RIPARIAN WOODY PLANT DIVERSITY, COMPOSITION, AND STRUCTURE ACROSS AN URBAN-RURAL LAND USE GRADIENT IN THE PIEDMONT OF GEORGIA, US

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RIPARIAN WOODY PLANT DIVERSITY, COMPOSITION, AND STRUCTURE ACROSS AN URBAN-RURAL LAND USE GRADIENT IN THE PIEDMONT OF GEORGIA, US

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RIPARIAN WOODY PLANT DIVERSITY, COMPOSITION, AND STRUCTURE

ACROSS AN URBAN-RURAL LAND USE GRADIENT IN

THE PIEDMONT OF GEORGIA, US

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DISSERTATION ABSTRACT

RIPARIAN WOODY PLANT DIVERSITY, COMPOSITION, AND STRUCTURE ACROSS AN URBAN-RURAL LAND USE GRADIENT IN THE PIEDMONT OF GEORGIA, US

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Riparian forests are increasingly threatened by urban expansion and land use change worldwide. Understanding the impacts of urbanization on riparian forests is critical because riparian areas provide a variety of important ecological services and are biological hotspots for species diversity. The overall goal of this work was to describe the relationships among landscape characteristics and woody plant diversity, structure, species composition, and plant functional traits of small order riparian corridors along an urban-rural land use gradient in the Georgia Piedmont, US. The objectives were to: (1) examine the influence of land use and urbanization indices on riparian woody plant species diversity and composition, (2) quantify changes in riparian forest structure across an urban-rural gradient, (3) elucidate changes in woody plant functional traits along an urban-rural gradient, and (4) compare trends in diversity, composition, structure, and trait charateristics in the mature forest stand and forest tree regeneration. This work demonstrates that changes in species diversity, composition, and structure are occurring in response to land use and the surrounding landscape matrix. Non-native invasive species appear to be driving many of the changes, specifically the shrub, *Ligustrum sinense*. Species richness was positively correlated to rural landscape characteristics and negatively related to urban characteristics. Shannon diversity was negatively associated with dominance of non-native species, especially for the forest regeneration layer. Urban sites were characterized by high richness of non-native species and several pioneer species. Developing sites were dominated by the non-native shrub, *Ligustrum sinense*, and several native overstory trees, mainly *Acer negundo*. While agricultural and managed forest sites were composed of ubiquitous species, the unmanaged forest type exhibited a structurally distinct midstory. Midstory tree biomass was positively related to forest cover and negatively related to impervious surface cover and shrub biomass was positively related to patch density. Urban and agriculture sites showed signs of recruitment failure. Species functional traits also varied across the gradient. Specifically, differences in leaf type, plant form, flood and shade tolerance, seed dispersal, pollination, growth rate, rooting characteristics, and life span were found. Flood tolerance was strongly reduced in the regeneration layer in urban riparian areas suggesting a potential shift in hydrologic function. Results from this study highlight the impact of urbanization on riparian forest plant biodiversity and structure.

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Style manual or journals used:

- Urban Ecosystems
- Plant Ecology
- Journal of Vegetation Science

Computer software used:

- SAS® version 9.1
- Sigma Plot® version 8.0
- ArcGIS® version 9.0
- FRAGSTATS® version 3.3
- PC-ORD® version 4.0
- Endnote® version 8.0
- Microsoft® Digital Image Pro 9.0
- Microsoft Office 2003
  - Word®
  - Excel®

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CHAPTER I

RIPARIAN WOODY PLANT DIVERSITY, COMPOSITION, AND STRUCTURE ACROSS AN URBAN-RURAL LAND USE GRADIENT IN THE PIEDMONT OF GEORGIA, US: AN INTRODUCTION

Natural riparian forests, one of the most diverse, complex, and dynamic terrestrial habitats on Earth (Naiman et al. 1993), serve as important regulators of aquatic-terrestrial linkages (Naiman and Decamps 1990). Riparian forests are unique landscape features in the southeastern United States because they are both ecotones between terrestrial and aquatic zones and corridors across regions (Malanson 1993). Therefore, riparian ecosystems have been the focus of research because they are of great ecological importance. Minor riparian forests are directly influenced by upland land use and therefore are important sources for water, sediments, nutrients, and organic matter for major floodplain ecosystems (Gomi et al. 2002). Brinson et al. (1981) estimated that 70% of natural riparian plant communities in the United States have been destroyed. In the Southeast, bottomland and riparian forests are now considered threatened ecosystems with 70-84% lost (Trani 2002). As interfaces between terrestrial and aquatic ecosystems, riparian forests are particularly sensitive to environmental change and may be the first element in the landscape to exhibit impacts from urbanization and land use change (Malanson 1993). Because small streams and their riparian zones provide important functions in the maintenance of biodiversity, water quality, and downstream ecosystems, understanding how they respond to urbanization and land use is crucial for proper management of local and regional natural resources.

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 has been identified as a hot spot for urbanization where forecasts indicate growth in urban area from about 8.1 million hectares in 1992 to 22.3 million hectares in 2020 and 32.8 million by 2040 (Wear 2002). Specifically, the Piedmont region of the Southeast, which extends southwest from Virginia to east-central Alabama, had the greatest rate of forestland conversion to urban uses between 1992-1997 (Figure 1) (USDA-NRCS 2006). Furthermore, Georgia ranked second to Texas for the highest average annual rate of land development in the United States between 1992-1997 (USDA-NRCS 2006). Late 19th and early 20th century agricultural development was the most common reason for clearing forests and caused lasting environmental damage due to irreversible soil loss in the southern Piedmont (Trimble 1974). Today, urbanization has surpassed agriculture as the primary cause of forestland loss in the South (Conner and Hartsell 2002) and may leave another permanent environmental legacy due to the spread of impervious surfaces associated with urban development (Arnold Jr. and Gibbons 1996). According to the Southern Resource Assessment (2002) conducted by the U.S. Forest Service, impacts of urban areas on forests extend far beyond city cores. Brown et al. (2005) suggest that exurban development, low-density housing (6-25 homes km^{-2}) around city fringes, is the fastest growing form of land use in the United States because the desire for rural housing locations combined with the opportunities and amenities of cities has greatly increased development along city fringes. Areas of new subdivisions (suburban) along the city fringe, where a mixing of housing and forestland occur (exurban), have been termed the Wildland-Urban Interface (WUI) (Radeloff et al. 2005).

The environmental impacts of development along the WUI are not well known but evidence suggests that urbanization influences forest structure, function, biodiversity, and composition, as well as the benefits derived from them (Macie and Hermansen 2002, Zipperer 2002). Habitat destruction and degradation resulting from human population growth are degrading water quality, increasing biodiversity loss, and changing terrestrial carbon storage (Primack 2002, Chen et al. 2006). Research examining the ecological impacts of urbanization in the United States has demonstrated significant biological and physical impacts along urban gradients, such as differences in soil characteristics along the palisades escarpment in New Jersey (Airola and Buchholz 1984), changes in bird and butterfly diversity around Palo Alto and Santa Clara, California (Blair 1996, Blair and Launer 1997, Rottenborn 1999), gradients in landscape pattern around Phoenix, Arizona (Luck and Wu 2002), negative effects on water quality in Baltimore, Maryland (Groffman et al. 2003), and shifts in nitrogen cycling around New York, NewYork (Zhu and Carreiro 2004). Porter et al. (2001) found significant differences in woody plant species diversity and structural attributes of urban versus rural vegetation around Oxford, Ohio. Two studies have specifically examined riparian vegetation along an urban-rural gradient. Patterns in species composition, especially non-native species, and species diversity were related to landscape fragmentation and land use along the Assiniboine River in Manitoba, Canada (Moffatt et al. 2004). The Long Term Ecological Research (LTER) ecosystem study on urbanization around Baltimore, Maryland reported shifts in riparian plant composition from lowland to upland species in more urbanized sites, where fluctuating water tables may create a “hydrologic drought” (Groffman et al. 2003).

Shifts in plant functional traits have also been described in response to disturbance and land use change and may offer a more general understanding of the influences and consequences of disturbance associated with land use on riparian vegetation (Rusch et al. 2003). Williams et al. (2005) reported that as disturbance from urbanization in Victoria, Australia increased, some plant functional traits of grassland species became less common while others expanded. Mayfield et al. (2005) suggested that deforestation in Costa Rica may change functional diversity and species assembly rules because species functional traits such as dispersal mechanism, fruit type, pollination vector, and growth form differed between forested and deforested habitats. Other influences on plant attributes in response to disturbance have been documented such as, leaf structure and flowering (Louault et al. 2005), life span and plant form (Diaz et al. 1999), and seed characteristics (Peco et al. 2005). Identifying shifts in dominant plant traits allows comparison of taxonomically distinct floras and exploration of consequences for ecosystem processes and functioning (Diaz and Cabido 2001) and has been suggested as an important step towards understanding ecosystem properties (Westoby and Wright 2006).

This study fills an important research gap in the effort to understand the ecological impacts of urbanization and land use by focusing on the biological and functional uniqueness of riparian forests along small order streams around a moderate sized city experiencing rapid growth in the southern Piedmont region. Columbus, Georgia is rapidly expanding, primarily towards the northeast because it is restricted from growth to the west by the Chattahoochee River and to the southeast by a military installation, Fort Benning. Urbanizing landscapes have facilitated the application of the gradient paradigm to the study of urban influences on ecosystems (McDonnell and Pickett 1990). The growth pattern of Columbus was used as an urban-to-rural land use gradient for ecological study. Three counties were selected in a south-to-north alignment representing an urban-to-rural gradient, including northern Muscogee County (Columbus), Harris County, and southern Troup County. Harris County has experienced high rates of suburban and exurban development evident by accelerated population growth, a 33% increase between the years 1990-2000, which is well above the national average of 13% (US Census Bureau, 2006). This research is part of a collaborative research effort and preliminary studies in the study area indicate significant changes in bird and vegetation assemblages, water quality, and stream biota (Lockaby et al. 2005).

As human population growth continues to climb, the pressures on our natural resources will inevitably increase. Elucidating the effects of urbanization and land use on riparian forests, particularly along headwater streams and the WUI, will contribute to understanding the consequences of urbanization on ecosystem biodiversity and functioning. The goal of this project was to provide information on the relationships between urbanization and land use and the condition and alteration of riparian forests along minor streams (1st- 3rd order streams) within sub-watersheds (< 2600 ha) of the

Chattahoochee River Basin in the Georgia Piedmont. Specific objectives were to: (1) examine the influence of land use and urbanization on riparian woody plant species diversity and composition, (2) quantify changes in riparian forest structure across an urban-rural gradient, (3) elucidate changes in woody plant functional traits along an urban-rural gradient, and (4) identify shifts in diversity, composition, structure, and trait characteristics in mature forest stands and regeneration layers.

In the first phase of the study, a subset of riparian sites (each site of a different predominant land use) representing the urban-to-rural land use gradient was sampled to identify trends that may be important indicators of riparian forest change due to land use intensity. Results from phase one are described in Chapter 2 and provide some evidence that riparian forests surrounded by urban areas exhibited decreases in species diversity, increases in non-native species, and shifts in forest structure. Chapter 2 highlights the need for more detailed studies addressing diversity, composition, and structural changes as well as addressing shifts in plant functional traits related to land use and hydrologic conditions.

Urbanization effects on forest composition and structure, especially in the forest regeneration layer may have significant consequences for forest sustainability. Chapter 3 takes a more thorough examination of the influence of land use and landscape pattern on diversity trends and species composition responses to various urbanization parameters by increasing the sampled communities from 6 to 17 and exploring additional relationships between landscape parameters and biodiversity and structural indices. Ramifications of the role urbanization and land use have on species composition and structure of forest regeneration are specifically examined.

While shifts in species composition may be obvious in some landscapes, shifts in the functional guilds within plant communities may be more obscure. Identifying correlations between land use and shifts in plant functional traits may prove useful when comparing different landscapes consisting of different plant assemblages. In Chapter 4, trends in riparian plant traits are identified across an urban-rural land use gradient and potential consequences for ecosystem functioning are explored. A link is made between changes in dominant plant traits and hydrology and urbanization.

Finally, Chapter 5 provides an overall synthesis of the research and results contained in each chapter. Continued development and expansion of hundreds of moderately sized cities, like Columbus, in the United States is inevitable. Conclusions drawn from this research project can contribute to the development of strategies that protect biodiversity and natural resources as urbanization proceeds.

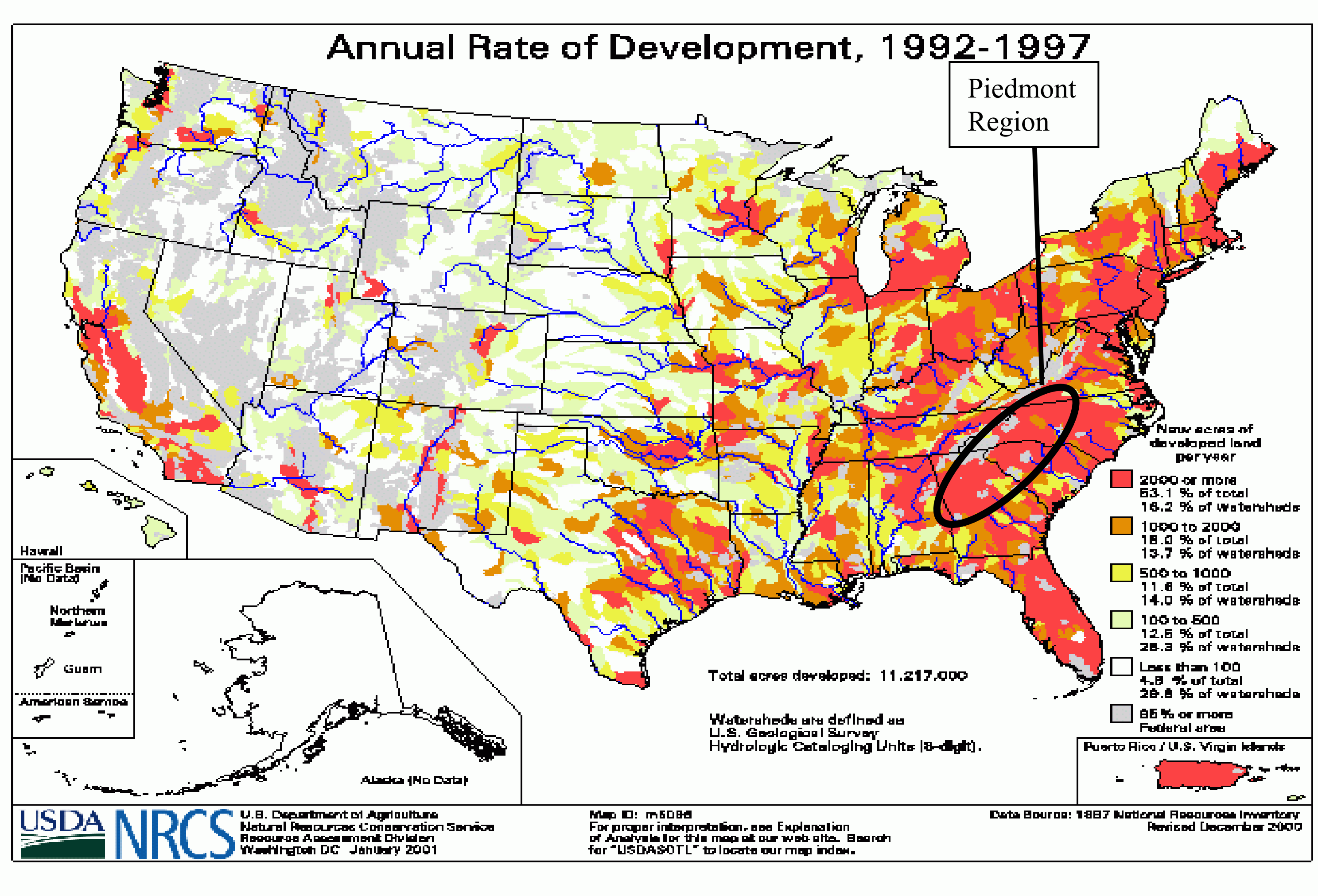

Figure 1: Annual rate of development for the United States, 1992-1997 NRCS
http://www.nrcs.usda.gov/technical/land

CHAPTER II

RIPARIAN WOODY PLANT DIVERSITY AND FOREST STRUCTURE ALONG AN URBAN-RURAL GRADIENT

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 along an urbanization gradient in West Georgia, US. 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 forest stands and regeneration layers for all riparian communities, the invasive, non-native shrub *Ligustrum sinense* was the most dominant species observed in the regeneration layers for urban, developing, and agricultural communities. The proportion of non-native species in forest stands and regeneration layers decreased and Shannon diversity of regeneration layers 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.

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, containing the most states with the greatest total acreage of land developed for urban uses between 1992-1997 (Cordell and Macie 2002). In the South, 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 and other important ecosystem functions may be impaired.

Human influences on forests in the South have had dramatic impacts on forest 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, and 3) the era of forest recovery and renewal, as shown by the 60% peak of forest cover in 1964 (Wear 2002). Today, strong economic growth is shaping the southern landscape. In October 2002, The Southern 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 total forest cover in much of the South has not declined due to shifting of agricultural land to forested landscapes, because of expanding 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 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. Urbanization may impose a another permanent 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 South of the 1990s, in which forests covered 56% relative to 28% in agriculture (cropland + pasture) in 1992 (Wear 2002), urbanization has now surpassed agriculture as the primary source of forest cover loss (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 (Kowarik 1993, Porter et al. 2001), vertebrate (Blair 1996) and insect (Blair and Launer 1997) assemblages, soils (Airola and Buchholz 1984, Dupouey et al. 2002), and water quality (Wear et al. 1998, Wang et al. 2001) 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 species richness (McKinney 2002) as well as adverse impacts on water quality (Tabacchi et al. 1998, Tabacchi et al. 2000, Gergel et al. 2002).

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 (Welsch 1991, Malanson 1993) and provide flood control during high rain events (Welsch et al. 2000). Humans, as well as aquatic biota and other animals, depend on these ecosystem services for well-being and habitat (Naiman et al. 1995). In addition, riparian forests provide aesthetic and recreational values. Studies also have 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 (Blair 1996, Rottenborn 1999, Cockle and Richardson 2003). Management of riparian buffer zones along streams adjacent to agriculture and managed forests has been implemented in some cases (Platts et al. 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 many-faceted impacts of urbanization on the biodiversity, 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). 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 agricultural land. I 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, I 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, US. The growth pattern of Columbus, Georgia provided a 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 mean annual precipitation and snowfall of 129.5 cm and 2.0 cm, respectively (NOAA 2005).

This study used watersheds as fundamental units 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 (Helms et al. 2005, Schoonover et al. 2005). 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.

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). Specific independent variables obtained from GIS analyses that were used in riparian vegetation analyses included: distance to urban center, percent impervious surfaces, and proportion of watershed covered by deciduous forest, evergreen forest, and agriculture (pasture). Each watershed exhibited a dominant land cover type including: mixed forests (M), evergreen forests-pine plantations (P), agriculture (A), developing-suburban (D), and urbanized (U) that reflected a gradient of increasing urban influences (Table 2). Refer to Lockaby et al. (2005) 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 70-m long transects were 100-m apart and extended 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 ≥ 2.5-cm DBH (diameter at 1.4-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 to species 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.

$$\text{Shannon Index (1949) } H' = -\sum_{i=1}^{s^*} (p_i \ln p_i) \qquad (1)$$

$$\text{Evenness } J' = \frac{H'}{H_{max}} \qquad (2)$$

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 i_{th} 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 those 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 mean 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-natives) were observed in the forest stand and 55 species (four non-natives) 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 dominant woody plant in forest stands and regeneration layers for riparian communities located closest to the urban center (Cooper Creek and Standing Boy Creek) with importance values of 64.2 and 70.2 for the forest stands, and 83.6 and 94.8 for the regeneration layers, respectively (Table 3). *Ligustrum sinense* was observed in the regeneration layer of five of the six riparian communities and was dominant in four of them (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 layers in most of the communities.

Site characteristics for the six riparian communities are described in Table 4. The percentage of non-native species in both the forest stands and regeneration layers showed a strong negative 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 also was found between the proportion of non-native species in the regeneration layers and the proportion of non-native species in the forest stands (Figure 2). Shannon diversity in the regeneration layers (Hr′) decreased linearly as the proportion of non-natives in the regeneration layers 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 (Table 2). 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, Hr′, and basal area demonstrated significant relationships 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% lost (Trani 2002) and rank high among forest types experiencing 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 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. Researchers have 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.

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 invasion by non-native species by providing a competitive advantage to invasive species (Tickner et al. 2001). The hydrological role of non-native, 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). This study is consistent with the findings of Merriam and Feil (2002) who reported 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 this study, riparian communities invaded by *Ligustrum sinense* exhibited decreased diversity. At small spatial scales, there is evidence that diverse communities exhibit higher productivity, stability, and resistance to biological invasions (Tilman 1999, Kennedy et al. 2002), because each species may occupy a unique niche and therefore respond differently to environmental changes (Ives et al. 2000). A significant decrease in basal area was also found as forest cover decreased along the urban gradient, which may reflect a decrease in forest productivity or a history of timber harvesting (Ramirez-Marcial et al. 2001, Sagar et al. 2003). 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. Changes in diversity and structure may subdue the ability of communities to maintain ecosystem stability and complexity (Yachi and Loreau 1999, Loreau et al. 2001).

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 (Tabacchi et al. 2000, Nilsson and Svedmark 2002) that requires interdisciplinary research. As part of a larger, integrative study at the rural-urban interface, data will be integrated with other facets of the overall West Georgia project to examine effects of water quality and hydrology on riparian forest communities along the urban gradient. This aquatic-terrestrial linkage is expected to prove useful for understanding the impacts of urbanization on riparian community ecology.

Acknowledgements

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

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 Urban	*Ligustrum sinense* Lour.*	64.2	*Ligustrum sinense* Lour.*	83.6
	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 Developing	*Ligustrum sinense* Lour.*	70.2	*Ligustrum sinense* Lour.*	94.8
	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

Riparian Community	**Forest stand species**	**IV$_{300}$ %**	**Regeneration layer species**	**IV$_{200}$ %**
Ossahatchie Creek Agriculture	*Carpinus caroliniana* Walt.	49.2	*Ligustrum sinense* Lour.*	57.6
	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
Sand Creek Pine	*Liquidambar styraciflua* L.	78.7	*Acer rubrum* L.	34.8
	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

Riparian Community	**Forest stand species**	**IV_{300} %**	**Regeneration layer species**	**IV_{200} %**
Clines Branch Mixed	*Liquidambar styraciflua* L.	43.2	*Acer rubrum* L.	65.4
	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* sp.	7.1
Blanton Creek Mixed	*Liriodendron tulipifera* L.	60.0	*Quercus nigra* L	40.0
	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

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

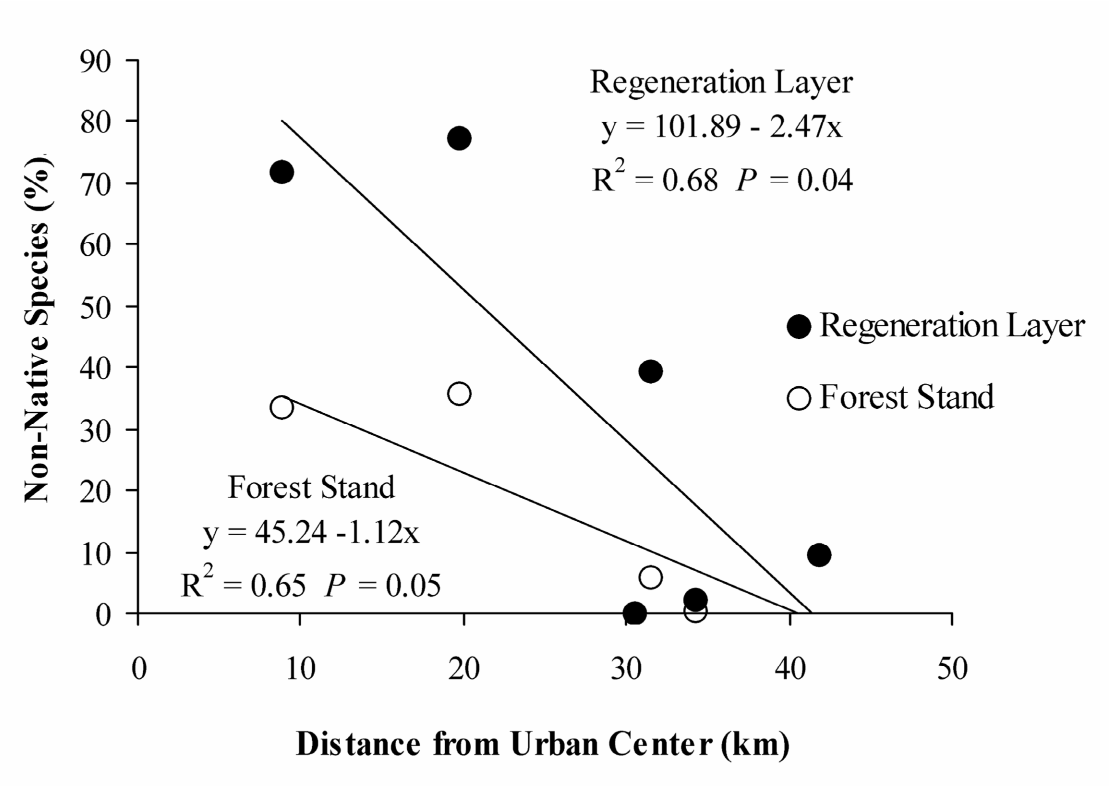

Figure 1: Linear regressions for the relationship between percent non-native species and distance from urban center for the forest stand and regeneration layer.

