Table 3). *Ligustrum sinense* was observed in the regeneration layer of five of the six riparian communities and was dominant in four of those communities (Table 3). In the urban riparian community (Cooper Creek), the non-native tree *Albizia julibrissin* Durazz. was a dominant species in the regeneration layer. *Liquidambar styraciflua* L. was a dominant species in all forest stands followed by *Quercus nigra* L. and *Carpinus caroliniana* Walt. *Liquidambar styraciflua* and *Quercus nigra* were also dominant species in the regeneration layer in most of the communities.

Site characteristics for the six riparian communities are described in Table 4. The percentage of non-native species in the forest stand and regeneration layer showed a strong

Table 3. Importance values (IV) for dominant species in the forest stand and regeneration layer in each riparian community

Riparian community	Forest stand species	IV_{300}	Regeneration layer species	IV_{200}
Cooper Creek	*Ligustrum sinense* Lour.*	64.2	*Ligustrum sinense* Lour.*	83.6
Urban	*Liquidambar styraciflua* L.	47.0	*Quercus nigra* L.	20.0
	Carpinus caroliniana Walt.	28.2	*Celtis laevigata* Nutt.	11.1
	Acer negundo L.	22.3	*Albizia julibrissin* Durazz.*	9.8
	Quercus nigra L.	21.6	*Acer negundo* L.	8.6
	Betula nigra L.	14.0	*Acer barbatum* Michx.	7.7
	Ulmus alata Michx.	11.8	*Prunus serotina* Ehrh.	7.7
Standing Boy Creek	*Ligustrum sinense* Lour.*	70.2	*Ligustrum sinense* Lour.*	94.8
Developing	*Carpinus caroliniana* Walt.	32.0	*Quercus nigra* L.	14.4
	Fraxinus pennsylvanica Marsh.	24.6	*Acer negundo* L.	12.7
	Liquidambar styraciflua L.	18.2	*Liquidambar styraciflua* L.	11.4
	Quercus nigra L.	17.1	*Carpinus caroliniana* Walt.	11.2
	Alnus serrulata (Ait.) Willd.	15.3	*Fraxinus pennsylvanica* Marsh.	11.1
	Acer negundo L.	11.3	*Acer barbatum* Michx.	11.0
Clines Branch	*Liquidambar styraciflua* L.	43.2	*Acer rubrum* L.	65.4
Mixed	*Acer rubrum* L.	27.7	*Quercus nigra* L.	21.6
	Kalmia latifolia L.	22.1	*Ostrya virginiana* (Mill) K. Koch	19.5
	Halesia tetraptera Ellis.	18.8	*Halesia tetraptera* Ellis.	12.0
	Quercus alba L.	17.8	*Carpinus caroliniana* Walt.	9.5
	Pinus taeda L.	17.7	*Quercus alba* L.	9.4
	Oxydendron arboreum (L.) DC.	16.3	*Vaccinium* spp.	7.1
Ossahatchie Creek	*Carpinus caroliniana* Walt.	49.2	*Ligustrum sinense* Lour.*	57.6
Agriculture	*Liquidambar styraciflua* L.	41.8	*Acer negundo* L.	37.9
	Acer negundo L.	31.7	*Quercus nigra* L.	26.1
	Quercus nigra L.	25.2	*Carpinus caroliniana* Walt.	12.7
	Ostrya virginiana (Mill.) K. Koch	21.8	*Acer barbatum* Michx.	12.0
	Pinus taeda L.	19.2	*Ostrya virginiana* (Mill.) K. Koch.	11.9
	Ligustrum sinense Lour.*	16.3	*Liquidambar styraciflua* L.	8.0
Blanton Creek	*Liriodendron tulipifera* L.	60.0	*Quercus nigra* L.	40.0
Pine	*Liquidambar styraciflua* L.	58.4	*Cornus florida* L.	29.2
	Cornus florida L.	41.2	*Ostrya virginiana* (Mill) K. Koch	18.9
	Quercus nigra L.	24.0	*Prunus serotina* Ehrh.	16.3
	Ostrya virginiana (Mill.) K. Koch.	22.3	*Carpinus caroliniana* Walt.	16.0
	Halesia tetraptera Ellis.	12.6	*Liriodendron tulipifera* L.	9.7
	Morus rubra L.	11.8	*Liquidambar styraciflua* L.	6.5
Sand Creek	*Liquidambar styraciflua* L.	78.7	*Acer rubrum* L.	34.8
Pine	*Acer rubrum* L.	55.5	*Liquidambar styraciflua* L.	29.0
	Betula nigra L.	33.1	*Ligustrum sinense* Lour.*	24.3
	Quercus nigra L.	18.9	*Fraxinus pennsylvanica* Marsh.	18.9
	Liriodendron tulipifera L.	18.1	*Cornus florida* L.	14.5
	Pinus taeda L.	16.3	*Quercus nigra* L.	11.1
	Cornus florida L.	10.4	*Halesia tetraptera* Ellis.	10.6