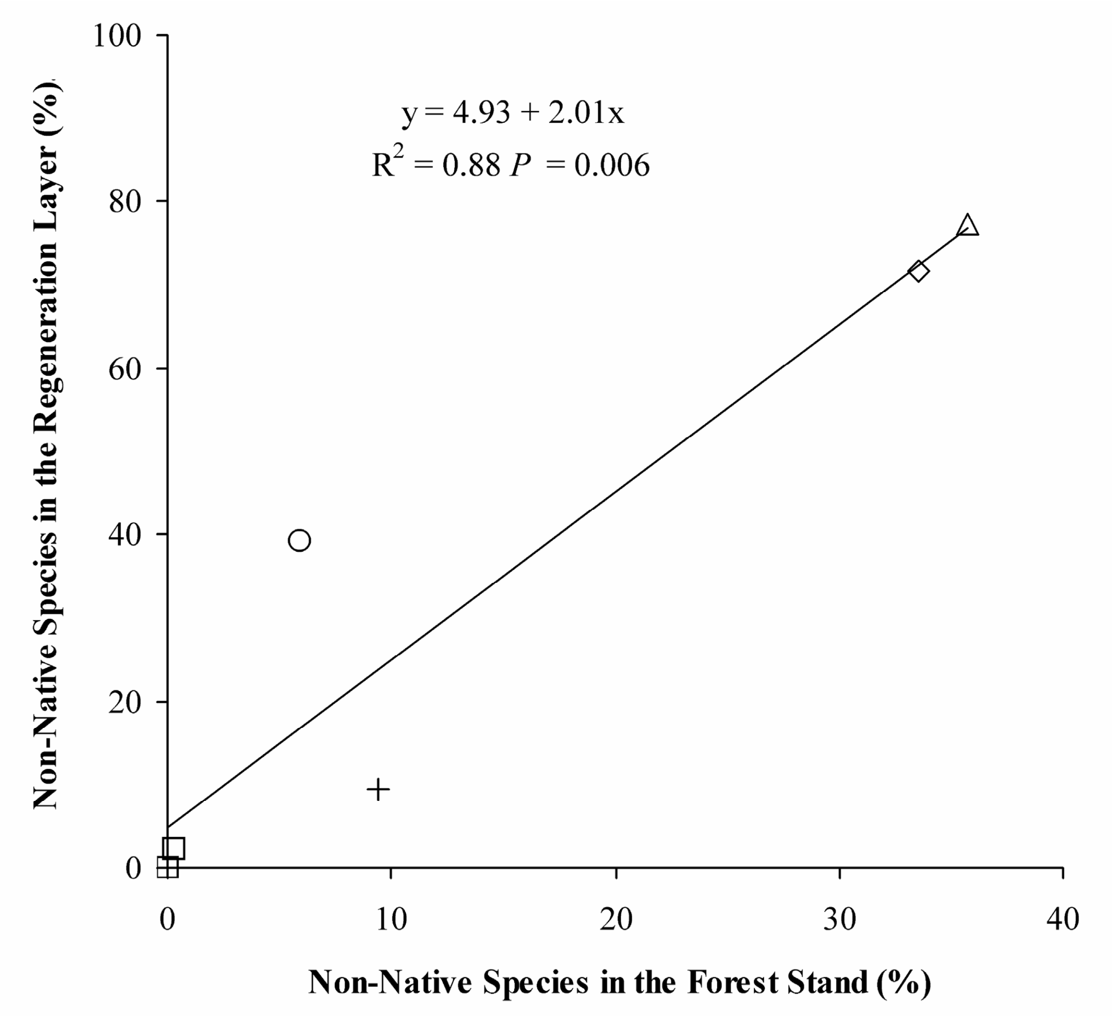

Figure 2: Linear regression for the relationship between percent non-native species in the forest stand and percent non-native species in the regeneration layer (Δ developing, ◊ urban, ○ agriculture, □ mixed, + pine).

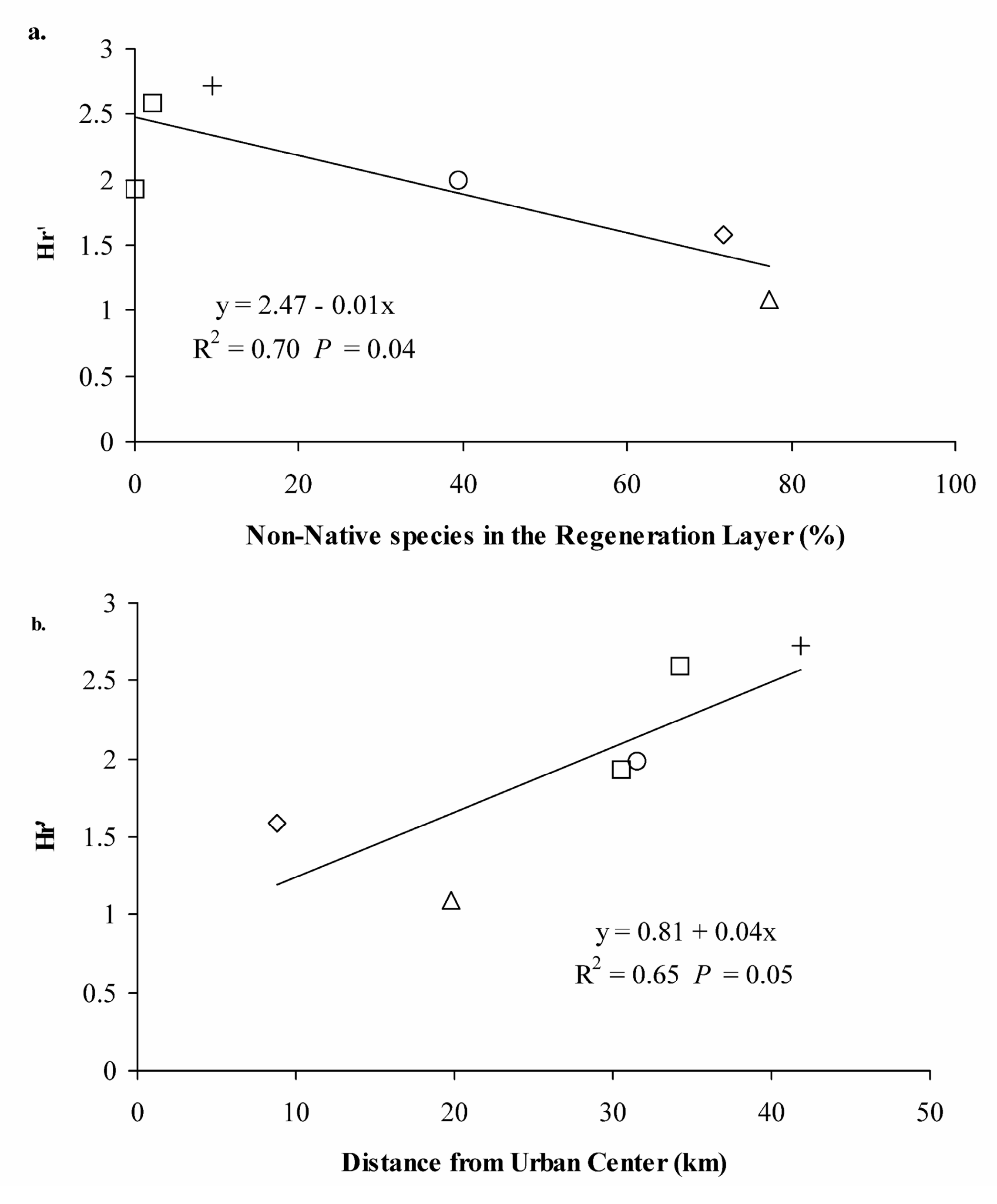

Figure 3: Linear regressions for the relationship between Shannon diversity of the regeneration layer (Hr′) and (a) percent of non-native species observed in the regeneration layer and (b) distance from the urban center (Δ developing, ◊ urban, ○ agriculture, □ mixed, + pine).

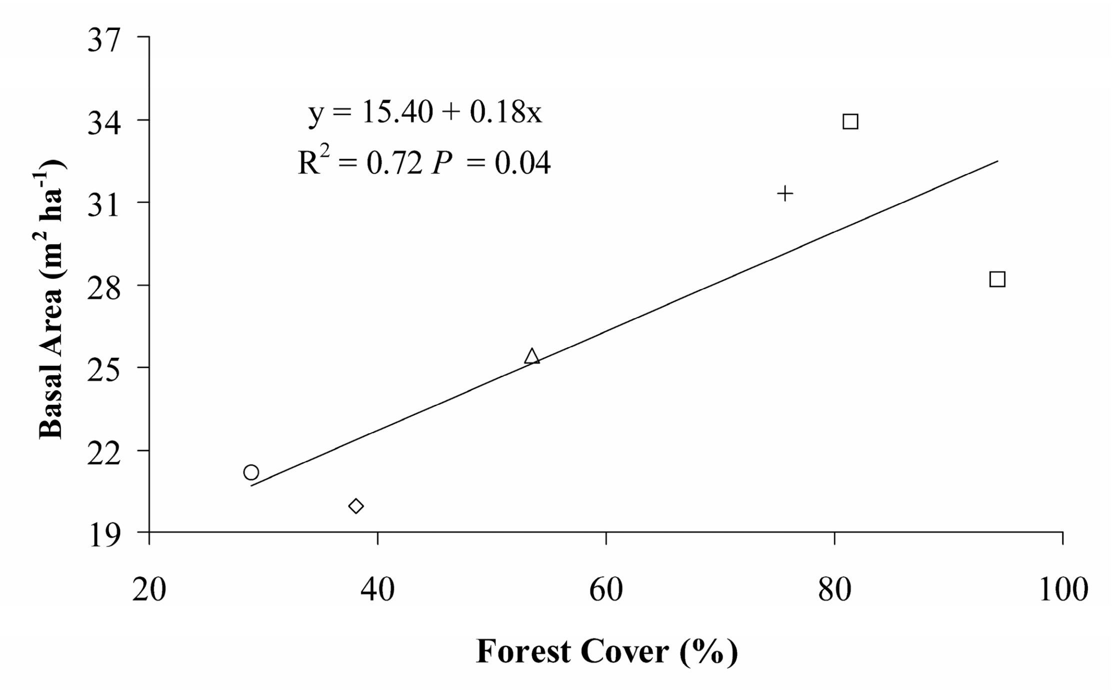

Figure 4: Linear regression for the relationship between basal area (m^2 ha^{-1}) and forest cover (% evergreen + % deciduous forest). (Δ developing, ◊ urban, ○ agriculture, □ mixed, + pine).

Appendix 1: Species encountered in sampling at all sites. Non-native species indicated by (*). Note: Plants were identified only to genus if species could not be determined.

Forest Stand *Scientific name*	**Regeneration Layer** *Scientific name*
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	*Callicarpa 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 sp.	*Crataegus* sp.
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.

Forest Stand *Scientific name*	**Regeneration Layer** *Scientific name*
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.
Oxydendrum 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.	*Sassafras albidum* (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* sp.
Salix nigra L.	*Vaccinium* sp.
Sambucus canadensis L.	
Sassafras albidum (Nutt.) Nees.	
Tilia americana L.	
Ulmus alata Michx.	
Ulmus americana L.	
Ulmus rubra Muhl.	
Vaccinium arboreum Marsh.	
Vaccinium elliottii Champ.	

CHAPTER III

IMPACTS OF URBANIZATION AND LAND USE ON RIPARIAN FOREST DIVERSITY, COMPOSITION, AND STRUCTURE IN THE PIEDMONT OF GEORGIA, US

Keywords: diameter distributions, forest regeneration, forest structure, *Ligustrum*, non-native species, urban gradient

Abstract

Riparian forests are increasingly threatened by urban expansion and land use change worldwide. This study described the relationships among landscape characteristics and woody plant diversity, structure, and composition of small order riparian corridors along an urban-rural land use gradient in the Georgia Piedmont, US. Relationships between biodiversity-structural indices and urbanization and landscape metrics, changes in woody plant species composition, and differences in biodiversity-structural indices and species composition between the mature forest stand and the riparian woody regeneration layer were examined. Patterns of riparian plant diversity, structure, and composition were related to landscape metrics and land use. Species richness was negatively associated with impervious surfaces and landscape diversity and positively associated with forest cover and largest forest patch index. Shannon species diversity was strongly related to the biomass of non-native species, especially for the regeneration layer. Urban sites were characterized by high richness of non-native and pioneer species. Developing sites were dominated by the non-native shrub, *Ligustrum sinense* Lour., and several native overstory trees, mainly *Acer negundo* L. While agricultural and managed forest sites were composed of ubiquitous species, unmanaged forest sites had a structurally distinct midstory indicative of reduced disturbance. Urban and agricultural land uses showed decreased leaf area index and native stem densities, and signs of overstory tree regeneration failure. Midstory biomass was positively related to forest cover and shrub biomass was positively related to landscape patch density. Results from this study highlight the impact of the surrounding landscape matrix upon riparian forest plant diversity and structure.

Introduction

Urbanization is a growing land use worldwide and poses a major threat to biodiversity (McKinney 2006). In the US, 6.5 million hectares of rural land were converted to urban land uses between 1992 and 1997, which implies an urbanization rate of over 1.2 million hectares annually (Cordell and Macie 2002). The desire for rural housing locations combined with the opportunities and amenities of cities has greatly increased development along city fringes. Brown et al. (2005b) suggest that exurban development, defined as low-density housing (6-25 homes km^{-2}) around city fringes, is the fastest growing form of land use in the United States. The southern states have experienced particularly high rates of urbanization: Georgia ranked second nationwide for the most land developed for urban uses between 1992-1997 (USDA-NRCS 2006). This trend is expected to continue as economic growth in the South progresses.

In the South, human land use has profoundly affected the environment. For example, agricultural development during the 17th-19th centuries resulted in tremendous soil erosion in much of the Southern Piedmont (Trimble 1974). Additionally, many natural forests were harvested during the booming timber industry of the 20th century (Wear 2002). While many lands have become reforested after agricultural and timber abandonment, pressures from urban development have become the leading cause of forestland loss in the Southeastern US (Wear 2002). To date, few studies in the southern region have addressed ecological issues related to urbanization (Zipperer 2002b) and little is known about the ecological consequences of urban expansion on biodiversity. The diversity of ecosystems and species associations in the

South, and human dependence on those natural resources, highlight the need for research on the environmental impacts of urbanization, so that informed decisions about future land use can be made.

Studying urbanization along a land use gradient is a useful approach for examining impacts of urban development and has the potential to identify critical areas of change along urban-rural interfaces (McDonnell and Pickett 1990). Some studies have documented important biological changes along urban-rural gradients such as impairment of water quality (Groffman et al. 2003; Schoonover et al. 2005), and degradation of stream habitat (Helms et al. 2005; Wang et al. 2001), as well as changes in animal abundance and composition (Blair and Launer 1997; Stratford and Robinson 2005) and changes in ecosystem processes (Groffman and Crawford 2003; McDonnell et al. 1997; Pouyat et al. 2002). Decreased species diversity, tree basal area, and plant density near urban areas have been reported (Guntenspergen and Levenson 1997; Moffatt et al. 2004; Porter et al. 2001). In preliminary studies, urban development has been shown to increase non-native invasive species richness and density in riparian forests in the southeastern United States (Burton et al. 2005; Loewenstein and Loewenstein 2005).

Understanding the impacts of urbanization on riparian forests is critical because riparian areas provide a variety of important ecological services and are sinks of high species richness (Naiman and Decamps 1997). Moffatt et al. (2004) and Groffman et al. (2003) found significant changes in species composition along the major riparian corridors of the Assiniboine River and Gywnns Falls along an urban-rural gradient in Manitoba, Canada and Baltimore, MD, respectively. Few studies have examined urbanization impacts on riparian forests of headwater streams. Headwater streams and their associated forests are tightly connected to upland land use and contribute significantly to downstream conditions (Gomi et al. 2002). Additionally, smaller cities are not exempt from the negative impacts of urbanization and many are expanding very rapidly.

The overall goal of this work was to describe the relationships among landscape characteristics and riparian woody plant diversity, composition, and structure along an urban-rural land use gradient in the Georgia Piedmont. Specific objectives were to: (1) identify relationships between biodiversity-structural indices and urbanization and landscape metrics, (2) detect changes in woody plant species composition along the urban-rural gradient, and (3) examine differences in biodiversity-structural indices and species composition between the mature forest stand and the riparian woody regeneration layer. I hypothesized that: (1) biodiversity indices would decrease in response to urbanization and importance of non-native species would increase; (2) urbanization would impact forest structure by reducing native plant densities, stand basal area, and canopy cover (leaf area), and increasing average tree diameter while reducing native tree recruitment; and (3) species composition would respond to landscape characteristics and land use, and would shift from riparian species to generalist or upland species as urban land use increased. This work builds on a preliminary study (Burton et al. 2005) that identified changes in species diversity, non-native species abundance, and stand basal area along this urban-rural gradient.

Materials and methods

Study area and sites

The study area was composed of 17 sites located in watersheds (300-2600 ha) of the Middle Chattahoochee River Basin arranged along a land use gradient extending northeast of Columbus, Georgia, US (Figure 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 (NOAA 2005). The southernmost site was located in Muscogee County near the urban center of Columbus, Georgia (32˚ 30.88´N, 84˚ 54.48´W). The remaining sites were embedded along the land use gradient extending northeast, scattered through Harris County and ending with the northernmost site in Troup County (32˚ 52.44´N, 84˚ 00.57´W) (Figure 1). The study area represents a rapidly urbanizing landscape where population statistics show that Muscogee County has a dense population (333 people km^{-2}) and is experiencing moderate growth (+4% per year) relative to Harris County where population density is low (20 people km^{-2}) but growth is rapid (+33% per year). The 33% population increase in Harris County is well above the national average of +13% per year (US Census 2000). Harris County is an excellent example of a location where increased rates of exurban (Brown et al. 2005b) and suburban development are occurring.

Study sites were predetermined from water quality/quantity and stream biota studies and were selected based on catchment size (< 2600 ha) and ranges in proportions of developed, forested, and agricultural land uses at a 30 m scale (Lockaby et al. 2005; Schoonover et al. 2005). Dominant land cover for each watershed was assessed using both supervised and unsupervised classification of 1 meter resolution digital March 2003 aerial photo imagery. Percentages of six major cover types (deciduous forest, evergreen forest, grass-pasture, impervious surface, water, and other) were obtained and the following five dominant land use types were determined based on dominant landcover: urban, developing, agriculture, managed forest (pine plantations), and unmanaged forest (mixed evergreen-deciduous forest) (Table 1). Developing sites were forested sites with active or recent development confirmed by ground truthing (Helms et al. 2005; Schoonover et al. 2005). Urban sites were represented by five sites and all other land use types were represented by three sites (Figure 1). Lockaby et al. (2005) provide a description of the image processing steps and classification methods used to assess watershed landcover/land use. Deciduous forest was primarily hardwood species such as *Quercus* spp., *Liriodendron tulipifera* L., and *Liquidambar styraciflua* L., but also included evergreen species such as *Pinus* spp. Evergreen forest is a common cover type and usually consisted of planted *Pinus taeda* L. at various stages of development. The grass cover type consisted of agricultural lands, which in the study area were pastures used for grazing cattle/horses and hay production as well as, residential lawns and recently harvested areas. Impervious surface is an important urbanization indicator (Gergel et al. 2002) and included features such as roads, rooftops, sidewalks, and driveways. In addition, landscape fragmentation and pattern data such as patch density, largest forest patch index and landscape diversity were calculated from the classified imagery using the program FRAGSTATS 3.3 (McGarigal et al. 2002) with the patch neighbor 8-cell rule option (Table 1). Patch density is the total number of all patches per 100 hectares within each watershed. As a measure of forest dominance, largest forest (deciduous and evergreen) patch index is the percentage of total watershed area occupied by the largest forest patch. Landscape diversity is the typical Shannon diversity index applied to the watershed landscape and in this case (McGarigal et al. 2002):

$$\text{Shannon diversity index} = -\sum_{i=1}^{m} (P_i \ln P_i) \qquad (1)$$

where P_i = proportion of the landscape occupied by patch type *i*, and *m* = number of patch types present in the landscape. Based on the original landscape classification (Lockaby et al. 2005), five patch types were impervious surface, forest (deciduous or evergreen), grass, water, and other (Table 1).

Field methods

Riparian vegetation data for the 17 sites were collected during the summer months (June-August) of 2003-2005. Forest stand data were collected once from each site over the three year period. The regeneration layer at 15 sites was sampled twice, once in 2004 and again in 2005. Second year regeneration was sampled in the same locations within the same month and week as the previous year. Two additional urban sites were added in 2005 and the forest stand and regeneration layer of those were sampled once in that year. Regeneration layer sampling was stratified among land use types so that each land use type was sampled at least once during each month

Each site was sampled using a total of 24 plots, each 0.01 ha in size, on six transects. The urban sites, however, varied in the number of plots (7-24 plots) because small size of the forest fragments restricted the number of plots in some cases. The first transect at each site was located at a pre-determined stream biota and/or hydrologic sampling point. The 70 m long transects extended perpendicular to and across the stream and were placed at 100 m intervals. On each transect, the forest stand was sampled in four 100 m^2 plots placed 15 m apart (two on each side of the stream). Within each 100 m^2 plot, all woody plants ≥ 2.5 cm at diameter at breast height (DBH, 1.4 m height) were identified to species and the DBH recorded. The woody plant regeneration layer was sampled using five 1 m^2 randomly chosen subplots in each 100 m^2 plot. All established (excludes germinants or seedlings with cotyledons present) woody stems < 2.5 cm DBH within the sub-samples were counted and identified. All species were described by one of the following plant forms: overstory tree, midstory tree, or shrub according to Hardin et al. (1996). Species nomenclature followed Godfrey (1988).

Biodiversity and structural indices

Woody vegetation biodiversity indices were calculated for the forest stand and regeneration layer at each site and included total number of species (species richness), Shannon diversity index (Shannon and Weaver 1949), and species evenness index (Pielou 1977). Non-native species were defined as those absent from the region prior to European settlement, according to Godfrey (1988). Species importance values were calculated as relative density + relative frequency + relative basal area (IV_{300}) for the forest stand and relative frequency + relative density (IV_{200}) for the regeneration layer.

Forest structure was characterized by diameter distributions, stem densities, quadratic mean diameter (Nyland 2002), basal area, aboveground biomass, and leaf area index. Predicted relative diameter distributions for each site were fit to empirical

DBH distributions of forest stands using the following two-parameter Weibull probability density function (with 2.5 cm as the minimum diameter class):

$$f(x) = cb^{-1} (xb^{-1})^{c-1} \exp[- (xb^{-1})^{c}] \text{ when } x \geq 2.5 \text{ cm} \qquad (2)$$

$$f(x) = 0 \text{ when } x < 2.5 \text{ cm}$$

where x is the probability density function for a random variable, b is the scale parameter which is related to the range of the distribution, and c describes the shape of the curve. When $c < 1$, the distribution displays a reversed J shape, but if $c > 1$ the shape becomes dome shaped (or flattened) to normally distributed. The parameters were estimated using the maximum likelihood estimation technique described by Johnson and Kotz (1970). To avoid overestimation of the small diameter classes, only empirical data from the overstory tree species were used to estimate diameter distributions.

Aboveground biomass for all woody species was estimated using existing DBH based allometric equations developed for each species or for species groups found on similar sites (Clark et al. 1985; Clark et al. 1986; Jenkins et al. 2003; Phillips 1981; Ter-Mikaelian and Korzukhin 1997). For multi-stemmed plants, each stem was treated as a separate individual. Aboveground biomass for the non-native shrub, *Ligustrum sinense* was determined using an allometric equation developed from a harvest of fifteen specimens from similar offsite locations covering the complete range (1.5 – 18.5 cm) of DBHs observed at each site. The allometric equation was developed using the power function in regression analysis (Clark et al. 1986; Jenkins et al. 2003) to relate whole plant dry-weight of *Ligustrum sinense* and the independent variable, DBH (cm):

$$y = aX^b;\ a = 0.214 \text{ and } b = 2.319\ \ (P < 0.001, R^2 = 0.99) \qquad (3)$$

where a and b are scaling coefficients, y is total whole plant aboveground biomass (kg dry weight), and X is measured DBH (cm).

As a measure of canopy cover or forest canopy shading, leaf area index (LAI) was sampled one meter from the forest floor 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 made along each transect and averaged by transect and then by site.

Ordination analyses

Species importance values for both the forest stand and regeneration layer were analyzed using ordination techniques. Using the program PC-ORD 4.0 (McCune and Mefford 1999) detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) were used as complementary approaches (Økland 1996) to relate species composition to landscape metrics and land use type, respectively (Moffatt et al. 2004). DCA is an indirect gradient analysis technique because environmental gradients are inferred from the species composition data. Default options were used and rare species were down-weighted (McCune et al. 2002). Because CCA uses multiple regression techniques to directly relate environmental variables to species composition (Palmer 1993), environmental variables were coded as land use type based on landscape metrics (Table 1) to avoid problems associated with multicollinearity of land cover percentages (King et al. 2005; Wagner and Fortin 2005). Using land use type as the “environmental variable” allows a direct examination of the influence of land use type on species composition. Site and species scores were standardized using Hill's (1979) method and the chi-squared distances for sites were optimized (Jongman et al. 1995). The Monte Carlo permutation was used to test the significance of the first axis eigenvalue, testing the null hypothesis of no relationship between the species and environmental matrix. Separate ordinations were conducted for the forest stand and the woody regeneration layer. All ordination analyses were based on species importance values and the regeneration layer data were pooled across the two sample years.

Statistical analyses

Analysis of variance was used to test for significant differences in landscape metrics and species importance among land uses. Tukey's HSD comparison test was used to separate means when the overall model was significant ($\alpha = 0.05$). Linear regression analyses were used to detect trends in biodiversity in response to landscape metrics and non-native plant abundance. Differences in slope parameters between the forest stand and regeneration layer were compared using dummy variable analysis. Pearson product-moment correlations were used to evaluate relationships between forest structure measures and DCA ordination scores with landscape metrics. For the regeneration layer, data were pooled across the two sample years. Tests for normality were conducted for all variables and density and species richness variables were log transformed to meet normality assumptions. Residual plots were used to check the equal variance assumption of these tests. All statistical analyses were conducted using SAS Software 9.1 (SAS Institute 2003).

Results

Land use/cover

Urban land use was characterized by significantly higher percent cover of impervious surfaces and had the lowest total forest cover, less than 40% (Table 1). Urban watersheds had the highest landscape diversity, because all patch types were present and the proportional distribution of area among them was more equitable compared to the other land uses (Table 1). This characteristic is consistent with Zipperer et al. (2000) who described urban landscapes as highly heterogeneous. Developing watersheds were not significantly different from the unmanaged forest (reference) sites in terms of impervious surfaces (1-3 %), forest cover (64-81 %), grass cover (13-28 %), and largest forest patch index (35-66 %), but had significantly higher patch density and landscape diversity suggesting more fragmentation than unmanaged forested sites (Table 1). These landscape characteristics fit the description of "exurban development" given by Brown et al. (2005b), where increasing rates of residential development are occurring in high quality, forested areas along the urban fringe. The agricultural land use type was characterized by high cover of grass (>35%), but grass cover was similar for both agriculture and urban land uses, most likely because of occurrence of residential lawns in urban areas. Urban and agriculture land uses also had the lowest largest forest patch indices, 6.1 and 25.2, respectively (Table 1). None of the landscape metrics for the managed forest sites were significantly different from unmanaged forest sites. Patch density and landscape diversity of managed forest sites were not significantly different from developing sites. Overall, landscape characteristics of the study sites conformed to the description given by Medley et al. (1995) of an urban-to-rural land use gradient.

Species diversity and composition

The forest stand

A total of 78 woody species (DBH ≥ 2.5 cm) were sampled in the forest stand across all sites (Appendix 1). Species richness showed significant relationships with landscape characteristics (Figure 2). For both the forest stand and the regeneration layer, species richness was positively related to percent forest cover and largest forest patch index and negatively related to percent impervious surface and landscape diversity. Shannon diversity and species evenness indices were not significantly related to any landscape characteristic (data not shown), but Shannon diversity was negatively related to increasing biomass of non-native species (Figure 3a).

Detrended correspondence analysis (DCA) ordinations were conducted to evaluate if species composition was related to landscape characteristics (Table 2). DCA axis 1 and 2 accounted for 31.9% and 15.3% of the variation, respectively, in the species data. The influence of landscape characteristics on riparian woody plant species composition was most evident along the 1st axis (Table 2). Impervious surfaces and landscape diversity showed negative correlations with the 1st axis, while forest cover and largest forest patch index showed significant positive correlations (Table 2). These landscape characteristics appear to represent the underlying cumulative effects of the land use (i.e. disturbance) gradient on species composition along axis 1 for the DCA ordination.

Canonical correspondence analysis (CCA) directly related land use to patterns in species composition. Only the eigenvalue for the first axis ($\lambda = 0.312$) was significant ($P < 0.05$) according to the Monte Carlo permutation test. The species-environment correlation for the first axis was 0.962, suggesting that land use was related to species composition along axis 1 for the forest stand (Figure 4). Although many species were common to all sites, some unique patterns emerged along the land use gradient. Urban sites were characterized by high richness of non-native species (*Albizia julibrissin* Durazz., *Sapium sebiferum* (L.) Roxb., and *Ligustrum* spp.) as well as pioneer species such as *Platanus occidentalis* L., *Prunus* spp., *Ulmus alata* Michx., *Pinus taeda* L., and *Quercus nigra* L. Common species to developing sites were a non-native shrub, *Ligustrum sinense*, and several native overstory trees, *Acer negundo* L., *Ulmus americana* L., *Salix nigra* L., and *Fraxinus pennsylvanica* L. In the developing sites, the importance of *Ligustrum sinense* was significantly higher when compared to three ubiquitous overstory trees (*Liquidambar styraciflua*, *Quercus nigra*, and *Liriodendron tulipifera*) (Figure 5a). Agriculture and managed forest land use types were dominated by several ubiquitous species such as *Liquidambar styraciflua* L., *Carya glabra* (Mill.) Sweet, *Acer rubrum* L., and *Liriodendron tulipifera* L. A group of midstory species (*Cornus florida* L., *Halesia tetraptera* Ellis., *Ostrya virginiana* (Mill.) K. Koch., *Sassafras albidum* (Nutt.) Nees. and *Oxydendrum arboreum* (L.) DC.) was present in the unmanaged forests. Other unique species for the unmanaged forest land use were *Magnolia acuminata* L., *Quercus shumardii* Buckl. and shrubs such as *Hamamelis virginiana* L., *Kalmia latifolia* L., *Vaccinium* sp. and *Rhododendron* sp.

The regeneration layer

Over the two year sample period, 68 woody species were sampled in the regeneration layer (stems < 2.5 cm DBH) across all sites. Diversity trends similar to those of the forest stand were observed for the regeneration layer. Species richness was positively associated with percent forest cover and largest forest patch index and negatively associated with percent impervious surface and landscape diversity (Figure 2). The Shannon diversity index was also negatively associated with non-native plant biomass (Figure 3a). The decrease in Shannon diversity in response to non-native plant biomass was significantly (P <0.001) greater for the regeneration layer than for the forest stand.

DCA ordination axis 1 and 2 represented 35.9% and 14.6% of the variation in species data for the regeneration layer, respectively, accounting for 50.5% of the total variation within the species data for the regeneration layer. Riparian woody plant recruitment patterns were related to landscape metrics mostly along axis 1 (Table 2). Similar to results observed for the forest stand, impervious surfaces and landscape diversity were negatively associated with the 1st axis, while forest cover and largest forest patch index showed a significant positive association. In addition, grass cover was negatively correlated with axis 1. Likewise, species patterns for the regeneration layer along DCA axis 1 appear to be responding to the underlying cumulative effects of the land use gradient.

Patterns in species composition of riparian woody plant recruitment, based on CCA, were also related to land use. The eigenvalue (λ= 0.342) for the 1st axis was significant (P < 0.05) according to the Monte Carlo permutation test and the species-environment correlation was 0.975 (Figure 6). Riparian species were essentially absent in the urban sites and non-native species were most common. In addition to some riparian species (as found in west-central Georgia), such as *Fraxinus pennsylvanica* Marsh., *Quercus michauxii* Nutt., *Gleditsia triacanthos* L., and *Magnolia virginiana* L., were present in the regeneration of the developing and agriculture sites, upland species such as *Carya tomentosa* (Poir.) Nutt. and *Juniperus virginiana* L. were also present. *Quercus nigra* L. was important for the managed and unmanaged forests. The semi-evergreen non-native shrub, *Ligustrum sinense*, was highly abundant in the agriculture, developing, and urban land uses, composing almost 50% of the stems in the agriculture communities and 75% of the stems in the urban and developing communities (Figure 3b). *Ligustrum sinense* was significantly more important when compared to three ubiquitous overstory tree species, *Liquidambar styraciflua*, *Quercus nigra*, and *Liriodendron tulipifera* (Figure 5b).

Forest structure

Forest structure was also related to landscape characteristics. Native stem density for both the forest stand and regeneration layer was positively correlated to percent forest cover and largest forest patch index, but negatively correlated to impervious surface cover and landscape diversity (Table 3). In the regeneration layer, native stem density was negatively correlated to non-native stem density (Figure 3b). Leaf area index (LAI) was lowest in the urban sites and highest in the forested sites and ranged from 2.86 to 5.97. LAI was negatively correlated to percent impervious surface and positively correlated to percent forest cover within the watershed (Table3).

Quadratic mean diameter ranged from 10.6 to 28.3 cm and was negatively correlated to forest cover (Table 3). Parameter ***c*** from the predicted diameter distributions for the two-parameter Weibull function was positively correlated with percent cover of grass within the watershed (Table 3). Basal area ranged from 14.59 to 45.33 m^2 ha^{-1} and showed no relationship with landscape metrics (Table 3). Average total aboveground biomass was 181.4 (urban), 104.1 (developing), 176.8 (agriculture), 141.2 (managed forest), and 161.2 (unmanaged forest) Mg ha^{-1}. Total and overstory tree biomass did not show any relationships with landscape metrics. Midstory tree biomass was positively correlated to forest cover, but negatively correlated to impervious surface and landscape diversity. Shrub biomass was positively related to patch density (Table 3). Urban sites were highly variable, representing the highest and lowest values for basal area and aboveground biomass (data not shown).

Discussion

Woody species diversity, composition, and structure were related to several important environmental gradients associated with land use/cover in the study area particularly impervious surfaces, forest cover, landscape diversity, and forest patch characteristics. Some studies (Moffatt et al. 2004; Porter et al. 2001) have documented peaks (unimodal response) in diversity (or species richness) in suburban (developing) landscapes. These results may support the intermediate disturbance hypothesis, which proposes that species diversity may be greatest where disturbance is intermediate in frequency, area, and intensity. In this study, species richness declined linearly as disturbance (urbanization) increased, as was also found by Ikeda (2003).

Mackey and Currie (2001) described studies where diversity did not consistently peak at intermediate levels of disturbance, particularly when the disturbance was human influenced. Shannon diversity and species evenness were not related to any landscape metric in this study, perhaps because abundance of non-native species superceded influences of the surrounding landscape matrix (Hopper et al. 2005). Developing sites (those located at the urban-rural interface) exhibited landscape characteristics similar to rural sites, such as high total forest cover and larger forest patches, but experienced pressures associated with urban development (i.e. forest fragmentation and non-native species invasion) similar to exurban development as described by Hansen et al. (2005).

Forest fragmentation and edge effects have been found to increase recruitment of invasive non-native species into forest interiors (Cadenasso and Pickett 2001; Yates et al. 2004). The structure of riparian areas themselves, functioning as corridors and aquatic-terrestrial ecotones, may inherently increase the risk of biological invasions (Renofalt et al. 2005). Invasive species have been reported to influence native species diversity, composition, and structure (Fierke and Kauffman 2006; Lichstein et al. 2004; Miller and Gorchov 2004). In this study, Shannon diversity declined with increasing biomass of non-native species. Brown et al. (2006) also reported significant declines in Shannon diversity in response to dominance by non-native species. The highly invasive shrub, *Ligustrum sinense*, was the most common non-native species found in this study and was essentially the only non-native woody plant observed in riparian communities of developing and urban sites. Morris et al. (2002) found that the growth and reproductive characteristics of *Ligustrum sinense* gave it a competitive advantage over a similar native species, *Forestiera ligustrina* (Michx.) Poir. *Ligustrum sinense* may completely suppress native tree recruitment as reported by others (Merriam and Feil 2002). In this study, as the density of non-native stems (mostly *Ligustrum sinense*) increased, the density of native stems significantly decreased. *Ligustrum sinense* was also more dominant than several common generalist tree species (*Liquidambar styraciflua*, *Quercus nigra*, and *Liriodendron tulipifera*). Increases in non-native plant recruitment, especially *Ligustrum sinense*, and reduced recruitment of native trees in urbanizing landscapes may result in degradation of communities into *Ligustrum* shrub thickets (Loewenstein and Loewenstein 2005).

CCA ordination demonstrated that species composition responded to dominant land use. For example, urban sites were composed of pioneer species, such as *Prunus* spp., *Ulmus alata*, and *Pinus taeda*. These results are consistent with Moffat et al. (2004), who reported more early successional and non-native species in urban riparian areas compared to rural riparian areas. In addition to *Ligustrum sinense*, the native tree *Acer negundo* was dominant in the developing sites and is common on sites experiencing human disturbance (Cowell 1998; Zipperer 2002a). Species composition for the agriculture and managed forest sites was dominated by ubiquitous species such as *Liriodrendron tulipifera* and *Liqidambar stryraciflua*. Groffman et al. (2003) reported that decreased importance of riparian tree species in response to urban land use in the northeastern United States was likely due to hydrologic changes associated with urban development. In this study, woody recruitment in the urban communities was composed of upland, generalist, and non-native species. While some riparian species were present in the developing and agriculture land use types, upland species such as *Carya tomentosa* and *Juniperus virginiana*, became more important potentially signifying species response to hydrologic change.

Eastern deciduous forests in North America often contain a distinct midstory canopy of small trees (Braun 1950). In this study, a distinct midstory canopy of native woody species was found in the unmanaged forest land use type but this midstory canopy was essentially absent for all other land use types. Little information is available about land use effects on forest midstory species. Rauscher et al. (1997) synthesized studies in southern Appalachian hardwood forests and documented the importance of disturbance, (i.e., fire and agriculture) for reducing shade tolerant midstory competition for oak-hickory regeneration on mesic sites. The CCA ordination showed species such as *Carya cordiformis* and *Quercus alba* were present in the forest stand on unmanaged forest sites, however many oak species were found to a lesser degree or were absent in the regeneration layer. In addition, the shade tolerant *Acer rubrum* was an important component of the forest stand and regeneration layer for the unmanaged forest type. *Acer rubrum* has been linked to reduced disturbance and oak regeneration limitation in Piedmont forests (McDonald et al. 2003). Presence of a shade tolerant midstory canopy and the importance of *Acer rubrum* may indicate reduced human disturbance in the unmanaged forests in this study. Midstory species and several native shrub species (*Chionanthus virginiana* L., *Lindera benzoin* (L.) Blume., and *Calycanthus floridus* L.) increased the overall diversity and species richness in unmanaged forests. Absence of these species for the other land use types potentially indicates that small-scale changes in landscape structure may significantly affect broad-scale (regional) species diversity (Brosofske et al. 1999).

In addition to shifts in species diversity and composition, impacts of land use on measures of forest structure were also observed. Rural land use showed a higher density of native stems, and urban and agriculture sites had higher mean tree diameters. Porter et al. (2001) found higher basal areas and stem densities in forests that were least affected by urban land use, while mean tree diameters increased in urban forests. In the urban sites, human preferences for open, park-like areas and vegetation maintenance (mowing) may be responsible for fewer small diameter trees and reduced woody plant recruitment observed in this study (Sharpe et al. 1986; Zipperer 2002a). Impacts from cattle grazing and trampling are possible reasons for a similar trend on the agricultural sites (Austrheim 2002). Reducing stem density can often increase overall diameter growth of the residual stand and over time maintain consistent basal area or "stand stocking level" (Nyland 2002), which may explain why no relationships between land use metrics and basal area were observed. Similar to Zipperer (2002a), who reported similar overall basal areas for remnant and regenerated urban forest patches, tradeoffs between mean tree diameters and stem densities, related to land use in this study, may have resulted in no shifts in overall basal area.

Total aboveground biomass was comparable to other biomass estimates of forested wetlands in the US (Giese et al. 2003; Lockaby and Walbridge 1998; Mitsch et al. 1991). Total aboveground biomass estimates were not significantly influenced by the landscape matrix, however the distribution of biomass among forest canopies (overstory, midstory, and shrub) was influenced by patch density, forest cover, and impervious surface cover. Watersheds exhibiting high forest cover had greater biomass in midstory while watersheds with high patch density had greater biomass in the shrub layer. Particularly, the developing sites increased biomass in the shrub layer likely due to the presence of *Ligustrum sinense*. Non-native, invasive plant species have been identified as a major contributor to human-induced environmental change (Vitousek et al. 1997). Litton et al. (2006) reported decreased sequestration of carbon in aboveground biomass following the invasion of a non-native grass in Hawaiian dry forests. Riparian forests may be important sinks for large quantities of carbon because of their relatively high productivity (Lockaby and Walbridge 1998) and urban forests may also be significant carbon sinks (Nowak and Crane 2002). However, changes in the distribution of carbon (biomass) among forest canopies (overstory, midstory, and shrub) influenced by invasion of non-native species may change ecosystem carbon storage at landscape and regional scales (Litton et al. 2006).

Diameter distributions are often used to assess forest structure and a reversed-J shaped curve indicates an uneven-aged forest (Nyland 2002). In general, exponentially high numbers of small diameter stems of overstory species are needed to insure recruitment of stems into the overstory through time (Nyland 2002). Sakkola et al. (2005) found significant differences in the Weibull distribution parameter ***c*,** which described the shape of the diameter distribution curve, among stands of Scots pine 10 to 60 years after peatlands were drained. As ***c*** approaches 1, the shape of the curve flattens and becomes dome-shaped rather than a reversed-J shape, which may indicate overstory tree regeneration failure in unevenaged forest stands (Johnson et al. 2002;

Nyland 2002). In this study, parameter ***c*** was positively correlated with grass cover, which was highest for the urban and agriculture sites. These results are consistent with results of West et al. (2000) who reported that agriculture practices contributed to regeneration failure of hardwoods in a sub-tropical forest. In addition to increased recruitment of non-native species, analysis of forest structure using the two-parameter Weibull function to predict diameter distributions also demonstrated that urban and agricultural land uses show signs of potential overstory tree regeneration failure (Nyland 2002).

In summary, the following changes in diversity, composition, and structure were observed across the urban-rural land use gradient. Species richness and Shannon diversity declined as urbanization and non-native plant biomass increased, respectively. Unmanaged forests had a structurally distinct midstory canopy composed of various small hardwood trees. Urban sites were composed mainly of upland and non-native species and developing sites showed a presence of upland species in the regeneration layer potentially signifying hydrologic changes. The shrub, *Ligustrum sinense* was the most abundant non-native species and appears to be a major factor influencing changes in composition and forest structure across the gradient. In the regeneration layer of the urban, developing, and agriculture sites, *Ligustrum sinense* had species importance values greater than three of the most common tree species found in the region. The forest regeneration layer had decreased native stem density as the density of non-natives (mostly *Ligustrum sinense*) increased. *Ligustrum sinense* increased the aboveground biomass of the shrub canopy in developing land use types and changes in the distribution of biomass among forest canopy layers may influence broad-scale carbon storage. Overstory recruitment failure in the forest stand (as shown by diameter distributions), declining density of native stems in the regeneration layer, and changes in species composition, suggest urbanization may greatly impact the integrity of riparian landscapes in the region.

This research highlights the significance of the surrounding landscape matrix on the diversity, composition, and structure of minor riparian forests in the Piedmont region of the southeastern US. Important implications of this research are potential impacts of declining diversity and compositional and structural changes on ecosystem processes and functioning, which has become a current area of scientific debate in the literature and intensive research (Hopper et al. 2005). A recent synthesis by Balvanera et al. (2006) suggests that diversity has positive effects on most ecosystem services. For instance, dominance by non-native species can significantly affect nutrient cycling in deciduous forests (Ashton et al. 2005). Reductions in riparian plant species richness may influence aquatic ecosystem functioning through complex trophic interactions related to leaf litter decomposition and feeding of stream biota (Lecerf et al. 2005). Diversity and composition of species functional traits are perhaps more important in governing ecosystem function than species diversity *per se* due to species complementarity and redundancy (Diaz and Cabido 2001; Grime 2002; Hopper et al. 2005). Changes in composition and vegetation structure, such as increases of evergreen species, may also affect stream flow and water cycles (Brown et al. 2005a).

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Table 1: Mean (± S.E.) landscape metrics based on 1 meter resolution digital aerial photo imagery for each land use type. Different letters indicate significant ($\alpha = 0.05$) differences between land use types (n=number of sites in each land use type).

Landscape Metric	Urban (n=5)	Developing (n=3)	Agriculture (n=3)	Managed Forest (n=3)	Unmanaged Forest (n=3)
Patch Type (% cover)					
Impervious surfaces	27.45 ± 4.64^{a}	2.83 ± 0.50^{b}	2.69 ± 0.48^{b}	1.71 ± 0.43^{b}	1.55 ± 0.19^{b}
Total forest †	39.91 ± 2.17^{c}	70.07 ± 3.09^{a}	55.05 ± 1.95^{b}	71.84 ± 2.25^{a}	78.76 ± 1.43^{a}
Grass	25.40 ± 3.89^{ab}	22.62 ± 2.51^{b}	38.85 ± 2.57^{a}	18.97 ± 1.23^{b}	15.47 ± 1.65^{b}
Water	1.29 ± 0.34^{a}	1.30 ± 0.34^{a}	2.13 ± 1.02^{a}	0.81 ± 0.12^{a}	0.41 ± 0.24^{a}
Other	3.90 ± 1.40^{a}	3.18 ± 0.22^{a}	1.29 ± 0.29^{a}	6.66 ± 2.91^{a}	3.81 ± 0.02^{a}
Fragmentation Metric					
Patch density 100 ha^{-1} ††	6.97 ± 0.86^{b}	19.28 ± 7.52^{a}	7.22 ± 0.27^{b}	10.74 ± 0.49^{ab}	9.39 ± 0.23^{b}
Landscape diversity	1.21 ± 0.02^{a}	0.82 ± 0.06^{b}	0.92 ± 0.06^{b}	0.76 ± 0.03^{bc}	0.65 ± 0.02^{c}
Largest forest patch index	6.12 ± 2.84^{b}	50.01 ± 9.03^{a}	25.21 ± 7.49^{b}	62.10 ± 3.15^{a}	61.75 ± 3.07^{a}

† Total forest cover = evergreen forest cover and deciduous forest cover combined.
†† Patch density reported in thousands per 100 ha.