Forest stand importance values (IV_{300}) = (relative density + relative basal area + relative frequency)
Regeneration layer importance values (IV_{200}) = (relative density + relative frequency)
Non-native species indicated by (*).

Table 4. Site characteristics for the six riparian communities

Site characteristic	Cooper Creek	Standing Boy Creek	Clines Branch	Ossahatchie Creek	Blanton Creek	Sand Creek
Density: stand (trees ha^{-1})	950	1388	1958	1058	1342	1233
Density: regeneration (stems ha^{-1})	1321	4888	3063	2125	1933	529
Basal area (m^2 ha^{-1})	20.0	25.4	28.2	21.2	33.9	31.3
Average DBH (cm)	12.7	12.1	10.9	12.6	13.9	8.9
No. species: stand (S_s)	24	31	37	23	32	24
No. species: regeneration (S_r)	23	23	27	23	32	20
Non-native: stand (%NN_s)	33.5	35.7	0	5.9	0.3	9.4
Non-native: regeneration (%NN_r)	71.8	77.2	0	39.4	2.2	9.4
Shannon diversity: stand (H_s)	2.26	2.45	2.92	2.48	2.5	2.19
Shannon diversity: regeneration (H_r)	1.58	1.09	1.93	1.99	2.59	2.72
Evenness: stand (J_s)	0.71	0.71	0.81	0.79	0.72	0.69
Evenness: regeneration (J_r)	0.50	0.35	0.58	0.64	0.75	0.91
Leaf area index (LAI, m^2 m^{-2})	4.98	5.45	4.86	4.04	5.09	4.70

correlation with distance to the urban center (figure 1). The proportion of non-native species decreased linearly as distance from the urban center increased. A strong, positive correlation was also found between the proportion of non-native species in the regeneration layer and the proportion of non-native species in the forest stand (figure 2). Diversity in the regeneration layer (H_r') decreased linearly as the proportion of non-natives in the regeneration layer increased and distance from the urban center decreased (figure 3). Watersheds exhibiting lowest forest cover (evergreen plus mixed forest) were the urban (Cooper Creek), developing (Standing Boy Creek), and agriculture (Ossahatchie Creek) communities. These stands also exhibited the lowest basal area (figure 4). All site characteristics were tested against land cover and urbanization parameters, however only the proportion of non-natives, H_r, and basal area demonstrated a significant relationship with a land cover or urbanization parameter.

Discussion

Because riparian forests provide important functions in the maintenance of biodiversity, water quality, and carbon storage, understanding how these forests respond to urbanization is crucial. In the United States, 6.5 million hectares of rural land were converted to developed urban land uses between 1992–1997 (Cordell and Macie, 2002). In the Southeast, bottomland and riparian forests are now considered threatened ecosystems with 70–84% loss (Trani, 2002) and rank high among forest types affected by fragmentation (Brinson and Malvarez, 2002). Natural riparian forests are some of the most diverse, complex, and dynamic terrestrial habitats on earth (Naiman *et al.*, 1993) and serve as important regulators

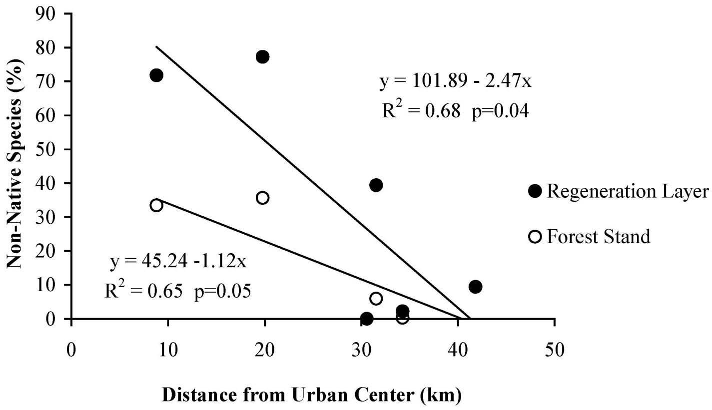

Figure 1. Linear regressions for the relationship between non-native species and distance from urban center for the stand and regeneration layer.