Table 2: Correlations between the landscape metrics and DCA axes 1 and 2 ordination scores for the forest stand and the regeneration layer (data pooled across two years).

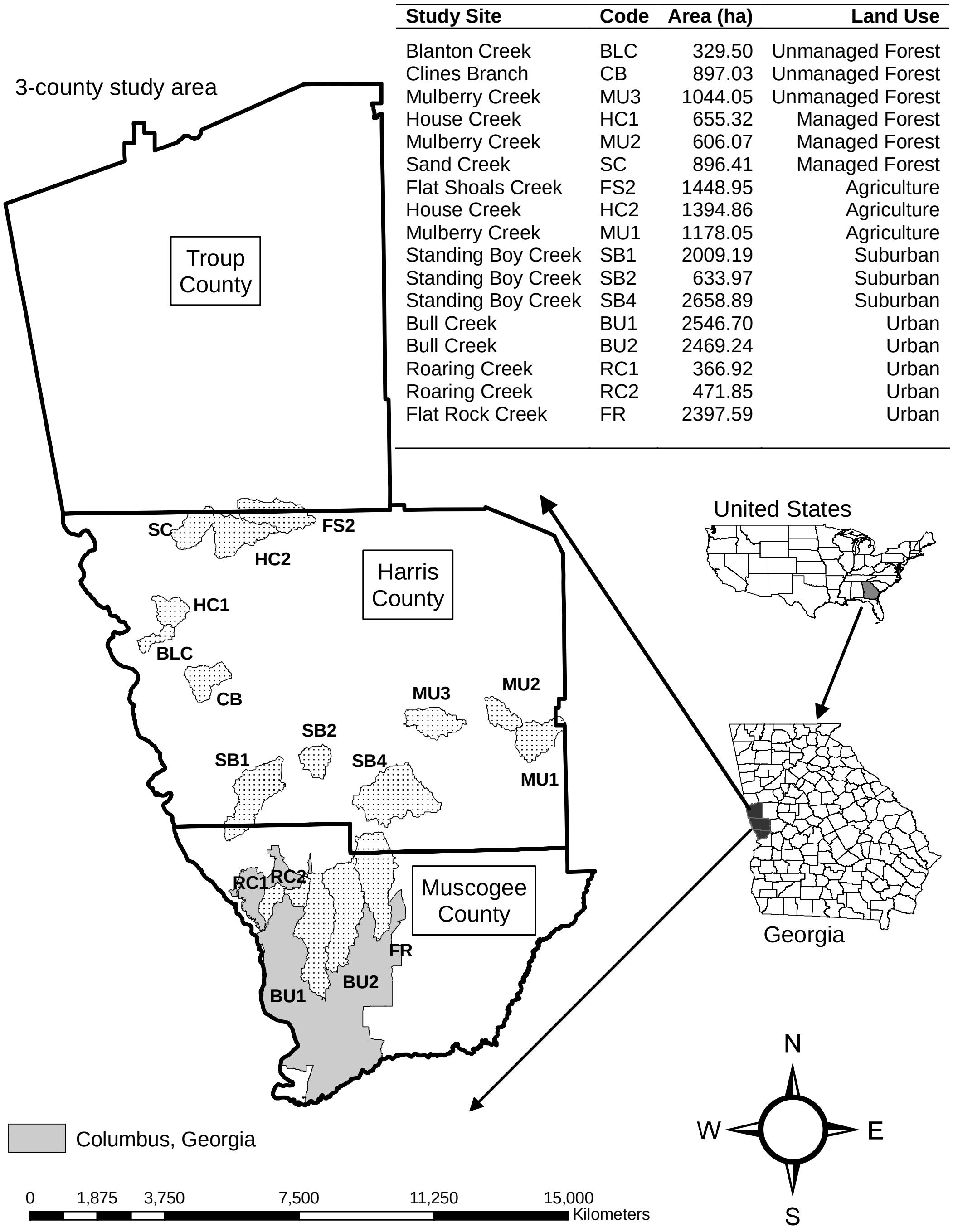
Landscape Metric	Forest Stand		Regeneration Layer	
	Axis 1	Axis 2	Axis 1	Axis 2
Impervious surface (%)	-0.60*	0.50*	-0.48*	-0.48*
Forest cover (%)	0.68*	-0.35	0.69**	-0.38
Grass cover (%)	-0.17	-0.19	-0.50*	-0.12
Patch density	-0.08	-0.27	-0.09	-0.36
Landscape diversity	-0.80**	0.27	-0.74**	0.24
Largest forest patch index	0.62*	-0.22	0.65**	-0.29

*$P < 0.05$; **$P < 0.001$

Table 3: Correlations between landscape metrics and structural indices of the 17 riparian sites. Density = number of native stems ha^{-1}; LAI = Leaf Area Index (m^{2} m^{-2}); Aboveground Biomass = Mg dry weight ha^{-1}; Basal Area (m^{2} ha^{-1}); QMD = quadratic mean diameter (cm); Parameter c = diameter distribution coefficient.

Structural Index	Impervious surfaces (%)	Forest cover (%)	Grass cover (%)	Patch density	Landscape diversity	Largest forest patch index
Density: Stand†	-0.61**	0.58**	-0.25	0.25	-0.43*	0.44*
Density: Regeneration†	-0.79**	0.70**	-0.16	0.24	-0.67**	0.56**
LAI	-0.50**	0.54**	-0.30	0.42*	-0.34	0.39
Total Aboveground Biomass	0.15	-0.34	0.37	-0.25	0.19	0.18
Overstory Biomass	0.14	-0.32	0.34	-0.25	0.17	-0.15
Midstory Biomass	-0.44*	0.41*	-0.04	0.15	-0.44*	0.30
Shrub Biomass	0.15	-0.18	0.07	0.53**	0.32	-0.28
Basal Area	0.12	-0.27	0.28	-0.23	0.19	-0.17
QMD	0.49**	-0.53**	0.37	-0.43*	0.28	-0.32
Parameter c	0.01	-0.29	0.51**	-0.18	-0.16	-0.18

† log$_{10}$ transformed
*$P < 0.1$; **$P < 0.05$



Study Site	Code	Area (ha)	Land Use
Blanton Creek	BLC	329.50	Unmanaged Forest
Clines Branch	CB	897.03	Unmanaged Forest
Mulberry Creek	MU3	1044.05	Unmanaged Forest
House Creek	HC1	655.32	Managed Forest
Mulberry Creek	MU2	606.07	Managed Forest
Sand Creek	SC	896.41	Managed Forest
Flat Shoals Creek	FS2	1448.95	Agriculture
House Creek	HC2	1394.86	Agriculture
Mulberry Creek	MU1	1178.05	Agriculture
Standing Boy Creek	SB1	2009.19	Suburban
Standing Boy Creek	SB2	633.97	Suburban
Standing Boy Creek	SB4	2658.89	Suburban
Bull Creek	BU1	2546.70	Urban
Bull Creek	BU2	2469.24	Urban
Roaring Creek	RC1	366.92	Urban
Roaring Creek	RC2	471.85	Urban
Flat Rock Creek	FR	2397.59	Urban

Figure 1: Location of study area and 17 study watershed sites within the Middle Chattahoochee River Basin for Muscogee, Harris, and Troup Counties, Georgia.

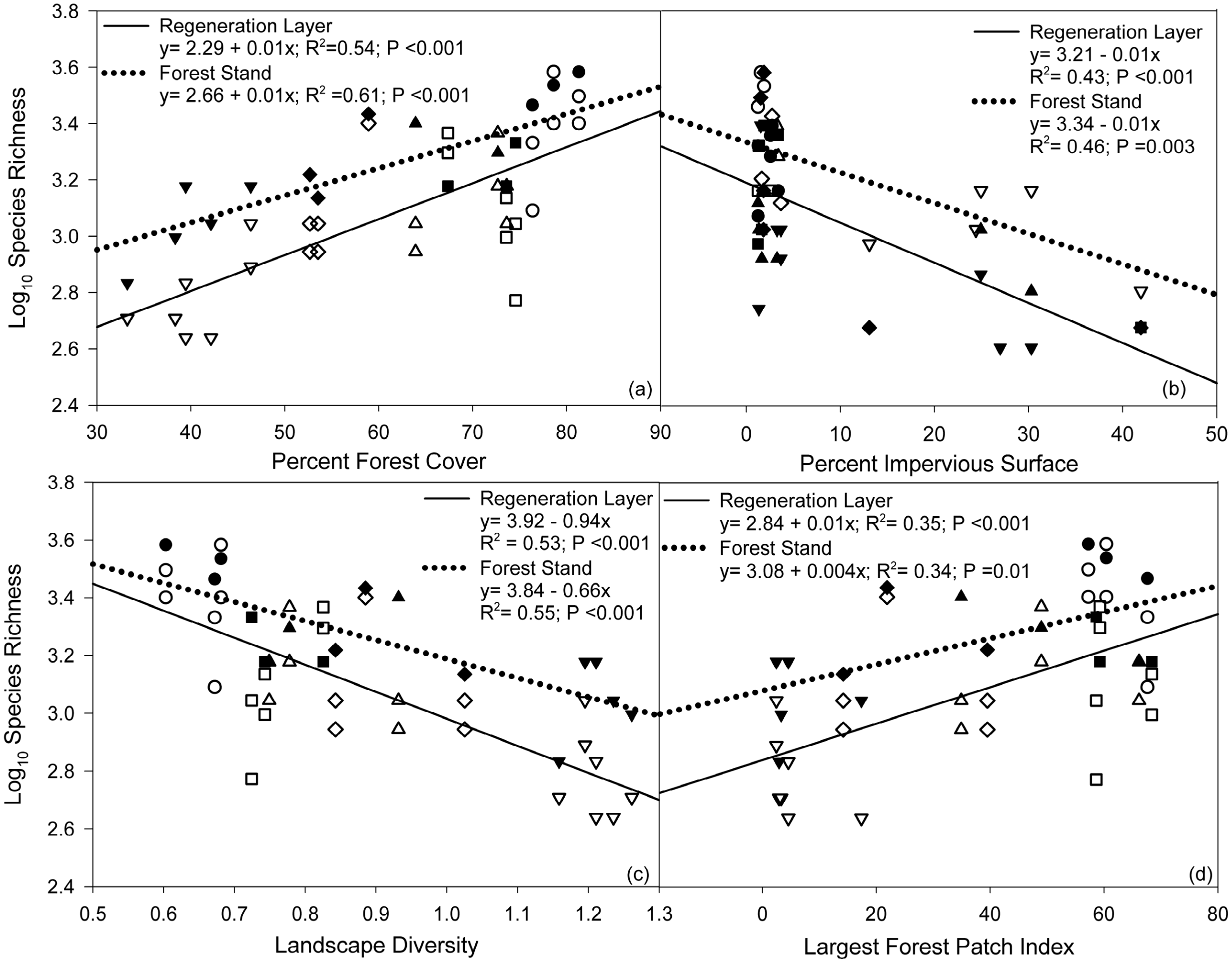


Figure 2: Linear regressions for the relationships between species richness and (a) percent forest cover, (b) percent impervious cover, (c) landscape diversity, and (d) largest forest patch index. Symbols represent dominant land use type: ● unmanaged forest, ■ managed forest, ♦ agriculture, ▲ developing, and ▼ urban. Closed symbols represent the forest stand and open symbols represent the regeneration layer.

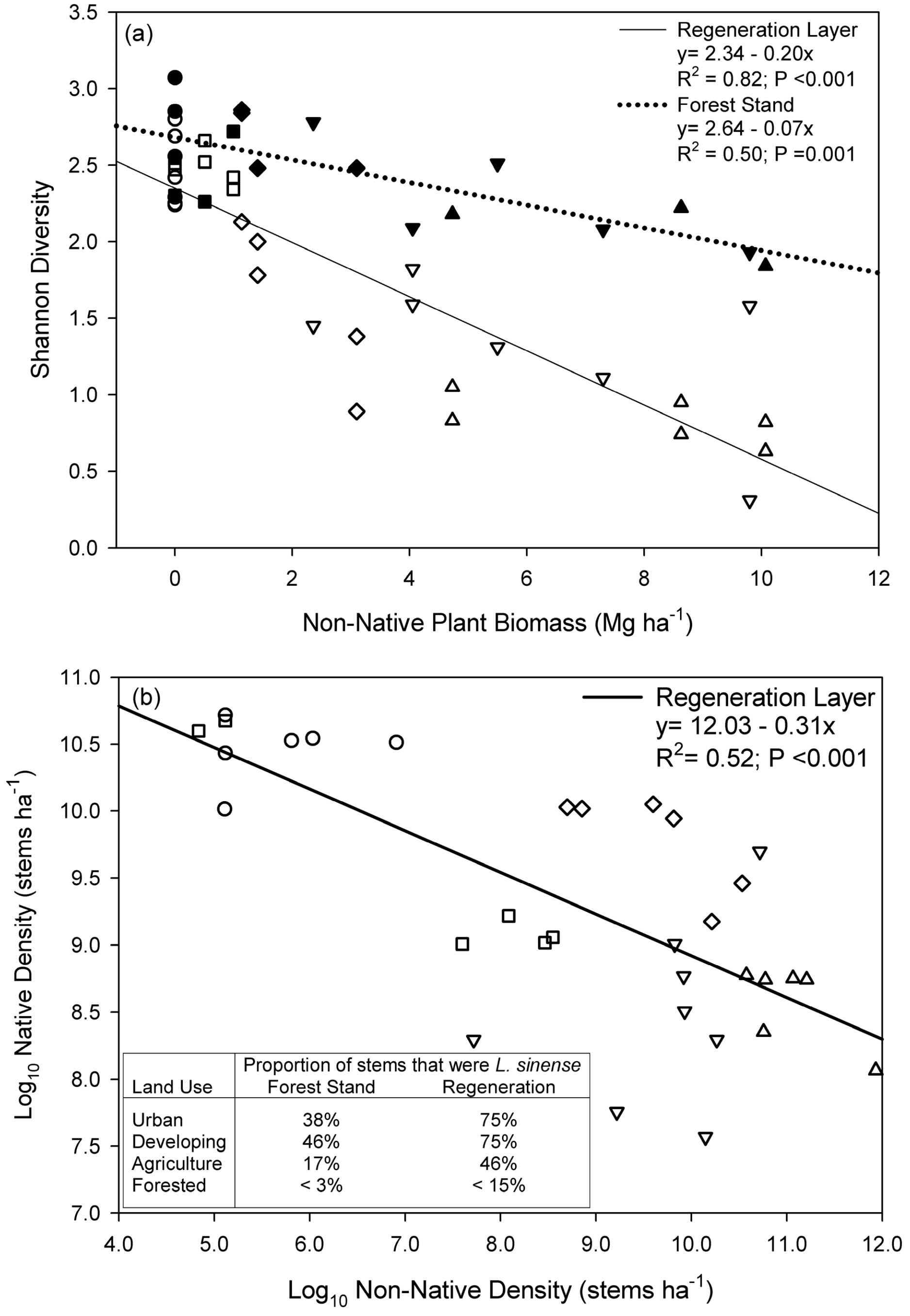


Figure 3: Linear regressions for the relationships between (a) the Shannon diversity index and the biomass of non-native species in the forest stand and regeneration layer, and (b) native stem density and non-native stem density in the regeneration layer. Symbols represent dominant land use type: ● unmanaged forest, ■ managed forest, ♦ agriculture, ▴ developing, and ▾ urban. Closed symbols represent the forest stand and open symbols represent the regeneration layer. Inset lists percent of total stems that were the non-native shrub, *Ligustrum sinense*, by land use type.

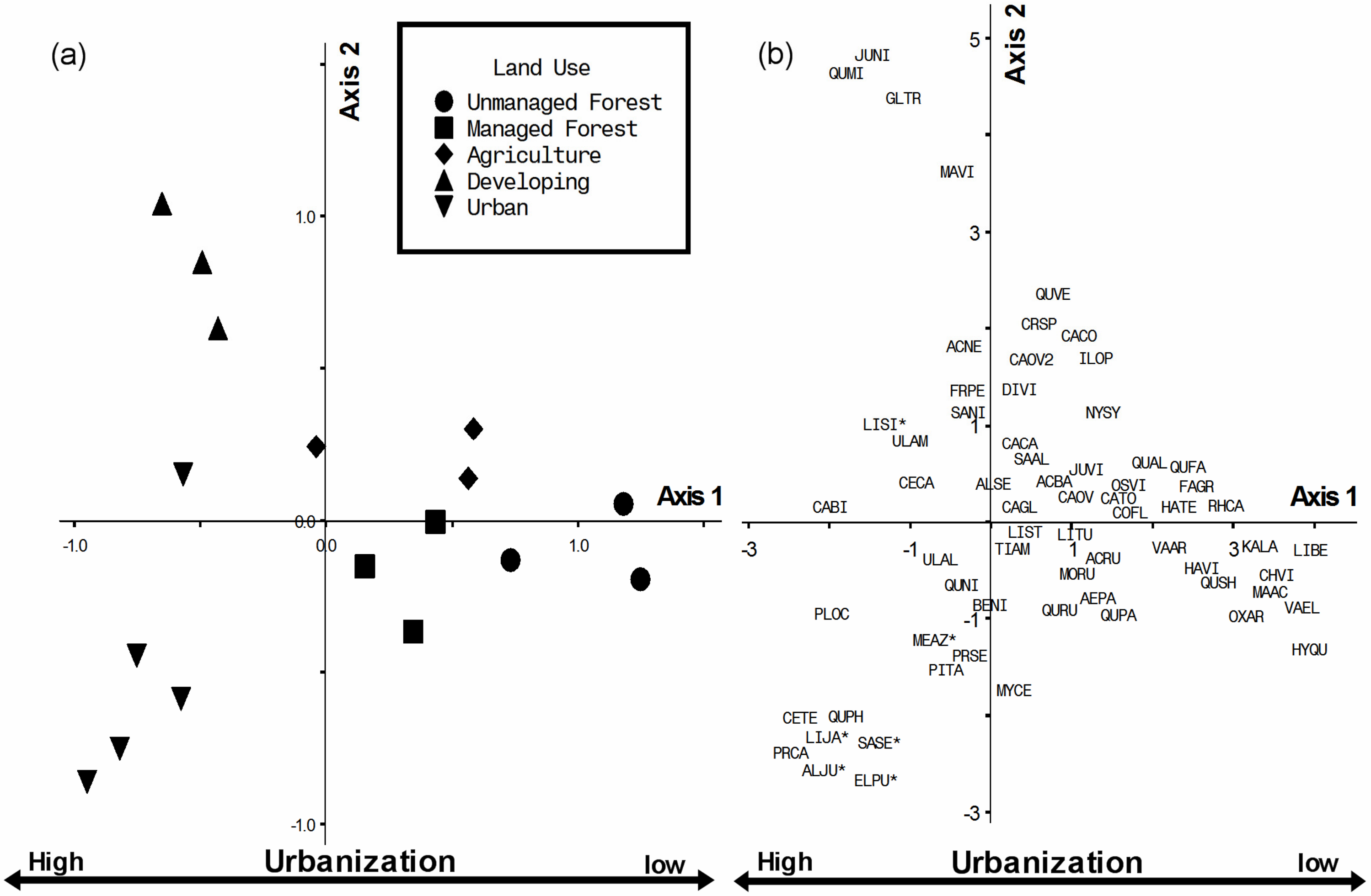


Figure 4: CCA ordination of a) 17 sites and, b) 77 species for the forest stands. Eigenvalues for the first two axes were 0.312 and 0.179, respectively. Sites and species are constrained by land use type. Only species occurring at more than one site are depicted. Non-native species indicated by (*). Species codes are listed in Appendix 1.

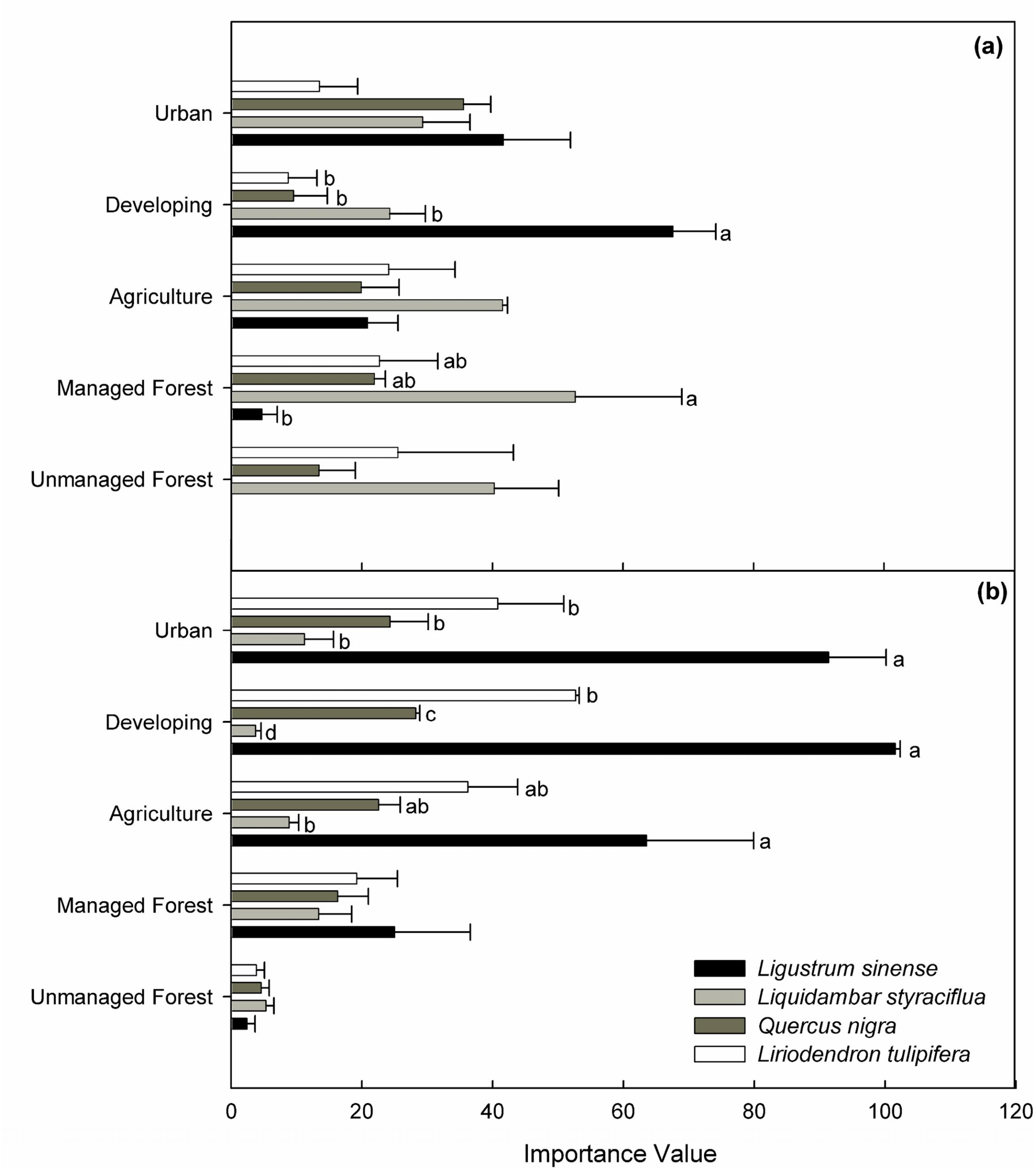


Figure 5: ANOVA of the mean importance value of three common overstory tree species and the non-native invasive shrub, *Ligustrum sinense*, in (a) the forest stand (IV_{300}) and (b) the regeneration layer (IV_{200}) by land use. Different letters indicate significant ($\alpha = 0.05$) differences between species.