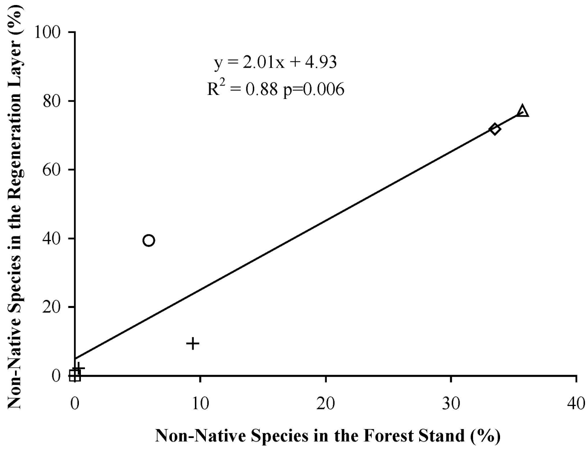

Figure 2. Linear regression for the relationship between percent non-native species in the stand and percent non-native species in the regeneration layer (△ developing, ◇ urban, ◯ agriculture, □ mixed, + pine).

of aquatic-terrestrial linkages (Naiman and Decamps, 1990). There is concern that riparian forests are particularly sensitive to environmental change (Malanson, 1993) and may be the first element in the landscape to exhibit impacts from urbanization. Research has documented strong physical and biological trends along urban gradients (McKinney, 2002), but important questions concerning ecosystem integrity remain. The level at which urbanization and land use change impact riparian vegetation assemblages and important ecosystem services is poorly understood.

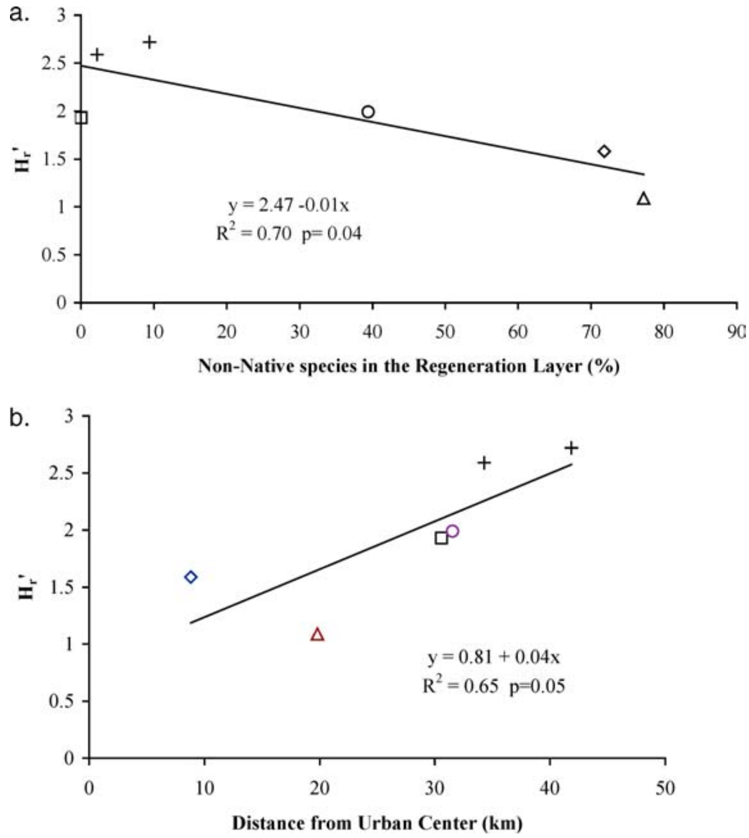

Figure 3. Linear regressions for the relationship between Shannon diversity of the regeneration layer (Hr') and (a) percent of non-native species observed in the regeneration layer and (b) distance from the urban center (Δ developing, ◇ urban, ◯ agriculture, □ mixed, + pine).