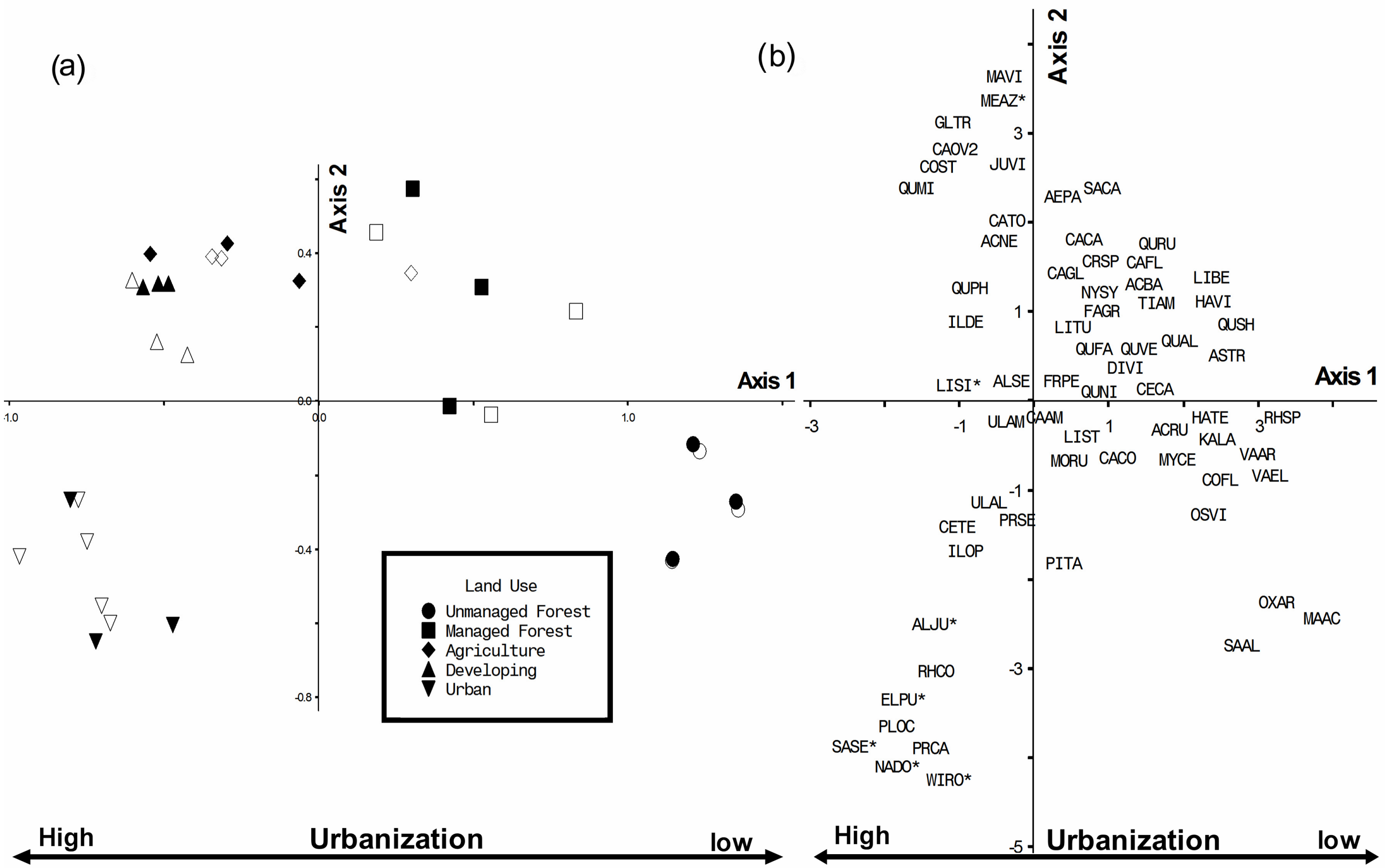


Figure 2: CCA ordination of a) 17 sites and b) 68 species for the regeneration layer pooled across two years. Closed symbols represent 2004 data and open symbols represent 2005 data. Eigenvalues for the first two axes were 0.342 and 0.119, respectively. Sites and species are constrained by land use type. Only species occurring at more than one site are depicted. Non-native species indicated by (*). Species codes are listed in Appendix 1.

Appendix 1: Species sampled across all 17 sites. Non-native species indicated by (*). Note: Plants were identified only to genus if species could not be determined. Nomenclature followed Godfrey (1988).

Species code	***Scientific name***
ACBA	*Acer barbatum* Michx.
ACNE	*Acer negundo* L.
ACRU	*Acer rubrum* L.
AEPA2	*Aesculus parviflora* Walt.
AEPA	*Aesculus pavia* L.
ALJU*	*Albizia julibrissin* Durazz.*
ALSE	*Alnus serrulata* (Ait.) Willd.
ASTR	*Asimina triloba* (L.) Dunal.
BENI	*Betula nigra* L.
CAAM	*Callicarpa americana* L.
CAFL	*Calycanthus floridus* L.
CACA	*Carpinus caroliniana* Walt.
CACO	*Carya cordiformis* (Wang.) K. Koch
CAGL	*Carya glabra* (Mill.) Sweet
CAOV	*Carya ovalis* (Wang.) Sarg.
CAOV2	*Carya ovata* (Mill.) K. Koch
CATO	*Carya tomentosa* (Poir.) Nutt.
CABI	*Catalpa bignonioides* Walt.
CETE	*Celtis tenuifolia* Nutt.
CECA	*Cercis canadensis* L.
CHVI	*Chionanthus virginicus* L.
COFL	*Cornus florida* L.
COST	*Cornus stricta* Lam.
CRSP	*Crataegus* spp.
DIVI	*Diospyros virginiana* L.
ELPU*	*Elaeagnus pungens* Thumb.*
FAGR	*Fagus grandifolia* Ehrh.
FRAM	*Fraxinus americana* L.
FRPE	*Fraxinus pennsylvanica* Marsh.
GLTR	*Gleditsia triacanthos* L.
HATE	*Halesia tetraptera* Ellis.
HAVI	*Hamamelis virginiana* L.
HYQU	*Hydrangea quercifolia* Bartr.
ILDE	*Ilex decidua* Walt.
ILOP	*Ilex opaca* Ait.
JUNI	*Juglans nigra* L.
JUVI	*Juniperus virginiana* L.

Species code	***Scientific name***
KALA	*Kalmia latifolia* L.
LIJA*	*Ligustrum japonica* Thunb.*
LISI*	*Ligustrum sinense* Lour.*
LIBE	*Lindera benzoin* (L.) Blume.
LIST	*Liquidambar styraciflua* L.
LITU	*Liriodendron tulipifera* L.
MAAC	*Magnolia acuminata* L.
MAGR	*Magnolia grandiflora* L.
MAMA	*Magnolia macrophylla* Michx.
MAVI	*Magnolia virginiana* L.
MEAZ*	*Melia azedarach* L.*
MORU	*Morus rubra* L.
MYCE	*Myrica cerifera* L.
NADO*	*Nandina domestica* Thunb.*
NYSY	*Nyssa sylvatica* Marsh.
OSVI	*Ostrya virginiana* (Mill.) K. Koch
OXAR	*Oxydendrum arboreum* (L.) DC.
PITA	*Pinus taeda* L.
PLOC	*Platanus occidentalis* L.
PRCA	*Prunus caroliniana* (Mill.) Ait.
PRSE	*Prunus serotina* Ehrh.
PSSI*	*Pseudocydonia sinensis*(Dum.-Cours.)Schneid*
QUAL	*Quercus alba* L.
QUFA	*Quercus falcata* Michx.
QULY	*Quercus lyrata* Walt.
QUMI	*Quercus michauxii* Nutt.
QUNI	*Quercus nigra* L.
QUPA	*Quercus pagoda* Raf.
QUPH	*Quercus phellos* L.
QURU	*Quercus rubra* L.
QUSH	*Quercus shumardii* Buckl.
QUVE	*Quercus velutina* Lam.
RHCA	*Rhododendron canescens* (Michx.) Sweet.
RHSP	*Rhododendron* sp.
RHCO	*Rhus copallinum* L.
WIRO*	*Rosa* sp.*
SANI	*Salix nigra* L.
SACA	*Sambucus canadensis* L.
SASE*	*Sapium sebiferum* (L.) Roxb.*
SAAL	*Sassafras albidum* (Nutt.) Nees.
TIAM	*Tilia americana* L.

Species code	***Scientific name***
ULAL	*Ulmus alata* Michx.
ULAM	*Ulmus americana* L.
ULRU	*Ulmus rubra* Muhl.
VAAR	*Vaccinium arboreum* Marsh.
VAEL	*Vaccinium elliottii* Champ.
VASP	*Vaccinium* sp.
VIRU	*Viburnum rufidulum* Raf.

CHAPTER IV

RIPARIAN WOODY PLANT TRAITS ACROSS AN URBAN-RURAL LAND USE GRADIENT IN THE GEORGIA PIEDMONT, US

Abstract

Questions: Are riparian woody plant traits related to the surrounding landscape matrix, dominant land use, and hydrologic regime? Are trends in plant traits that are related to urbanization and hydrology also evident in the riparian woody plant regeneration layer?

Location: This study was conducted in the Piedmont physiographic region of the southeastern US near Columbus, Georgia.

Methods: Study sites were characterized using urbanization and hydrologic indices. Data on woody plant species composition were collected from 17 forest communities along headwater streams representing an urban-to-rural land use gradient. Plant species were described by morphological, physiological, and reproductive trait groups. A community × trait matrix was obtained and Detrended Correspondence Analysis (DCA) ordinations were used to identify trends in plant traits. Correlative analyses were used to relate urbanization and hydrologic indices to plant traits.

Results: Ordination analyses indicated that riparian woody plant traits were related to the surrounding landscape matrix, land use, and hydrologic regime. Traits such as leaf evergreeness, fast growth rate, shallow rooting, animal seed dispersal, and shrub plant form were associated with urban communities and flashy stream flow. In general, the regeneration layer and the forest stand showed similar relationships between trait importance and ordination axes. In the regeneration layer, flood tolerance in urban environments showed decreased importance values.

Conclusions: Changes in riparian woody plant traits related to landscape and hydrologic characteristics are occurring and may have significant implications for ecosystem functioning and structure as urbanization continues.

Nomenclature: Godfrey (1988)

Abbreviations: DCA= Detrended Correspondence Analysis; DBH= Diameter at Breast Height

Key Words: DCA ordination, ecosystem function, functional traits, trait matrix, urbanization

Introduction

Worldwide, urbanization and land use change are occurring at extraordinary rates and have been identified as major threats to global environmental quality and our natural resources (Vitousek 1994). Currently in the US, 1.2 million hectares of land are converted to urban land uses annually (Cordell and Macie 2002). The southern states have experienced particularly high rates of urbanization: Georgia ranks second nationwide for the most land developed for urban uses between 1992-1997 (USDA-NRCS 2006b). Often, highly populated cities are surrounded by irregular rings of decreasing exurban development (6-25 homes km^{-2}), which Brown (2005) suggests is the fastest growing land use in the US. Urbanizing landscapes have facilitated the application of the gradient paradigm to the study of urban influences on ecosystems (McDonnell and Pickett 1990).

The structure and composition of the surrounding landscape matrix have been linked to shifts in vegetation diversity, composition, and structure along urban gradients, such as decreased species richness, diversity, and basal area (Guntenspergen and Levenson 1997; Moffatt et al. 2004; Porter et al. 2001). There is evidence that, along urban gradients, abundance of non-native, invasive species in riparian forests greatly affects species composition and structure (Burton et al. 2005; Loewenstein and Loewenstein 2005; Moffatt et al. 2004). Groffman et al. (2003) reported distinct shifts in riparian vegetation composition from wetland species to upland species along a rural to urban gradient and suggested that urbanization may have induced hydrologic drought. Riparian forests have great ecological importance in terms of maintenance of water quality (Malanson 1993), hydrological processes (Tabacchi et al. 2000), and maintaining regional biodiversity. Shifts in diversity and structure may have critical ramifications for the long term ecological integrity of riparian ecosystems.

A plant functional trait approach may offer a more general understanding of the influences and consequences of disturbance associated with land use on riparian vegetation (Rusch et al. 2003). Trait-based analyses have become an increasingly popular approach for comparing and describing plant communities (McIntyre et al. 1999). Describing plant communities by plant traits increases the ability to compare and contrast taxonomically distinct floras and also helps summarize the high biodiversity found in many ecosystems (Diaz et al. 1999). Identifying shifts in dominant plant traits may also allow exploration of the consequences of urbanization on ecosystem processes and functioning (Diaz and Cabido 1997; Diaz and Cabido 2001). For example, species functional traits such as dispersal mechanism, fruit type, pollination vector, and growth form differed between forested and deforested habitats in Costa Rica, suggesting that deforestation may change functional diversity and species assembly rules (Mayfield et al. 2005). Diaz and Cabido (1997) measured plant traits over a steep climatic gradient and discussed how shifts in species traits across the gradient may affect ecosystem processes such as productivity, biomass turnover, nutrient cycling, and water uptake in response to global climate change.

Several studies have examined the influence of land uses, such as logging and grazing, on shifts in plant functional traits and report that dominant plant functional groups change in response to disturbance (Diaz et al. 1992; Diaz et al. 1999; Louault et al. 2005; Peco et al. 2005). Grime (2002) suggests that continuously and severely disturbed systems may be dominated by plants with life history traits such as fast growth rate, short life span, shallow rooting depth, shade intolerance, and evergreen leaf type, and that these may alter ecosystem functioning. Shifts in ecosystem properties are anticipated in urbanizing environments due to increasing anthropogenic alteration and disturbance. For instance, hydrological gradients are often created along urbanization gradients due to stream channeling and effects of storm drainage systems in human dominated environments (Feminella and Walsh 2005; Finkenbine et al. 2000; Schoonover 2005). Groffman et al. (2003) suggested that riparian regeneration is tightly dependent on the hydrology of the adjacent stream. Williams et al. (2005) examined functional traits of grassland species along an urban-rural gradient in Australia and found that dominance of plants with particular combinations of traits increased the probability of local extinction in urban areas. However, application of the trait-based approach to the urban-rural gradient concept in riparian areas has been largely unexplored.

The overall goal of this study was to identify changes in woody riparian plant traits along an urban-rural land use gradient in the Piedmont physiographic region of Georgia. This research addressed two primary questions focusing on nine morphological, physiological, and reproductive plant traits that may serve as indicators of environmental change or may significantly influence ecological processes or function. First, are riparian woody plant traits related to the surrounding landscape matrix, dominant land use, and hydrologic regime? Second, are trends in woody plant traits that are related to urbanization and hydrology also evident in the riparian woody plant regeneration layer? Hypotheses tested include: (1) plant traits characteristic of disturbed environments would be positively associated with urban land use, (2) plant traits such as rooting depth and flood tolerance would be positively related to hydrologic characteristics and, (3) woody regeneration layer plant traits would exhibit relationships with the landscape matrix similar to the forest stand.

Materials and methods

Study area

Columbus, a moderate sized city in the Georgia Piedmont, was the study area for this research. Columbus is rapidly expanding towards the northeast because it is restricted in growth to the west by the Chattahoochee River and to the southeast by a military installation (Fort Benning). The growth pattern of Columbus provided the urban-to-rural land use gradient for ecological study. Seventeen sites were arranged between 32˚30′ N, 84˚54′ W and 32˚52′ N, 84˚00′ W within three counties in a south-to-north alignment representing an urban-to-rural land use gradient. These counties included Muscogee County (Columbus), Harris County, and extreme southern Troup County (Figure 1). A comparison of the population statistics for Muscogee and Harris Counties reveals that Muscogee County had a relatively high population (186,291 people) in 2000, yet a low percent increase (4%) between 1990-2000. Harris County had a much lower population (23,695 people) but has experienced accelerated development (a population increased 33% between 1990 and 2000) well above the national average of 13% (US Census 2000).

The study area ranges in elevation between 100 and 250 m above sea level and consists of gently rolling hills. Soils in the region were transformed during the 17th-19th centuries due to locally severe soil erosion from intensive agricultural practices, mostly from cotton farming (Trimble 1974). Soils are typically Udults with exposed loamy to clayey subsoil. Although the booming timber industry in the 20th century left much of the region denuded, today much of the land has reverted to mixed deciduous forests or has been planted with pines. Oak (*Quercus* spp.), pine (*Pinus* spp.), and hickory (*Carya* spp.) are the predominant taxa of contemporary upland forests (Cowell 1998). Lowland forests also include *Quercus* spp., *Pinus* spp., and *Carya* spp., but *Acer* spp., *Liquidambar styraciflua* L., *Liriodendron tulipifera* L., and *Fraxinus* spp. are also common (Cowell 1998). Piedmont forests also exhibit a distinct mid-story canopy of various small tree species including (but not limited to), *Cornus* spp., *Cercis canadensis* L., and *Oxydendrum arboreum* (L.) DC (Braun 1950).

Landscape classification

This study used the watershed as the fundamental unit in which to study the impacts of urbanization on riparian woody plant traits. The 17 sites were located in watersheds within the Middle Chattahoochee River Basin in West Georgia, arranged along a land use gradient extending northeast of Columbus, GA. The study area is composed of urban and suburban land use around the city of Columbus and a mixture of pasture land, managed pine plantations of *Pinus tadea* L. at various ages of stand development, and unmanaged mixed evergreen-deciduous forests. The 17 study sites were predetermined from water quality/quantity and stream biota studies and were selected based on catchment size (< 2600 ha) and ranges in proportions of developed, forested, and agricultural land uses at a 30 m scale (Lockaby et al. 2005; Schoonover et al. 2005). Dominant land cover for each watershed was assessed using both supervised and unsupervised classification of 1 meter resolution digital March 2003 aerial photo imagery. Percentages of six major cover types (deciduous forest, evergreen forest, grass-pasture, impervious surface, water, and other) were obtained and the following five dominant land use types were determined based on dominant landcover: urban, developing, agriculture, managed forest (pine plantations), and unmanaged forest (mixed evergreen-deciduous forest) (Table 1). Developing sites were forested sites with active or recent development confirmed by ground truthing (Helms et al. 2005; Schoonover et al. 2005). Urban sites were represented by five sites and all other land use types were represented by three sites (Figure 1). Lockaby et al. (2005) provide a description of the image processing steps and classification methods used to assess watershed landcover/land use. In addition, landscape fragmentation and pattern data such as patch density, largest forest patch index, and landscape Shannon diversity, were calculated from the classified imagery using the program FRAGSTATS 3.3 (McGarigal et al. 2002) with the patch neighbor 8-cell rule option (Table 1). Patch density is the total number of patches per 100 hectares within each watershed. As a measure of forest dominance, largest forest (deciduous and evergreen) patch index is the percentage of total landscape area occupied by the largest forest patch. Landscape Shannon diversity is the typical Shannon diversity index applied to the watershed landscape, in this case:

$$\text{Shannon diversity index} = -\sum_{i=1}^{m} (P_i \ln P_i) \tag{1}$$

where P_i = proportion of the landscape occupied by patch type i, and m = number of patch types present in the landscape. Based on the original landscape classification

(Lockaby et al. 2005), five patch types were impervious surface, forest (deciduous or evergreen), grass, water, and other (Table 1). More detailed descriptions of the fragmentation metrics used can be found in McGarigal et al. (2002).

Hydrologic characteristics

Base flow index for the 17 watersheds was obtained from concurrent water quality studies (Crim 2006 unpublished data; Schoonover 2005). Base flow index is the proportion of water contributing to the stream as groundwater versus surface runoff (Σ predicted baseflow/ Σ observed baseflow) (Schoonover et al. 2005). A high base flow index indicates significant streamflow contribution from groundwater (stable hydrographs) whereas watersheds with a low baseflow index are predominantly recharged from surface runoff inputs (flashy flows). In general, base flow index for the 17 watersheds indicated that urban and developing watersheds had a low base flow index relative to the agricultural and forested watersheds (Appendix 1).

Field sampling

The forest stands of 17 riparian sites were sampled during the summer months (June-August) of 2003-2005. Generally, 24 plots were arranged along six transects at each site, although urban sites varied between 7-24 plots because the size of the forest fragments restricted the number of possible plots in some cases. The first transect at each site was located at a pre-determined stream biota and/or hydrologic sampling point. Transects were placed 100 m apart and extended perpendicular to and across each stream. On each 70 m transect, the forest stand was sampled in four 100 m^2

plots, placed 15 m apart with two on either side of the stream. Within each plot all woody stems $\geq$ 2.5 cm were identified to species and the diameter at breast height (DBH) was recorded. The woody plant regeneration layer was sampled at all sites during the summer of 2005 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. The order of community sampling was stratified among land use types to ensure each land use type was sampled at least once during each summer month. Species nomenclature followed Godfrey (1988).

Vegetation and plant trait data

For each riparian community, species importance values were calculated as relative density + relative frequency + relative basal area (IV_{300}) for the forest stand and relative frequency + relative density (IV_{200}) for the regeneration layer. Nine morphological, physiological, and reproductive trait groups were identified for this study. Plant traits that indicate environmental change (hydrology, disturbance regime) or may influence ecosystem processes (nutrient and water cycling) were of particular interest. Each trait group consisted of two to three trait states coded as positive or negative (1 or 0) (Appendix 2) for a total for 24 traits for all woody species found in the both the forest stand and regeneration layer (Table 2). Classifications were based on readily available published data for each species, particularly Burns and Honkala (1990), the PLANTS Database (USDA-NRCS 2006a), Samuelson and Hogan (2006), and Dirr (1998). Appendix 2 contains the trait data for all species and the sources used to score species for each trait. Efforts were made to compare multiple sources when available. Finally, the data were arranged in matrices for the analysis where matrix **W** described the riparian community by species importance value found across the study area and matrix **B** described the presence/absence (1 or 0) of each trait by species.

Data analyses

In order to identify the importance of each trait in each riparian community the community × species matrix was multiplied by the species × trait matrix to obtain a community × trait matrix (i.e. **B'W**). Methods for calculating the community × trait matrix followed that of Diaz and Cabido (1997), Diaz et al. (1999), and Peco et al. (2005). The value in each cell of the community × trait matrix was the sum of importance value of each species that was positive for that trait in each community. There were no transformations of the species importance or trait matrices. Using the program PC-ORD 4.0 (McCune and Mefford 1999) detrended correspondence analysis (DCA) of the community × trait matrices was conducted for the forest stand and regeneration layer to identify gradients in plant traits related to urbanization and hydrology. Default options were selected and rare species were down-weighted in PC-ORD (McCune et al. 2002). Correlation analyses associating DCA axes with urbanization and hydrologic indices were used to relate urbanization and hydrologic gradients to changes in trait importance. Correlation analyses were conducted to identify relationships between trait importance and DCA ordination axes for both the forest stands and regeneration layers.

Results

DCA ordinations indicated that riparian woody plant traits were related to the surrounding landscape matrix, land use, and hydrologic characteristics (Figures 2 and 3). Landscape metrics were significantly correlated with the 1st axis for both the forest stand and regeneration layer ordinations (Table 3). Specifically landscape characteristics associated with urban land use, impervious surfaces and landscape diversity, were negatively correlated with axis 1 for both the forest stand and regeneration layer. In contrast, characteristics associated with rural land use, forest cover and largest forest patch index, were positively correlated with axis 1. Patch density and the percent of the watershed in grass cover were not significantly related to the distribution of riparian communities and plant traits along axis 1 (Table 3). Base flow index was positively correlated with ordination scores along axis 1. The 1st axis for both ordinations appears to represent the underlying cumulative effects of the urban-rural land use gradient on riparian woody plant traits. No landscape metrics were significantly related to the 2nd axis (Table 3).