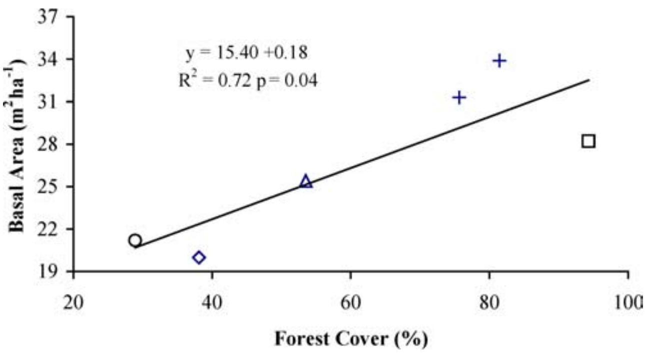

Figure 4. Linear regression for the relationship between basal area (m^2 ha^{-1}) and forest cover (% evergreen + % deciduous forest). (Δ developing, ◇ urban, ◯ agriculture, □ mixed, + pine).

This study indicates that diversity, presence of non-native species and basal area are related to percent forest cover within the watershed and distance from urbanization. Moreover, the presence of non-native woody plants was related to a reduction in riparian woody plant diversity. Although cause and effect cannot be tested by this work, these results highlight the importance of past or present land use in understanding changes in biodiversity. Environmental changes due to anthropogenic influences, such as hydrologic shifts, changing microclimates and fragmentation, have been shown to influence riparian plant community composition (Nilsson and Svedmark, 2002). Changes in water table levels and soil moisture may promote the invasion of non-native species by providing a competitive advantage to invasive species (Tickner *et al.*, 2001). The hydrological role of invasive species, such as *Ligustrum sinense*, is not well understood, and the potential impacts on ecosystem structure and function by non-natives remains uncertain (Tickner *et al.*, 2001). Our study is consistent with the findings of Merriam and Feil (2002) who found that the presence of *Ligustrum sinense* in mixed hardwood forest in North Carolina significantly reduced native plant diversity and almost completely suppressed the growth of native tree regeneration.

In our study, riparian communities invaded by *Ligustrum sinese* exhibited decreased diversity. At small spatial scales, there is evidence that diverse communities exhibit higher productivity, stability, and resistance to biological invasions (Kennedy *et al.*, 2002; Tilman, 1999), because each species may occupy a unique niche and respond differently to environmental changes (Ives *et al*., 2000). We also found a significant decrease in basal area as forest cover decreased along the urban gradient, which may reflect a decrease in forest productivity or a history of timber harvesting (Sagar *et al.*, 2003; Ramrez-Marcial *et al*., 2001). Decreasing basal area and diversity in the regeneration layer along the urban gradient may be related to the intensity of anthropogenic disturbance, such as the reduction of forest cover and increased sources of non-native, invasive species. Consequently, changes in diversity and structure may subdue the ability of communities to maintain ecosystem stability and complexity (Loreau *et al.*, 2001; Yachi and Loreau, 1999).

Grime (2002) suggests that continuously and severely disturbed systems may experience shifting life history traits that can result in declines in productivity and carbon storage but nonetheless confer properties such as high resilience. However, important functional attributes of riparian tree species may be lost. Groffman *et al.* (2003) described how changes in water flow due to urbanization around Baltimore, Maryland have created a "hydrologic drought" in riparian areas resulting in compositional shifts from lowland to upland species. Hydrologic changes may be most obvious in riparian tree regeneration (Dixon, 2003). The relationship between hydrology and riparian plant composition has been identified as an important research gap (Nilson and Svedmark, 2002; Tabacchi *et al.*, 2000) that requires interdisciplinary research. As part of a larger, integrative study at the rural-urban interface, we will integrate data with other facets of the overall West Georgia project to examine effects of water quality, particularly hydrology, on riparian forest communities along the urban gradient. We expect this aquatic-terrestrial linkage to prove useful for understanding the impacts of urbanization on riparian ecology.