DCA ordination separated several trends in plant traits along the urban-rural gradient (axis 1) in both the forest stands (Figure 2) and regeneration layers (Figure 3). Evergreen leaf type, fast growth rate, and shallow rooting habit were associated with urban communities (Table 4). Animal seed dispersal, shrub plant form, intermediate shade tolerance, and medium life span were also prevalent in urban communities. Plants traits associated with rural communities were deciduous leaf type, water or gravity seed dispersal, midstory tree form, shade tolerance, slow growth rate, deep rooting habit, and long life span (Table 4). Trends were consistent for both the forest stands and regeneration layers. More correlations between plant traits and axis 1 were detected for the regeneration layer.

Several trends differed between forest layers. Overstory tree form, intermediate flood tolerance, shade intolerance, wind seed dispersal and pollination, medium growth rate, and short life span were not significantly related to axis 1 for the forest stand but were all positively correlated with the 1st axis of the regeneration layer ordination. Animal pollination was strongly and negatively correlated to the 1st axis in the regeneration layer but not in the forest stand. Flood intolerance was positively correlated to axis 1 in the forest stand but was negatively correlated to the 1st axis in the regeneration layer.

Discussion

A trait-based approach was used to examine relationships between plant traits and community structure in riparian forests along an urban-rural gradient to better understand potential consequences of urbanization and land use on ecosystem functioning. Fast growth rates and moderate life spans were prevalent in urban environments while slow growth rates and long life spans where characteristic of rural environments. Diaz et al. (1999) reported predominance of short life spans and fast growth rates for xerophytic woodlands under severe disturbance from logging and grazing land uses. Trends in shade tolerance were consistent with Metzer (2000) who found shade tolerant species were positively correlated with larger forest fragments and suggested that this trait is more sensitive to forest fragmentation than shade intolerance. Forest cover, largest forest patch index, and shade tolerance were all positively correlated with rural riparian communities while landscape diversity, a measure of fragmentation, was characteristic of urban environments where shade tolerance was uncommon. In contrast to Metzer (2000) who found no relationship between shade intolerance and fragmentation, shade intolerance was more prevalent in the regeneration layer of urban riparian communities where fragmentation is probably high. However, intermediate shade tolerance showed a strong positive relationship with urban communities suggesting that disturbance may favor the dominance of intermediate shade tolerant species (Rebertus and Meier 2001).

Urban and agricultural landscapes have been characterized by traits that result in low dispersability (Verheyen et al. 2003). Wind and gravity dispersed traits were more prevalent in rural riparian communities in the study area. Wind and gravity dispersal is generally less efficient than animal dispersal because transport distances are usually less and therefore finding suitable habitat for survival may be reduced (Van der Pijl 1982). Farwig et al. (2006) reported the number of animal dispersed seeds of *Prunus africana* was highest in fragmented and disturbed forests and suggested that animal dispersal may be more effective in fragmented and disturbed environments. In general, animal dispersal distances are greatest and may increase the probability of finding suitable habitat. In contrast, Williams et al. (2005) documented increased extinction risk of wind-dispersed grassland species in urban areas because colonization capacity was severely reduced in fragmented habitats. However, Metzer (2000) found that all dispersal types were influenced by the landscape matrix in Brazilian tropical forests but at different spatial scales. While animal pollination and dispersal may be more efficient vectors in urban environments, extinction risk may be high because the structure of urban environments may negatively affect landscape connectivity for many bird, insect, and small mammal species (Blair and Launer 1997; Cockle and Richardson 2003; Rottenborn 1999; Stratford and Robinson 2005; Williams et al. 2005). Mayfield et al. (2006) suggested animal-mediated dispersal plays a major role in community assembly in human-altered landscapes illustrating the importance of human landscape alteration on plant-animal interactions.

Urban environments exhibited increasing importance of the evergreen leaf type. Prevalence of leaf evergreeness and leaf longevity has been linked to lower photosynthesis rates, lower nutrient loss rates, and slower rates of decomposition in nutrient poor environments (Aerts 1995). Lamb and Mallik (2003) found that evergreeness increased in prevalence along a riparian zone-forest ecotone and suggested that this trait may provide an advantage in the drier upland forest environment. Previous research in this study area indicated that species composition and structure in urban and developing land use types were significantly influenced by the non-native, evergreen invasive shrub, *Ligustrum sinense* Lour. (Burton et al. 2005). Non-native invasive plants can significantly affect ecosystem structure and influence ecological functioning (Ashton et al. 2005; Lecerf et al. 2005). Plant traits associated with *Ligustrum sinense*, such as evergreen leaf type, shrub plant form, and shallow rooting were greatly increased in invaded communities.

Riparian vegetation and species functional traits are tightly connected to stream hydrology (Grime 2001; Groffman et al. 2003). Walsh et al. (2005) described the “urban stream syndrome” and suggested that urban riparian zones may exhibit reduced water and nutrient infiltration because natural terrestrial pathways are often bypassed due to stormwater drainage networks. Data collected from this study area indicated a decrease in baseflow and an increase in overland flow in urban and developing areas (i.e. low base flow index) (Schoonover 2005) suggesting urban sites may be drier and experience more physical disturbance from overland flow than the rural sites (Groffman et al. 2003). Base flow index was significantly related to axis 1 of the DCA ordinations showing a hydrologic gradient co-occured with the urbanization gradient. Allan (2004) suggested that co-varying natural and human induced gradients are common in urban ecosystems. Fast growth rate was prevalent in the urban sites perhaps in response to increased disturbance from overland flow. Flood tolerance showed an interesting pattern in the urban sites. Flood tolerance was prevalent in the forest stand but the regeneration layer show increased importance of flood intolerance. These results are consistent with Groffman et al. (2003) who reported shifts to upland, flood intolerant species in urban riparian areas as a result of an induced hydrologic drought. A potential consequence of flood intolerance in the regeneration layer combined with increasing importance of evergreeness in urban riparian areas is drier and nutrient deficient soils or decreased nutrient uptake.

Conclusions

This work provides more specific information about potential changes in ecological function across the urban gradient by demonstrating that differences in riparian woody plant traits are related to landscape and hydrologic characteristics. Specifically, differences in leaf type, plant form, flood and shade tolerance, seed dispersal, pollination, growth rate, rooting characteristics, and life span were found and these may have implications for ecosystem function and structure as urbanization continues. Examination of the regeneration layer provided insights into the potential influence of current landscape conditions on future riparian vegetation traits. Most notably, flood tolerance was strongly reduced in the regeneration layer in urban riparian areas suggesting a potential shift in hydrologic function. Whether all plant species or just a few representatives of each functional type are critical to maintain functional ecosystems is highly debated in the literature but species functional traits can strongly influence ecosystem properties (Hopper et al. 2005). Identifying functional trait patterns can be useful for understanding the conservation potential of disturbed landscapes (Mayfield et al. 2006). Results from this study provide important information about changes in functional traits that may affect ecosystem function and services in the region and suggest how functional traits may be similarly influenced around the world as urbanization continues.

Acknowledgements

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Table 1: Mean (± S.E.) landscape metrics based on 1 meter resolution digital aerial photo imagery for each land use type. n=number of sites in each land use type.

Landscape Metric	Urban (n=5)	Developing (n=3)	Agriculture (n=3)	Managed Forest (n=3)	Unmanaged Forest (n=3)
<u>Patch Type (% cover)</u>					
Impervious surfaces	27.45 ± 4.64	2.83 ± 0.50	2.69 ± 0.48	1.71 ± 0.43	1.55 ± 0.19
Evergreen forest	28.34 ± 1.92	39.03 ± 1.12	30.15 ± 6.91	45.10 ± 1.58	45.99 ± 2.22
Deciduous forest	14.96 ± 3.55	31.04 ± 4.14	24.90 ± 5.49	26.83 ± 1.10	32.76 ± 2.55
Total forest[†]	39.91 ± 2.17	70.07 ± 3.09	55.05 ± 1.95	71.84 ± 2.25	78.76 ± 1.43
Grass	25.40 ± 3.89	22.62 ± 2.51	38.85 ± 2.57	18.97 ± 1.23	15.47 ± 1.65
Water	1.29 ± 0.34	1.30 ± 0.34	2.13 ± 1.02	0.81 ± 0.12	0.41 ± 0.24
Other	3.90 ± 1.40	3.18 ± 0.22	1.29 ± 0.29	6.66 ± 2.91	3.81 ±0.02
<u>Fragmentation Metric</u>					
Patch density $100ha^{-1}$ [††]	6.97 ± 0.86	19.28 ± 7.52	7.22 ± 0.27	10.74 ± 0.49	9.39 ± 0.23
Landscape Shannon diversity	1.21 ± 0.02	0.82 ± 0.06	0.92 ± 0.06	0.76 ± 0.03	0.65 ± 0.02
Largest forest patch index	6.12 ± 2.84	50.01 ± 9.03	25.21 ± 7.49	62.10 ± 3.15	61.75 ± 3.07

[†] Total forest = evergreen forest and deciduous forest combined.
[††] Patch density reported in thousands.

Table 2: Nine trait groups and 24 trait states used in the trait matrix with descriptions used to score woody plant species.

Trait Group	Trait States	Trait Description
Leaf Type	Deciduous	Maintain photosynthetic leaves for only one growing season
	Evergreen	Retention of photosynthetic leaves for more than one growing season (Chabot and Hicks 1982)
Plant Form	Shrub	Multiple stemmed woody plant usually < 4m tall with erect, spreading, or prostrate stems
	Midstory tree	Usually single stemmed woody plant that at maturity is < 6 m tall
	Overstory tree	Single stemmed woody plant that at maturity is > 6 m tall (Hardin et al. 1996)
Shade Tolerance	Tolerant Intermediate Intolerant	The shade tolerance relative to other species (USDA-NRCS 2006a)
Flood Tolerance	Tolerant	Species that are able to survive saturated or flooded soils for several months during the growing season
	Intermediate	Species that are able to survive saturated or flooded soils for short periods of a few days to a few weeks
	Intolerant	Species that are not able to survive even short periods of soil saturation or flooding (Clark and Benforado 1980)
Seed Dispersal	Wind	Diaspores with structures that assist with wind dispersal such as wings or hairlike pappus
	Water/Gravity	Diaspores that can float or have no apparent dispersal mechanism (includes gravity dispersed seeds)
	Animal	Diaspores usually are attractive, edible, or have adhesive mechanisms carried by animal (Van der Pijl 1982)
Pollination	Wind	Perianth highly reduced, absent or deciduous with unobstructed stigmas, color and scent are insignificant
	Animal	Perianth is attractive by conspicuous smell, color or configuration, pollen sticky, anthesis synchronized with activity of pollinator (includes hummingbirds) (Faegri and Van der Pijl 1966)
Growth Rate	Slow Medium Fast	The growth rate relative to other species (USDA-NRCS 2006a)
Rooting	Shallow	Rooting depth < 60 cm
	Deep	Rooting depth ≥ 60 cm
Life Span	Short Medium Long	The life span relative to other species (USDA-NRCS 2006a)

Table 3: Pearson correlation coefficients between landscape metrics and the first two axes of the DCA ordination of the riparian community × traits matrices. NS= P > 0.05; *= P ≤ 0.05; **= P < 0.01; ***= P < 0.001

	Forest Stand				Regeneration Layer			
Landscape Metric	AXIS 1		AXIS 2		AXIS 1		AXIS 2	
Impervious surface (%)	-0.71	**	-0.30	NS	-0.57	*	0.37	NS
Forest (%)	0.68	**	0.38	NS	0.65	**	-0.17	NS
Grass (%)	-0.22	NS	-0.25	NS	-0.32	NS	-0.33	NS
Patch density	-0.13	NS	0.48	NS	-0.11	NS	-0.01	NS
Landscape diversity	-0.78	***	-0.28	NS	-0.71	***	0.25	NS
Largest forest patch	0.61	*	0.20	NS	0.63	**	-0.18	NS
Base flow index	0.66	**	-0.47	NS	0.57	*	-0.42	NS

Table 4: Pearson correlation coefficients between the 24 plant traits and the first two DCA axes of the riparian community × traits matrices. NS= $P > 0.05$; * $P \leq 0.05$; ** $P < 0.01$; *** $P < 0.001$

		Forest Stand				Regeneration Layer			
Trait Group	Trait State	AXIS 1		AXIS 2		AXIS 1		AXIS 2	
Leaf Type	Evergreen	-0.84	***	0.04	NS	-0.99	***	0.16	NS
	Deciduous	0.84	***	-0.04	NS	0.99	***	-0.11	NS
Plant Form	Shrub	-0.74	***	0.41	NS	-0.98	***	-0.12	NS
	Midstory tree	0.66	**	0.67	**	0.75	***	-0.35	NS
	Overstory tree	0.10	NS	-0.92	***	0.84	***	0.31	NS
Shade Tolerance	Tolerant	0.77	***	0.41	NS	0.92	***	0.04	NS
	Intermediate	-0.72	***	0.31	NS	-0.99	***	-0.08	NS
	Intolerant	-0.25	NS	-0.83	***	-0.51	*	0.01	NS
Flood Tolerance	Tolerant	-0.46	*	-0.61	*	0.55	*	0.63	*
	Intermediate	0.20	NS	0.43	NS	0.68	***	-0.30	NS
	Intolerant	0.61	**	0.02	NS	-0.86	***	-0.25	NS
Seed Dispersal	Wind	0.17	NS	0.17	NS	0.80	***	0.32	NS
	Water/gravity	0.57	*	-0.41	NS	0.52	*	0.24	NS
	Animal	-0.49	*	0.13	NS	-0.89	***	-0.28	NS
Pollination	Wind	-0.03	NS	-0.25	NS	0.93	***	-0.10	NS
	Animal	0.03	NS	0.25	NS	-0.96	***	0.03	NS
Growth Rate	Slow	0.81	***	0.15	NS	0.81	***	-0.33	NS
	Medium	0.34	NS	0.71	*	0.77	***	-0.27	NS
	Fast	-0.80	***	-0.54	*	-0.91	***	0.39	NS
Rooting	Shallow	-0.90	***	-0.06	NS	-0.90	***	0.32	NS
	Deep	0.89	***	0.06	NS	0.91	***	0.27	NS
Life Span	Short	0.17	NS	0.31	NS	0.71	***	0.25	NS
	Medium	-0.78	***	0.22	NS	-0.92	***	-0.11	NS
	Long	0.69	***	-0.43	NS	0.80	***	0.00	NS

Study Site	Code	Area (ha)	Land Use Type
Blanton Creek	BLC	329.50	Unmanaged Forest
Clines Branch	CB	897.03	Unmanaged Forest
Mulberry Creek	MU3	1044.05	Unmanaged Forest
House Creek	HC1	655.32	Managed Forest
Mulberry Creek	MU2	606.07	Managed Forest
Sand Creek	SC	896.41	Managed Forest
Flat Shoals Creek	FS2	1448.95	Agriculture
House Creek	HC2	1394.86	Agriculture
Mulberry Creek	MU1	1178.05	Agriculture
Standing Boy Creek	SB1	2009.19	Developing
Standing Boy Creek	SB2	633.97	Developing
Standing Boy Creek	SB4	2658.89	Developing
Bull Creek	BU1	2546.70	Urban
Bull Creek	BU2	2469.24	Urban
Roaring Creek	RC1	366.92	Urban
Roaring Creek	RC2	471.85	Urban
Flat Rock Creek	FR	2397.59	Urban

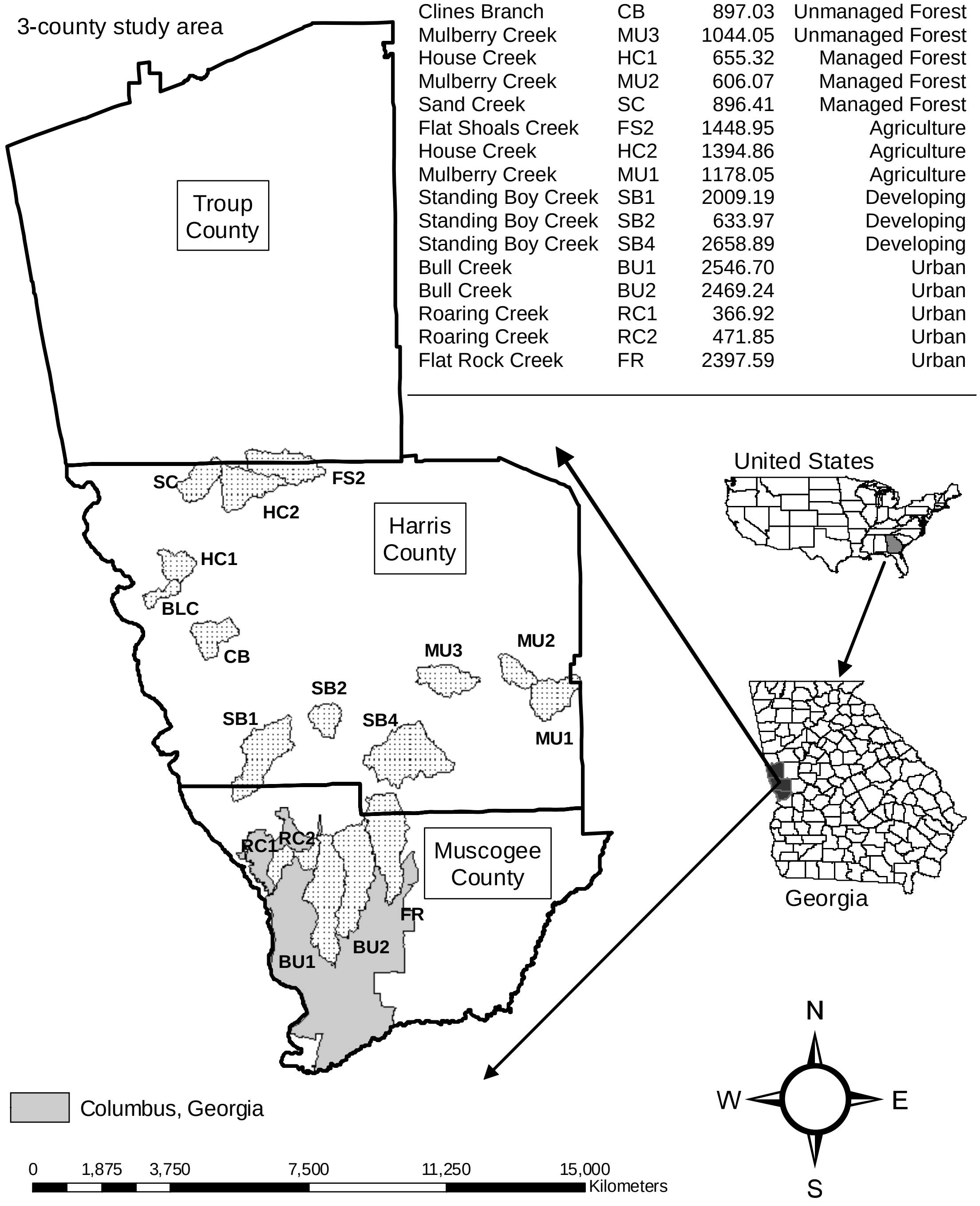

Figure 1: Location of study area and 17 study watershed sites within the Middle Chattahoochee River Basin for Muscogee, Harris, and Troup Counties, Georgia.

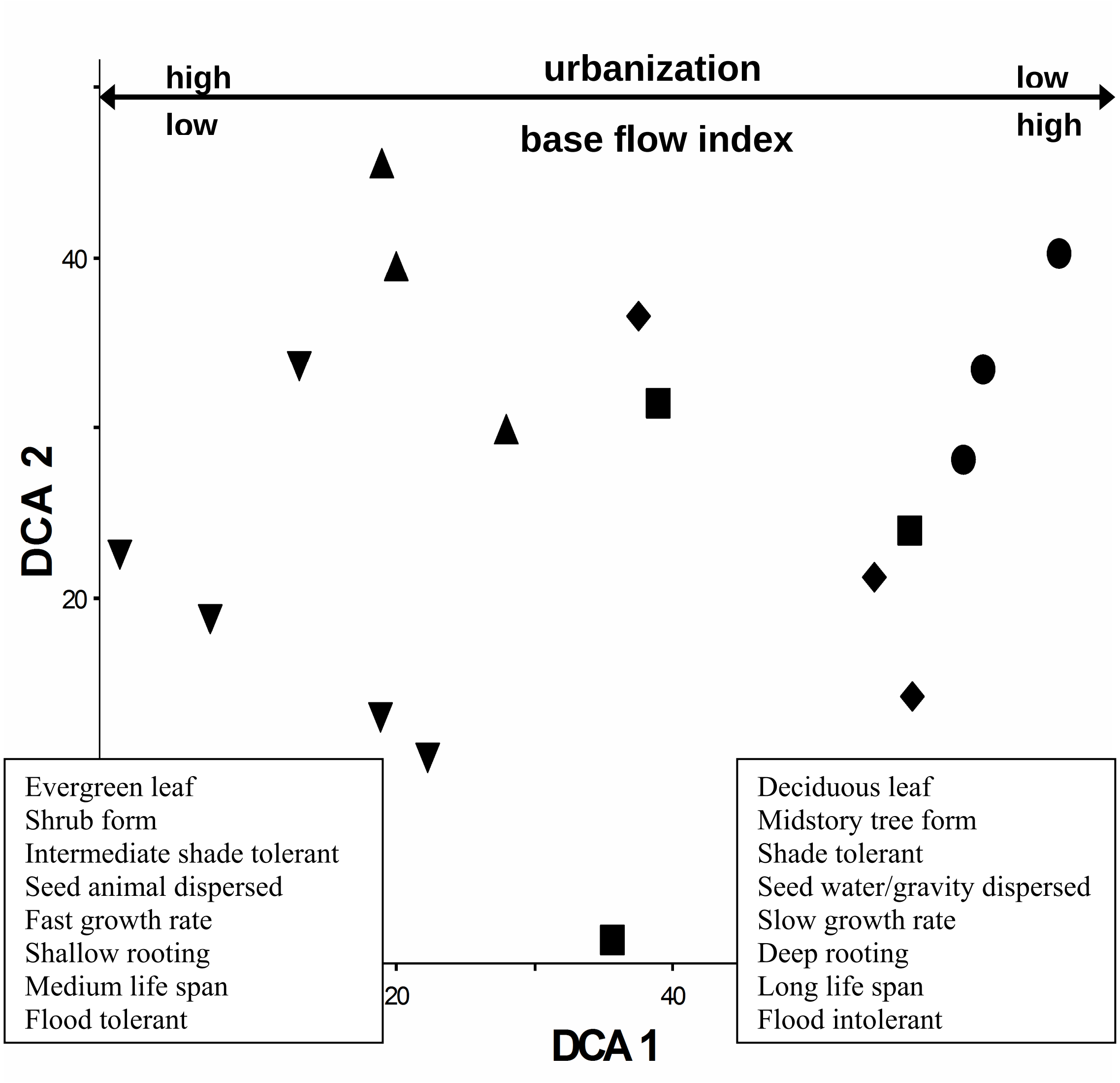

Figure 2: DCA ordination of the riparian community × trait matrix for the forest stand. Plant traits correlated with axis 1 are displayed in boxes (see Table 4). Symbols represent dominant land use types of each stand: ● unmanaged forest, ■ managed forest, ♦ agriculture, ▲ developing, and ▼ urban.

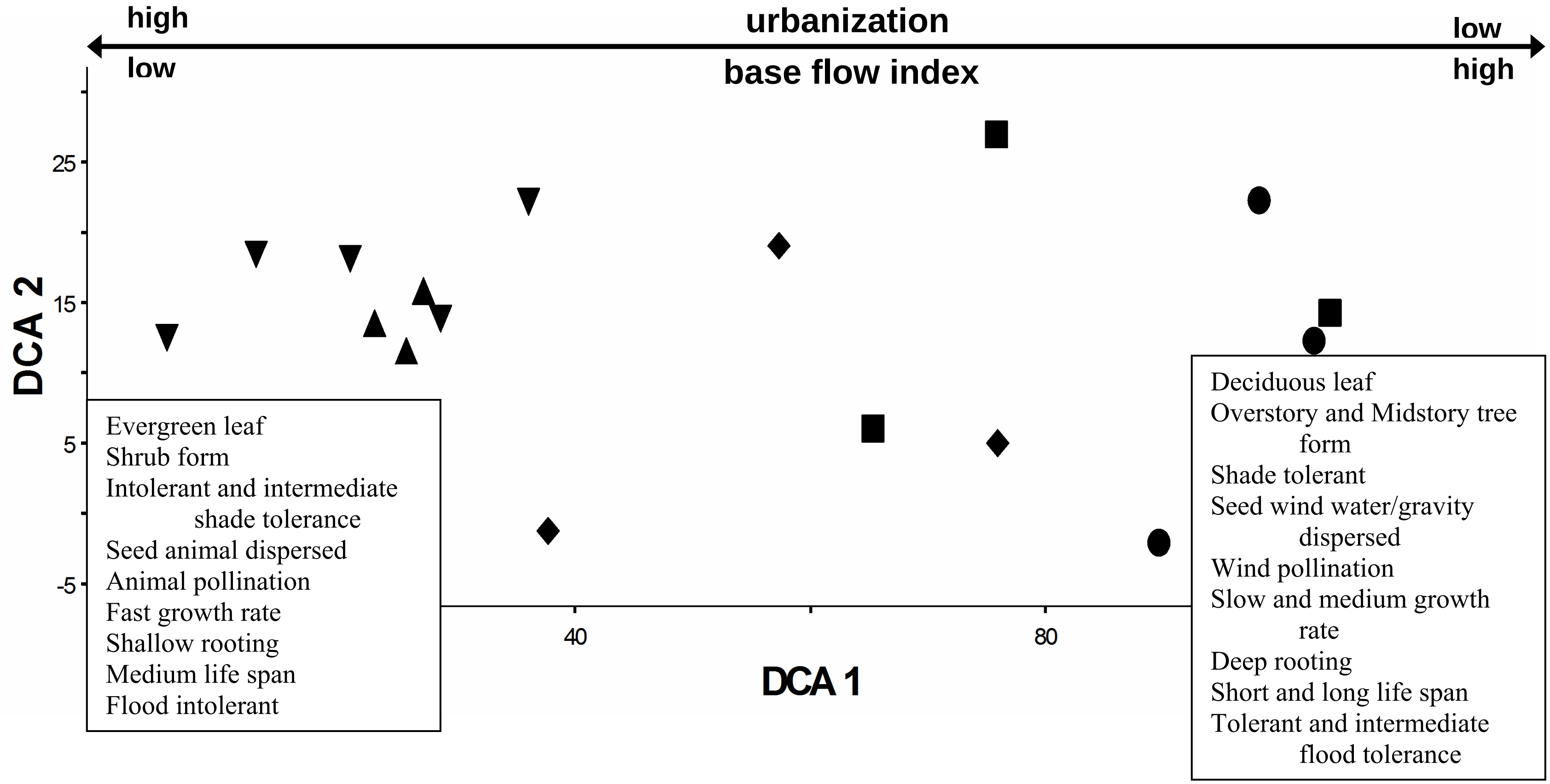

Figure 3: DCA ordination of the riparian community × trait matrix for the regeneration layer. Plant traits correlated with axis 1 are displayed in boxes (see Table 4). Symbols represent dominant land use types of each stand: ● unmanaged forest, ■ managed forest, ♦ agriculture, ▲ developing, and ▼ urban.

Appendix 1: Base flow index for the 17 watersheds

Site	Land use type	Base flow index[†]
BLC	Unmanaged forest	0.65
CB	Unmanaged forest	0.42
MU3	Unmanaged forest	0.21
HC1	Managed forest	0.55
MU2	Managed forest	0.21
SC	Managed forest	0.49
FS2	Agriculture	0.82
HC2	Agriculture	0.81
MU1	Agriculture	0.28
SB1	Developing	0.13
SB2	Developing	0.13
SB4	Developing	0.10
BU1	Urban	0.32
BU2	Urban	0.03
RC1	Urban	0.13
RC2[‡]	Urban	-----
FR[‡]	Urban	0.45

Base flow data obtained from Schoonover (2005) unless otherwise noted.
[‡] Data source (Crim 2006 unpublished data)

Appendix 2: Plant trait data for Piedmont woody riparian forest species.

Scientific name	**Leaf Type**	**Plant Form**	**Shade Tolerance**	**Flood Tolerance**	**Moisture Requirement**	**Seed Dispersal†**	**Pollination†**	**Growth Rate**	**Rooting Habit**	**Lifespan**	**References**
Acer barbatum Michx.	Deciduous	Midstory	Tolerant	Intermediate	Intermediate	Wind	Wind	Medium	Shallow	Medium	1-3
Acer negundo L.	Deciduous	Overstory	Intolerant	Tolerant	Wet or Dry	Wind	Wind	Fast	Shallow	Short	1-4
Acer rubrum L.	Deciduous	Overstory	Tolerant	Tolerant	Wet or Dry	Wind	Wind	Fast	Shallow	Short	1-3, 5, 6
Aesculus parviflora Walt.	Deciduous	Shrub	Tolerant	Intermediate	Moist	Water/ gravity	Animal	Medium	Shallow	Long	1
Aesculus pavia L.	Deciduous	Shrub	Tolerant	Intermediate	Moist	Water/ gravity	Animal	Medium	Shallow	Long	1
Albizia julibrissin Durazz. *	Deciduous	Overstory	Intolerant	Intolerant	Wet or Dry	Wind	Wind	Fast	Shallow	Medium	1
Alnus serrulata (Ait.) Willd.	Deciduous	Shrub	Intolerant	Tolerant	Wet	Water/ gravity	Wind	Medium	Shallow	Medium	1
Asimina triloba (L.) Dunal.	Deciduous	Shrub	Tolerant	Intolerant	Intermediate	Animal	Animal	Slow	Shallow	Short	1, 3, 5
Betula nigra L.	Deciduous	Overstory	Intolerant	Tolerant	Wet	Wind	Wind	Fast	Shallow	Medium	1-3, 7
Callicarpa americana L.	Deciduous	Shrub	Intermediate	Intermediate	Intermediate	Animal	Animal	Medium	Shallow	Medium	1
Calycanthus floridus L.	Deciduous	Shrub	Tolerant	Intermediate	Intermediate	Water/ gravity	Animal	Medium	Deep	Medium	1, 8
Carpinus caroliniana Walt.	Deciduous	Midstory	Tolerant	Intermediate	Intermediate	Animal	Wind	Slow	Deep	Medium	1-3, 6
Carya cordiformis Wang.	Deciduous	Overstory	Intolerant	Tolerant	Wet	Water/ gravity	Wind	Slow	Deep	Medium	1, 2
Carya glabra (Mill.) Sweet	Deciduous	Overstory	Intolerant	Intolerant	Dry	Water/ gravity	Wind	Slow	Deep	Medium	1, 2
Carya ovalis (Wang.) Sarg.	Deciduous	Overstory	Intolerant	Intolerant	Dry	Water/ gravity	Wind	Slow	Deep	Medium	1, 2
Carya ovata (Mill.) K. Koch	Deciduous	Overstory	Intermediate	intolerant	Intermediate	Water/ gravity	Wind	Slow	Deep	Long	1, 2
Carya tomentosa (Poir.) Nutt.	Deciduous	Overstory	Intermediate	Intolerant	Wet or Dry	Water/ gravity	Wind	Slow	Deep	Long	1, 2
Catalpa bignonioides Walt.	Deciduous	Overstory	Intolerant	Tolerant	Wet	Water/ gravity	Animal	Fast	Shallow	Long	1, 4

Scientific name	**Leaf Type**	**Plant Form**	**Shade Tolerance**	**Flood Tolerance**	**Moisture Requirement**	**Seed Dispersal†**	**Pollination†**	**Growth Rate**	**Rooting Habit**	**Lifespan**	**References**
Celtis tenuifolia Nutt.	Deciduous	Midstory	Tolerant	Intermediate	Intermediate	Animal	Wind	Medium	Shallow	Medium	1, 4, 9
Cercis canadensis L.	Deciduous	Midstory	Tolerant	Intolerant	Intermediate	Animal	Animal	Fast	Shallow	Short	1, 2, 8
Chionanthus virginicus L.	Deciduous	Midstory	Tolerant	Intermediate	Intermediate	Animal	Animal	Slow	Deep	Short	1, 8
Cornus florida L.	Deciduous	Midstory	Tolerant	Intolerant	Intermediate	Animal	Animal	Medium	Shallow	Short	1-3, 8, 10
Cornus stricta Lam.	Deciduous	Shrub	Tolerant	Intermediate	Wet	Animal	Animal	Medium	Shallow	Medium	1, 8
Crataegus spp.	Deciduous	Midstory	Tolerant	Intolerant	Intermediate	Animal	Animal	Slow	Shallow	Medium	1, 8
Diospyros virginiana L.	Deciduous	Overstory	Tolerant	Tolerant	Wet or dry	Animal	Wind	Slow	Deep	Long	1-3, 8
Elaeagnus pungens Thumb.*	Evergreen	Shrub	Intolerant	Tolerant	Wet	Animal	Animal	Fast	Shallow	Short	1, 8
Fagus grandifolia Ehrh.	Deciduous	Overstory	Tolerant	Intolerant	Wet	Water/ gravity	Wind	Slow	Shallow	Long	1-3, 6, 8
Fraxinus americana L.	Deciduous	Overstory	Intolerant	Tolerant	Wet	Wind	Wind	Medium	Deep	Medium	1, 2, 8
Fraxinus pennsylvanica Marsh.	Deciduous	Overstory	Intolerant	Tolerant	Wet	Wind	Wind	Medium	Deep	Short	1-5, 8
Gleditsia triacanthos L.	Deciduous	Overstory	Intolerant	Tolerant	Wet	Animal	Wind	Fast	Shallow	Medium	1-4, 8
Halesia tetraptera Ellis.	Deciduous	Midstory	Tolerant	Intolerant	Intermediate	Water/ gravity	Animal	Slow	Deep	Medium	1, 4, 8
Hamamelis virginiana L.	Deciduous	Shrub	Tolerant	Intolerant	Intermediate	Wind	Wind	Slow	Deep	Long	1, 4, 8
Hydrangea quercifolia Barr.	Deciduous	Shrub	Tolerant	Intolerant	Intermediate	Wind	Animal	Medium	Shallow	Medium	1, 8
Ilex decidua Walt.	Deciduous	Shrub	Tolerant	Intermediate	Intermediate	Animal	Animal	Fast	Deep	Medium	1, 3, 8
Ilex opaca Ait.	Evergreen	Midstory	Tolerant	Intermediate	Intermediate	Animal	Animal	Slow	Deep	Medium	1-3, 6, 8
Juglans nigra L.	Deciduous	Overstory	Intolerant	Intermediate	Wet	Water/ gravity	Wind	Slow	Deep	Medium	1-4, 8
Juniperus virginiana L.	Evergreen	Midstory	Intolerant	Intermediate	Intermediate	Animal	Wind	Slow	Deep	Medium	1, 4, 10

Scientific name	**Leaf Type**	**Plant Form**	**Shade Tolerance**	**Flood Tolerance**	**Moisture Requirement**	**Seed Dispersal†**	**Pollination†**	**Growth Rate**	**Rooting Habit**	**Lifespan**	**References**
Kalmia latifolia L.	Evergreen	Shrub	Tolerant	Intermediate	Wet	Wind	Animal	Slow	Deep	Long	1, 8
Ligustrum japonica Thumb.*	Evergreen	Shrub	Tolerant	Intermediate	Intermediate	Animal	Animal	Fast	Shallow	Medium	1
Ligustrum sinense Lour.*	Evergreen	Shrub	Intermediate	Intermediate	Intermediate	Animal	Animal	Fast	Shallow	Medium	1, 2, 11
Lindera benzoin (L.) Blume.	Deciduous	Shrub	Tolerant	Intermediate	Wet	Animal	Animal	Slow	Deep	Long	1, 8
Liquidambar styraciflua L.	Deciduous	Overstory	Intolerant	Tolerant	Wet and Dry	Water/ gravity	Wind	Fast	Deep	Long	1-3, 5, 6
Liriodendron tulipifera L.	Deciduous	Overstory	Intolerant	Intolerant	Intermediate	Wind	Animal	Fast	Deep	Medium	1-3
Magnolia acuminata L.	Deciduous	Overstory	Intermediate	Intolerant	Intermediate	Animal	Animal	Fast	Deep	Medium	1, 2, 8
Magnolia grandiflora L.	Evergreen	Overstory	Tolerant	Intolerant	Intermediate	Animal	Animal	Fast	Deep	Long	1, 2, 6, 8
Magnolia macrophylla Michx.	Deciduous	Overstory	Intermediate	Intolerant	Intermediate	Animal	Animal	Fast	Deep	Medium	1, 8
Magnolia virginiana L.	Evergreen	Overstory	Intermediate	Tolerant	Wet	Animal	Animal	Medium	Deep	Medium	1-3, 8
Melia azedarach L.*	Deciduous	Overstory	Intolerant	Intermediate	Intermediate	Animal	Animal	Fast	Deep	Medium	1, 8
Morus rubra L.	Deciduous	Overstory	Tolerant	Intolerant	Intermediate	Animal	Wind	Medium	Shallow	Medium	1-3, 8
Myrica cerifera L.	Evergreen	Shrub	Intermediate	Tolerant	Intermediate	Animal	Wind	Medium	Shallow	Long	1, 2
Nandina domestica Thunb.*	Evergreen	Shrub	Intermediate	Intolerant	Intermediate	Animal	Wind	Fast	Deep	Long	1, 8
Nyssa sylvatica Marsh.	Deciduous	Overstory	Tolerant	Tolerant	Wet or Dry	Animal	Animal	Medium	Deep	Medium	1-3
Ostrya virginiana (Mill.) K. Koch	Deciduous	Midstory	Tolerant	Intolerant	Wet or Dry	Wind	Wind	Medium	Deep	Short	1-3, 8
Oxydendrum arboreum (L.) DC.	Deciduous	Midstory	Tolerant	Intolerant	Wet or Dry	Wind	Animal	Medium	Deep	Medium	1, 2, 8
Pinus taeda L.	Evergreen	Overstory	Intolerant	Intermediate	Intermediate	Wind	Wind	Fast	Shallow	Medium	1-3, 10

Scientific name	**Leaf Type**	**Plant Form**	**Shade Tolerance**	**Flood Tolerance**	**Moisture Requirement**	**Seed Dispersal†**	**Pollination†**	**Growth Rate**	**Rooting Habit**	**Lifespan**	**References**
Platanus occidentalis L.	Deciduous	Overstory	Intolerant	Tolerant	Wet	Water/ gravity	Wind	Medium	Deep	Long	1-3
Prunus caroliniana (Mill.) Ait.	Evergreen	Midstory	Tolerant	Intolerant	Intermediate	Animal	Animal	Fast	Shallow	Short	1, 8, 12
Prunus serotina Ehrh.	Deciduous	Overstory	Intolerant	Intolerant	Intermediate	Animal	Animal	Fast	Deep	Medium	1-3, 8, 12
Pseudocydonia sinensis (Dum.-Cours.)Schneid*	Deciduous	Shrub	Intolerant	Intermediate	Intermediate	Water/ gravity	Wind	Slow	Shallow	Medium	8
Quercus alba L.	Deciduous	Overstory	Intermediate	Intolerant	Intermediate	Animal	Wind	Slow	Deep	Long	1-4, 6, 10
Quercus falcata Michx.	Deciduous	Overstory	Intermediate	Intolerant	Dry	Animal	Wind	Medium	Deep	Long	1-3
Quercus lyrata Walt.	Deciduous	Overstory	Intermediate	Tolerant	Wet	Animal	Wind	Slow	Shallow	Long	1-33
Quercus michauxii Nutt.	Deciduous	Overstory	Intolerant	Intermediate	Wet	Animal	Wind	Medium	Deep	Medium	1-4, 10
Quercus nigra L.	Deciduous	Overstory	Intolerant	Tolerant	Wet or Dry	Animal	Wind	Fast	Deep	Medium	1-4, 6
Quercus pagoda Raf.	Deciduous	Overstory	Intolerant	Intermediate	Wet	Animal	Wind	Medium	Deep	Medium	1-4
Quercus phellos L.	Deciduous	Overstory	Intolerant	Tolerant	Wet	Animal	Wind	Fast	Shallow	Long	1-4
Quercus rubra L.	Deciduous	Overstory	Intermediate	Intermediate	Intermediate	Animal	Wind	Medium	Deep	Long	1, 2, 4, 10
Quercus shumardii Buckl.	Deciduous	Overstory	Intolerant	Intermediate	Intermediate	Animal	Wind	Medium	Deep	Long	1-4
Quercus velutina Lam.	Deciduous	Overstory	Intermediate	Intolerant	Dry	Animal	Wind	Slow	Deep	Medium	1, 2, 4
Rhododendron canescens (Michx.) Sweet.	Deciduous	Shrub	Intermediate	Intolerant	Intermediate	Wind	Animal	Slow	Shallow	Long	1
Rhododendron spp.	Deciduous	Shrub	Intermediate	Intolerant	Intermediate	Wind	Animal	Slow	Shallow	Long	1
Rhus copallinum L.	Deciduous	Shrub	Intolerant	Intermediate	Intermediate	Animal	Wind	Slow	Shallow	Medium	1
Rosa spp.*	Deciduous	Shrub	Intolerant	Intolerant	Intermediate	Animal	Animal	Fast	Shallow	Medium	1
Salix nigra L.	Deciduous	Overstory	Intolerant	Tolerant	Wet	Wind	Wind	Fast	Shallow	Short	1, 3
Sambucus canadensis L.	Deciduous	Shrub	Intolerant	Tolerant	Wet	Animal	Animal	Fast	Shallow	Medium	1
Sapium sebiferum (L.) Roxb.*	Deciduous	Overstory	Intolerant	Tolerant	Wet or Dry	Animal	Wind	Fast	Shallow	Medium	1

Scientific name	**Leaf Type**	**Plant Form**	**Shade Tolerance**	**Flood Tolerance**	**Moisture Requirement**	**Seed Dispersal†**	**Pollination†**	**Growth Rate**	**Rooting Habit**	**Lifespan**	**References**
Sassafras albidum (Nutt.) Nees.	Deciduous	Midstory	Intolerant	Intolerant	Intermediate	Animal	Animal	Medium	Shallow	Medium	1-3
Tilia americana L.	Deciduous	Overstory	Tolerant	Intermediate	Intermediate	Wind	Animal	Fast	Shallow	Medium	1, 2
Ulmus alata Michx.	Deciduous	Overstory	Tolerant	Intermediate	Intermediate	Wind	Wind	Fast	Deep	Short	1-3
Ulmus americana L.	Deciduous	Overstory	Intermediate	Tolerant	Wet	Wind	Wind	Medium	Deep	Medium	1-3, 5
Ulmus rubra Muhl.	Deciduous	Overstory	Tolerant	Intolerant	Wet	Wind	Wind	Medium	Deep	Medium	1-3
Vaccinium arboreum Marsh.	Evergreen	Shrub	Tolerant	Intolerant	Intermediate	Animal	Animal	Slow	Shallow	Long	1
Vaccinium elliottii Champ.	Deciduous	Shrub	Intermediate	Intolerant	Intermediate	Animal	Animal	Slow	Shallow	Medium	1
Vaccinium spp.	Deciduous	Shrub	Intermediate	Intolerant	Intermediate	Animal	Animal	Slow	Shallow	Medium	1
Viburnum rufidulum Raf.	Deciduous	Shrub	Intermediate	Intermediate	Wet	Animal	Animal	Slow	Deep	Medium	1

* Non-native species

† Animal includes insect pollination and dispersal.

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CHAPTER V

SUMMARY AND CONCLUSION

Riparian forests are distinctive landscape features in the southeastern United States and provide a variety of important ecological benefits such as acting as reservoirs of biotic diversity and regulating aquatic-terrestrial linkages. Riparian forests are increasingly threatened by urban expansion and land use change, especially in the southeast. This research focused on small order streams because they and their associated forests are tightly connected to upland land use and contribute significantly to downstream conditions. The goal of this research was to elucidate the impacts of urbanization on riparian forests and identify ecological trends along an urban-rural land use gradient in the Piedmont physiographic region of the southeastern USA. Specific objectives were to: (1) examine the influence of land use and urbanization indices on riparian woody plant species diversity and composition, (2) quantify changes in riparian forest structure across an urban-rural gradient, (3) elucidate changes in woody plant functional traits along an urban-rural gradient, and (4) examine trends in diversity, composition, structure, and trait charateristics in the mature forest stand and regeneration layer.

Results from this work indicate the following trends across the urban-rural gradient:

Diversity and Composition

- Of the diversity indices examined, (species richness, Shannon diversity, evenness) only species richness was related to measured landscape metrics.
- Species richness was high in landscapes exhibiting high forest cover and large forest patches (ie. unmanaged forest, managed forest, and developing land uses).
- Shannon diversity increased and importance of non-native species decreased with distance from the urban core.
- For the regeneration layer, the Shannon diversity index showed a stronger decline in response to non-native plant invasion than the forest stand.
- Non-native species were abundant in the developing, urban, and agriculture land use types.
- *Ligustrum sinense* was the most abundant and widespread woody non-native species.
- Species composition was related to land use. Urban sites were dominated by early successional species; developing sites were dominated by non-native (*Ligustrum sinense*) and pioneer species (*Acer negundo*); agriculture and managed forest sites were dominated by ubiquitous species such as *Liquidambar styraciflua*, *Quercus nigra*, and *Liriodendron tulipifera*; and unmanaged forest sites were characterized *Acer rubrum* and a midstory of small tree species.
- In general, species composition was similar between the forest stand and regeneration layer, but the regeneration layer showed increased importance of a few upland species for the developing and agricultural land use types.
- Urban sites were composed mostly of upland, generalist, or non-native species.
- Urban, developing, and agriculture sites showed high importance of the non-native *Ligustrum sinense* and reduced recruitment of common native tree species such as *Liquidambar styraciflua*, *Quercus nigra*, and *Liriodendron tulipifera*.

Forest Structure

- Native species density was positively related to forest cover.
- Mean stem diameter was highest in the urban and agriculture sites.
- Aboveground biomass and basal area were not significantly related to landscape characteristics. Midstory tree biomass was positively related to forest cover and negatively related to impervious surface, and shrub biomass was positively related to patch density.
- Diameter distributions for sites with high grass cover (urban and agriculture) showed reduced recruitment of small diameter stems.

Woody Plant Traits

- Urban sites were dominated by: evergreen leaf habit, shrub plant form, intermediate shade tolerance, animal seed dispersal, fast growth rate, shallow rooting depth, and medium life span.
- Rural sites were dominated by: deciduous leaf habit, midstory tree form, shade tolerance, wind or gravity seed dispersal, slow growth rate, deep rooting, and long life span.
- For the regeneration layer, overstory tree form and medium growth rate increased in importance for the rural sites and animal pollination increased in importance for the urban sites.
- Flood tolerance for the urban sites shifted from tolerant in the forest stand to intolerant in the regeneration layer.

Future directions

This work demonstrated important relationships between riparian forest composition and structure, and the surrounding landscape matrix. Other natural environmental variables that have been found to significantly influence riparian plant communities, such as soil properties, topography, and hydrologic gradients may override land use effects or co-vary with changes in the landscape matrix. In addition, plant community response to land use change and disturbance may be non-linear and respond at different scales. Historical influences may also play a major role in shaping current vegetation characteristics. Incorporating these variables into future studies may provide a more holistic analysis of the urban-rural gradient approach. While developing specific management guidelines was not the goal of this work, these results could be used to guide biodiversity conservation in land use planning and reserve design. In conclusion, this study identifies important changes in diversity, forest structure, and composition of species and functional traits along an urban gradient and provides a better understanding of consequences to ecosystem function associated with urban development.