Appendix 1

Species sampled across all sites

Forest stand	Regeneration layer
Acer barbatum Michx.	*Acer barbatum* Michx.
Acer negundo L.	*Acer negundo* L.
Acer rubrum L.	*Acer rubrum* L.
Albizia julibrissin Durazz.∗	*Acer saccharinum* L.
Alnus serrulata (Ait.) Willd.	*Albizia julibrissin* Durazz.*
Aesculus pavia L.	*Alnus serrulata* Wild.
Betula nigra L.	*Aesculus pavia* L.
Carpinus caroliniana Walt.	*Asimina triloba* (L.) Dunal.
Carya cordiformis Wang.	*Betula nigra* L.
Carya glabra (Mill.) Sweet	*Calicarpa americana* L.
Carya ovalis (Wang.) Sarg.	*Calycanthus floridus* L.
Carya ovata (Mill.) K. Koch	*Carpinus caroliniana* L.
Carya tomentosa (Poir.) Nutt.	*Celtis laevigata* Nutt.
Cercis canadensis L.	*Celtis tenuifolia* Nutt.
Cornus florida L.	*Cercis canadensis* L.
Cornus stricta Lam.	*Cornus florida* L.
Crataegus spp.	*Crataegus* spp.
Crataegus spathulata Michx.	*Diospyros virginiana* L.
Diospyros virginiana L.	*Elaeagnus pungens* Thumb.*
Fagus grandifolia Ehrh.	*Fagus grandifolia* Ehrh.
Fraxinus americana L.	*Fraxinus pennsylvanica* Marsh.
Fraxinus pennsylvanica Marsh.	*Halesia tetraptera* Ellis.
Halesia tetraptera Ellis.	*Hamamelis virginiana* L.
Hamamelis virginiana L.	*Ilex opaca* Ait.
Hydrangea quercifolia Barr.	*Juniperus virginiana* L.
Ilex decidua Walt.	*Kalmia latifolia* L.
Ilex opaca Ait.	*Ligustrum japonica* Thumb.*
Juglans nigra L.	*Ligustrum sinense* Lour.*
Juniperus virginiana L.	*Lindera benzoin* (L.) Blume.
Kalmia latifolia L.	*Liquidambar styraciflua* L.
Ligustrum japonica Thumb.*	*Liriodendron tulipifera* L.
Ligustrum sinense Lour.*	*Morus rubra* L.
Liquidambar styraciflua L.	*Myrica cerifera* L.
Liriodendron tulipifera L.	*Nyssa sylvatica* L.
Magnolia virginiana L.	*Ostrya virginiana* (Mill.) K. Koch.

(*Continued on next page*.)

(*Continued*).

Forest Stand	Regeneration Layer
Melia azedarach L.*	*Pinus taeda* L.
Morus rubra L.	*Prunus caroliniana* (Mill.) Ait.
Myrica cerifera L.	*Prunus serotina* Ehrh.
Nyssa sylvatica Marsh.	*Quercus alba* L.
Ostrya virginiana (Mill.) K. Koch	*Quercus falcata* Michx.
Oxydendron arboreum (L.) DC.	*Quercus lyrata* Walt.
Pinus taeda L.	*Quercus michauxii* Nutt.
Platanus occidentalis L.	*Quercus nigra* L.
Prunus serotina Ehrh.	*Quercus rubra* L.
Pseudocydonia sinensis(Dum.-Cours.)Schneid*	*Quercus* spp.
Quercus alba L.	*Rhododendron* spp.
Quercus falcata Michx.	*Sambucus canadensis* L.
Quercus lyrata Walt.	*Sapium sebiferum* (L.) Roxb.*
Quercus michauxii Nutt.	*Sassafrass albidium* (Nutt.) Nees.
Quercus nigra L.	*Tilia americana* L.
Quercus phellos L.	*Ulmus alata* Michx.
Quercus velutina Lam.	*Ulmus americana* L.
Rhododendron canescens (Michx.) Sweet.	*Ulmus* spp.
Salix nigra L.	*Vaccinium* spp.
Sambucus canadensis L.	
Sassafras albidium (Nutt.) Nees.	
Tilia americana L.	
Ulmus alata Michx.	
Ulmus americana L.	
Ulmus rubra Muhl.	
Vaccinium arboreum Marsh.	
Vaccinium elliotii Champ.	

Non-native species indicated by (*).
Note: Plants were identified only to the genus group if species could not be determined.

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