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APPENDIX

APPENDIX A: Landcover percentages and fragmentation data for each study site in West Georgia

Table 1: Percent landcover data based on 1-meter resolution imagery (March 2003) for each study site.

Watershed Code	% Evergreen Forest	% Deciduous Forest	% Grass Cover[†]	% Impervious Surface	% Water	% Other	% Total Forest [††]
BLC	48.13	28.24	18.61	1.24	0.00	3.79	76.37
BU1	20.89	12.34	22.71	41.94	0.71	1.41	33.23
BU2	30.49	15.88	24.94	24.93	1.63	2.11	46.38
CB	48.31	32.99	13.00	1.53	0.38	3.78	81.30
FR	30.89	7.44	38.19	13.08	2.15	8.25	38.33
FS2	30.71	28.21	35.79	2.74	1.51	1.05	58.92
HC1	47.84	26.73	19.55	1.33	0.68	3.87	74.57
HC2	30.47	22.22	43.95	1.64	0.76	0.96	52.68
MU1	29.26	24.27	36.80	3.68	4.12	1.86	53.54
MU2	42.39	24.98	16.53	2.57	1.05	12.48	67.37
MU3	41.55	37.06	14.80	1.88	0.86	3.85	78.61
RC1	28.38	11.06	27.10	30.30	1.62	1.53	39.45
RC2	28.07	14.07	26.98	24.4	0.28	6.2	42.14
SB1	38.61	35.01	20.32	1.83	0.73	3.51	73.62
SB2	37.34	35.35	19.90	3.39	1.26	2.76	72.68
SB4	41.15	22.76	27.64	3.27	1.91	3.26	63.92
SC	44.80	28.79	20.84	1.24	0.71	3.62	73.59

[†] % Grass cover includes lawns, cut-over areas, and pasture land

[††] % Forest category is % Evergreen + % Deciduous forest

Table 2: Fragmentation data and landscape characteristics based on 1-meter resolution imagery (March 2003) for each study site.

Watershed Code	No. Patches 100ha^{-1} (PD)	No. Grass Patches 100ha^{-1} (PDAG)	Largest Patch Index (LPI)	Largest Forest Patch Index (LPIFOR)	Largest Mean Forest Patch Index (MNFOR)	Shannon Diversity (SHDI)	Evenness (SHEI)
BLC	9537.58	6365.63	67.62	67.62	0.1062	0.67	0.485
BU1	5017.24	2835.04	38.48	2.93	0.0188	1.16	0.720
BU2	5618.31	2991.05	22.39	2.45	0.0255	1.20	0.743
CB	9702.11	6703.10	57.24	57.24	0.1847	0.60	0.375
FR	8765.92	2606.78	11.35	3.30	0.0190	1.26	0.784
FS2	6720.13	4451.05	21.91	21.91	0.0312	0.89	0.550
HC1	10247.21	7896.87	58.65	58.65	0.1702	0.72	0.450
HC2	7629.27	3946.80	39.52	39.52	0.0160	0.84	0.524
MU1	7301.91	3732.92	14.21	14.21	0.0187	1.03	0.637
MU2	11710.40	7266.56	59.27	59.27	0.0367	0.83	0.592
MU3	8936.85	6831.56	60.40	60.40	0.1779	0.68	0.423
RC1	6196.80	2966.28	11.09	4.56	0.0145	1.21	0.752
RC2	9246.73	4165.70	17.39	17.39	0.0341	1.24	0.768
SB1	10813.17	8432.06	66.15	66.15	0.1261	0.75	0.466
SB2	12747.63	10651.94	48.98	48.98	0.0944	0.78	0.483
SB4	34281.88	21976.30	34.92	34.92	0.0103	0.93	0.579
SC	10253.73	7258.95	68.39	68.39	0.0866	0.74	0.462

Note: Fragmentation and landscape parameters were obtained from FRAGSTATS (McGarigal 2002). Complete definitions of parameters can be found at the website: http://www.umass.edu/landeco/research/fragstats/fragstats.html

APPENDIX B: Location data and community summaries for each site sampled in West Georgia.

Watershed Code: BLC
Name of Stream: Blanton Creek
Land Use Category: Unmanaged Forest
Geographic Coordinates*: 32.75515 N -85.10477 W

Forest Stand	
Leaf Area Index - LAI ($m^2\ m^{-2}$)	5.09
Basal Area ($m^2\ ha^{-1}$)	33.7
Stem density (stems ha^{-1})	1525
Heterogeneity index†	66.4
Quadratic Mean Diameter – QMD (cm)	16.78
Biomass (Mg ha^{-1})	199.5
Overstory	184.6
Midstory	15.3
Shrub	0.35
Non-native	0.0
Species richness	32
Shannon diversity	2.56
Species evenness	0.74

Regeneration Layer	2004	2005
Stem density‡	42167	38833
Class1	4500	1000
Class2	32667	33000
Class3	5000	4833
Species richness	29	25
Shannon diversity	2.42	2.42
Species evenness	0.72	0.73

Watershed Code: BU1
Name of Stream: Bull Creek
Land Use Category: Urban
Geographic Coordinates*: 32.53323 N -84.93153 W

Forest Stand	
Leaf Area Index - LAI ($m^2 m^{-2}$)	2.86
Basal Area ($m^2 ha^{-1}$)	33.0
Stem density (stems ha^{-1})	525
Heterogeneity index †	79.6
Quadratic Mean Diameter – QMD (cm)	28.3
Biomass (Mg ha^{-1})	240.0
Overstory	234.6
Midstory	3.8
Shrub	1.7
Non-native	4.1
Species richness	17
Shannon diversity	2.09
Species evenness	0.74

Regeneration Layer	2004	2005
Stem density‡	55417	19083
Class1	49167	6583
Class2	5583	12083
Class3	667	333
Species richness	17	18
Shannon diversity	1.59	1.81
Species evenness	0.56	0.63

Watershed Code: BU2
Name of Stream: Bull Creek
Land Use Category: Urban
Geographic Coordinates*: 32.51465 N -84.90808 W

Forest Stand	
Leaf Area Index - LAI ($m^2\,m^{-2}$)	4.98
Basal Area ($m^2\,ha^{-1}$)	25.6
Stem density (stems ha^{-1})	1616
Heterogeneity index †	78.9
Quadratic Mean Diameter – QMD (cm)	13.6
Biomass (Mg ha^{-1})	111.6
Overstory	104.6
Midstory	2.1
Shrub	7.5
Non-native	9.8
Species richness	24
Shannon diversity	1.93
Species evenness	0.61

Regeneration Layer	2004	2005
Stem density‡	33368	264526
Class1	7895	237789
Class2	22632	22632
Class3	2842	4105
Species richness	23	24
Shannon diversity	1.6	0.31
Species evenness	0.50	0.10

Watershed Code: CB
Name of Stream: Clines Branch
Land Use Category: Unmanaged Forest
Geographic Coordinates*: 32.73548 N -85.06503 W

Forest Stand	
Leaf Area Index - LAI (m^2 m^{-2})	4.86
Basal Area (m^2 ha^{-1})	28.0
Stem density (stems ha^{-1})	2504
Heterogeneity index †	82.9
Quadratic Mean Diameter – QMD (cm)	11.93
Biomass (Mg ha^{-1})	162.6
Overstory	142.4
Midstory	16.2
Shrub	3.6
Non-native	0.0
Species richness	36
Shannon diversity	2.85
Species evenness	0.79

Regeneration Layer	2004	2005
Stem density‡	44583	59167
Class1	22083	13750
Class2	21083	43917
Class3	1417	1500
Species richness	31	35
Shannon diversity	2.24	2.25
Species evenness	0.65	0.63

Watershed Code: FR
Name of Stream: Flat Rock Creek
Land Use Category: Urban
Geographic Coordinates*: 32.51762 N -84.87995 W

Forest Stand	
Leaf Area Index - LAI (m^2 m^{-2})	4.88
Basal Area (m^2 ha^{-1})	45.3
Stem density (stems ha^{-1})	2571
Heterogeneity index †	85.2
Quadratic Mean Diameter – QMD (cm)	14.98
Biomass (Mg ha^{-1})	290.4
Overstory	282.5
Midstory	3.7
Shrub	5.7
Non-native	5.5
Species richness	20
Shannon diversity	2.51
Species evenness	0.84

Regeneration Layer	2004	2005
Stem density‡	-	67143
Class1	-	5714
Class2	-	48286
Class3	-	13143
Species richness	-	18
Shannon diversity	-	1.31
Species evenness	-	0.48

Watershed Code: FS2
Name of Stream: Flat Shoals Creek
Land Use Category: Agriculture
Geographic Coordinates*: 32.87383 N -85.01158 W

Forest Stand	
Leaf Area Index - LAI ($m^2 m^{-2}$)	5.05
Basal Area ($m^2 ha^{-1}$)	23.2
Stem density (stems ha^{-1})	1042
Heterogeneity index †	59.7
Quadratic Mean Diameter – QMD (cm)	16.8
Biomass (Mg ha^{-1})	156.3
Overstory	154.0
Midstory	1.3
Shrub	1.0
Non-native	1.1
Species richness	31
Shannon diversity	2.84
Species evenness	0.83

Regeneration Layer	2004	2005
Stem density‡	54667	33750
Class1	26000	4333
Class2	24917	25500
Class3	3750	3917
Species richness	32	33
Shannon diversity	2.13	2.86
Species evenness	0.62	0.81

Watershed Code: HC1
Name of Stream: House Creek
Land Use Category: Managed Forest
Geographic Coordinates*: 32.8006 N -85.09788 W

Forest Stand	
Leaf Area Index - LAI ($m^2 m^{-2}$)	5.97
Basal Area ($m^2 ha^{-1}$)	24.7
Stem density (stems ha^{-1})	1525
Heterogeneity index †	78.1
Quadratic Mean Diameter – QMD (cm)	14.3
Biomass (Mg ha^{-1})	153.5
Overstory	144.5
Midstory	7.9
Shrub	1.0
Non-native	1.0
Species richness	28
Shannon diversity	2.72
Species evenness	0.82

Regeneration Layer	2004	2005
Stem density‡	17583	15833
Class1	4250	2083
Class2	12167	11917
Class3	1167	1833
Species richness	17	22
Shannon diversity	2.34	2.42
Species evenness	0.82	0.78

Watershed Code: HC2
Name of Stream: House Creek
Land Use Category: Agriculture
Geographic Coordinates*: 32.83525 N -85.03463 W

Forest Stand	
Leaf Area Index - LAI ($m^2 m^{-2}$)	3.22
Basal Area ($m^2 ha^{-1}$)	34.1
Stem density (stems ha^{-1})	646
Heterogeneity index †	70.6
Quadratic Mean Diameter – QMD (cm)	25.9
Biomass (Mg ha^{-1})	257.8
Overstory	242.2
Midstory	12.5
Shrub	3.1
Non-native	3.1
Species richness	25
Shannon diversity	2.48
Species evenness	0.77

Regeneration Layer	2004	2005
Stem density‡	72333	59000
Class1	35333	8583
Class2	35000	49333
Class3	2000	1083
Species richness	20	22
Shannon diversity	0.89	1.38
Species evenness	0.30	0.45

Watershed Code: MU1
Name of Stream: Mulberry Creek
Land Use Category: Agriculture
Geographic Coordinates*: 32.65412 N -84.73007 W

Forest Stand	
Leaf Area Index - LAI ($m^2 m^{-2}$)	4.04
Basal Area ($m^2 ha^{-1}$)	21.1
Stem density (stems ha^{-1})	1279
Heterogeneity index [†]	85.0
Quadratic Mean Diameter – QMD (cm)	14.5
Biomass (Mg ha^{-1})	116.3
Overstory	93.1
Midstory	21.6
Shrub	1.6
Non-native	1.4
Species richness	23
Shannon diversity	2.48
Species evenness	0.79

Regeneration Layer	2004	2005
Stem density[‡]	58167	42833
Class1	20250	4333
Class2	35250	37667
Class3	2667	833
Species richness	22	21
Shannon diversity	2.00	1.61
Species evenness	0.65	0.53

Watershed Code: MU2
Name of Stream: Mulberry Creek
Land Use Category: Managed Forest
Geographic Coordinates*: 32.71125 N -84.7714 W

Forest Stand	
Leaf Area Index - LAI (m^2 m^{-2})	4.81
Basal Area (m^2 ha^{-1})	15.9
Stem density (stems ha^{-1})	1681
Heterogeneity index †	87.5
Quadratic Mean Diameter – QMD (cm)	10.6
Biomass (Mg ha^{-1})	78.2
Overstory	68.7
Midstory	7.4
Shrub	2.1
Non-native	0.0
Species richness	24
Shannon diversity	2.30
Species evenness	0.72

Regeneration Layer	2004	2005
Stem density‡	56625	50500
Class1	1092	7000
Class2	2642	42833
Class3	42	667
Species richness	31	28
Shannon diversity	2.47	2.51
Species evenness	0.72	0.75

Watershed Code: MU3
Name of Stream: Mulberry Creek
Land Use Category: Unmanaged Forest
Geographic Coordinates*: 32.69007 N -84.85343 W

Forest Stand	
Leaf Area Index - LAI ($m^2 m^{-2}$)	-
Basal Area ($m^2 ha^{-1}$)	23.0
Stem density (stems ha^{-1})	1496
Heterogeneity index †	85.7
Quadratic Mean Diameter – QMD (cm)	14.0
Biomass (Mg ha^{-1})	121.6
Overstory	94.6
Midstory	26.5
Shrub	0.6
Non-native	0.0
Species richness	34
Shannon diversity	3.07
Species evenness	0.87

Regeneration Layer	2004	2005
Stem density‡	50583	48500
Class1	16417	10083
Class2	33000	36833
Class3	1167	1583
Species richness	31	37
Shannon diversity	2.68	2.80
Species evenness	0.78	0.78

Watershed Code: RC1
Name of Stream: Roaring Creek
Land Use Category: Urban
Geographic Coordinates*: 32.5398 N -84.96247 W

Forest Stand	
Leaf Area Index - LAI ($m^2 m^{-2}$)	3.82
Basal Area ($m^2 ha^{-1}$)	14.6
Stem density (stems ha^{-1})	1025
Heterogeneity index [†]	76.8
Quadratic Mean Diameter – QMD (cm)	17.1
Biomass (Mg ha^{-1})	78.8
Overstory	74.6
Midstory	2.2
Shrub	2.0
Non-native	2.0
Species richness	24
Shannon diversity	2.78
Species evenness	0.87

Regeneration Layer	2004	2005
Stem density[‡]	29667	31000
Class1	2167	4333
Class2	19667	23000
Class3	7833	3667
Species richness	19	16
Shannon diversity	1.45	1.45
Species evenness	0.49	0.52

Watershed Code: RC2
Name of Stream: Roaring Creek
Land Use Category: Urban
Geographic Coordinates*: 32.52555 N -84.99038 W

Forest Stand	
Leaf Area Index - LAI (m^2 m^{-2})	4.53
Basal Area (m^2 ha^{-1})	29.2
Stem density (stems ha^{-1})	1267
Heterogeneity index †	58.1
Quadratic Mean Diameter – QMD (cm)	17.1
Biomass (Mg ha^{-1})	186.1
Overstory	180.3
Midstory	1.3
Shrub	4.5
Non-native	7.3
Species richness	21
Shannon diversity	2.08
Species evenness	0.68

Regeneration Layer	2004	2005
Stem density‡	-	34167
Class1	-	1417
Class2	-	25833
Class3	-	6917
Species richness	-	19
Shannon diversity	-	1.11
Species evenness	-	0.38

Watershed Code: SB1
Name of Stream: Standing Boy Creek
Land Use Category: Developing
Geographic Coordinates*: 32.60122 N -85.0249 W

Forest Stand	
Leaf Area Index - LAI ($m^2 m^{-2}$)	4.63
Basal Area ($m^2 ha^{-1}$)	20.3
Stem density (stems ha^{-1})	1196
Heterogeneity index †	88.8
Quadratic Mean Diameter – QMD (cm)	14.7
Biomass (Mg ha^{-1})	108.3
Overstory	102.1
Midstory	1.3
Shrub	4.9
Non-native	4.7
Species richness	24
Shannon diversity	2.18
Species evenness	0.69

Regeneration Layer	2004	2005
Stem density‡	171250	93917
Class1	106417	3167
Class2	58667	81667
Class3	6167	9083
Species richness	25	22
Shannon diversity	0.83	1.05
Species evenness	0.26	0.34

Watershed Code: SB2
Name of Stream: Standing Boy Creek
Land Use Category: Developing
Geographic Coordinates*: 32.64545 N -84.94848 W

Forest Stand	
Leaf Area Index - LAI ($m^2\ m^{-2}$)	4.25
Basal Area ($m^2\ ha^{-1}$)	17.9
Stem density (stems ha^{-1})	2008
Heterogeneity index †	83.9
Quadratic Mean Diameter – QMD (cm)	10.7
Biomass (Mg ha^{-1})	92.9
Overstory	82.4
Midstory	4.1
Shrub	10.1
Non-native	10.1
Species richness	27
Shannon diversity	1.84
Species evenness	0.56

Regeneration Layer	2004	2005
Stem density‡	390333	183250
Class1	312000	7500
Class2	72083	170083
Class3	6250	5667
Species richness	30	25
Shannon diversity	0.63	0.82
Species evenness	0.19	0.25

Watershed Code: SB4
Name of Stream: Standing Boy Creek
Land Use Category: Developing
Geographic Coordinates*: 32.6303 N -84.89395 W

Forest Stand	
Leaf Area Index - LAI ($m^2 m^{-2}$)	5.45
Basal Area ($m^2 ha^{-1}$)	20.7
Stem density (stems ha^{-1})	2100
Heterogeneity index †	73.1
Quadratic Mean Diameter – QMD (cm)	11.2
Biomass (Mg ha^{-1})	111.0
Overstory	89.3
Midstory	12.9
Shrub	10.2
Non-native	8.6
Species richness	30
Shannon diversity	2.22
Species evenness	0.65

Regeneration Layer	2004	2005
Stem density‡	167500	81250
Class1	106417	83
Class2	54167	75750
Class3	6917	5417
Species richness	22	21
Shannon diversity	0.74	0.95
Species evenness	0.22	0.31

Watershed Code: SC
Name of Stream: Sand Creek
Land Use Category: Managed Forest
Geographic Coordinates*: 32.84565 N -85.07468 W

Forest Stand	
Leaf Area Index - LAI (m^2 m^{-2})	4.70
Basal Area (m^2 ha^{-1})	30.9
Stem density (stems ha^{-1})	1383
Heterogeneity index †	74.3
Quadratic Mean Diameter – QMD (cm)	16.9
Biomass (Mg ha^{-1})	191.9
Overstory	189.1
Midstory	1.5
Shrub	0.5
Non-native	0.5
Species richness	24
Shannon diversity	2.26
Species evenness	0.71

Regeneration Layer	2004	2005
Stem density‡	12000	10667
Class1	1833	833
Class2	7583	7583
Class3	2583	2250
Species richness	24	21
Shannon diversity	2.66	2.52
Species evenness	0.84	0.83

*Geographic Coordinates correspond to the location of Transect 1 (T1) for each site. See Appendix C for transect directions.

†Heterogeneity Index (HI) is the spatial heterogeneity in species composition within a site and was calculated as the mean percent dissimilarity (PD) (Collins 1992):

PD = 1 - PS

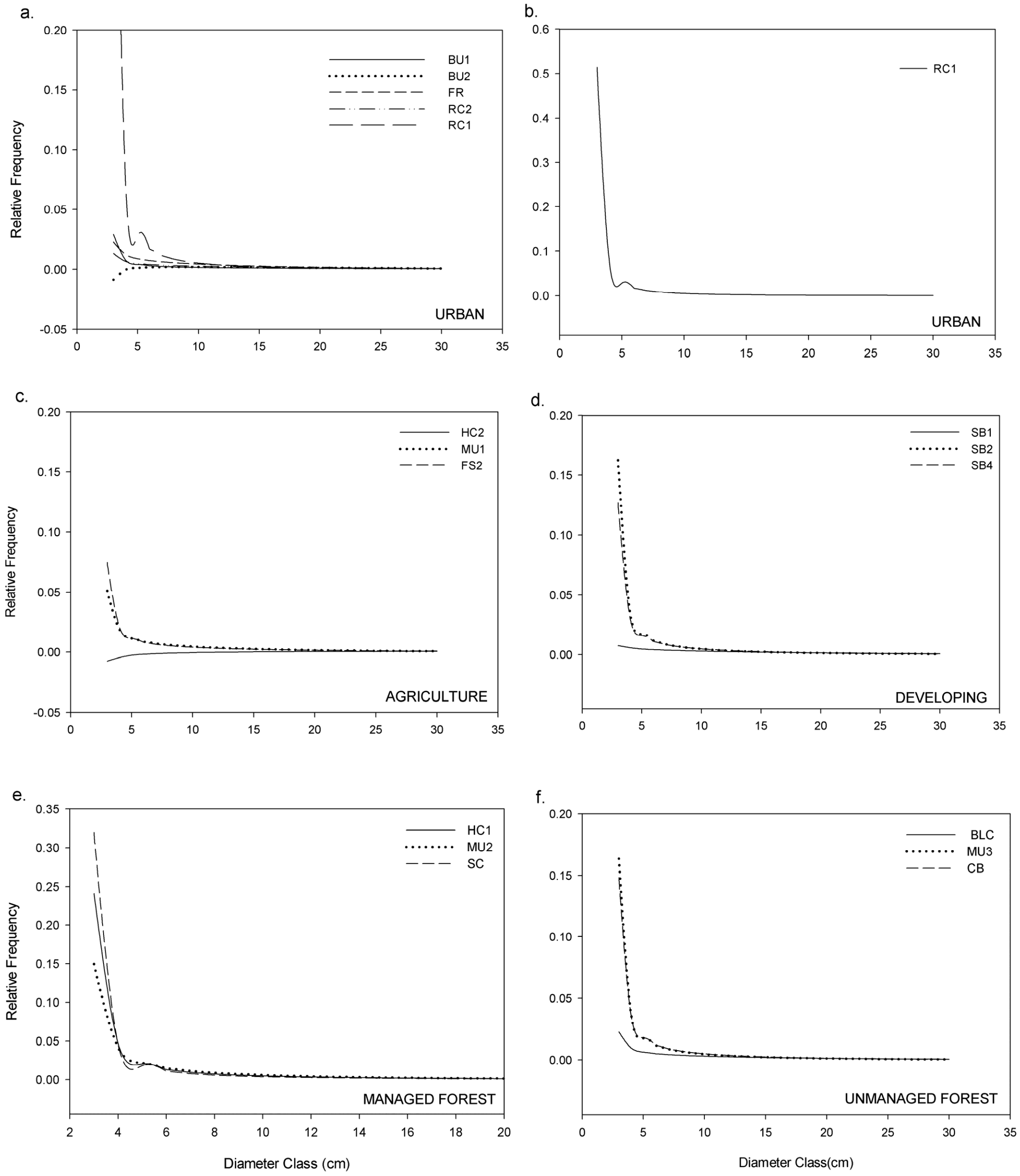
$PS = 1 - 0.5 \sum_{i=1}^{s} | p_a - p_b |$; where PS is the percent similarity, p_a is the proportional cover of species p in plot a, p_b is the proportional cover of species p in plot b, and s is the total number of species. PD was calculated for all possible two-way combinations of plots for each site, resulting in 276 values for a site with 24 plots. Within-site heterogeneity was the average of the 276 values.

[‡] Regeneration stem density size class definitions: Class 1= germinate, cotyledons present; Class 2= height ≤1m; Class 3= height > 1m.

APPENDIX C: Transect directions for each site sampled in West Georgia.

Site-Transect	Bearing 1	Bearing 2	Site-Transect	Bearing 1	Bearing 2
BLC-T1	100	280	MU1-T4	280	90
BLC-T2	100	280	MU1-T5	220	40
BLC-T3	54	234	MU1-T6	280	100
BLC-T4	90	270	MU2-T1	50	230
BLC-T5	90	270	MU2-T2	70	250
BLC-T6	80	260	MU2-T3	70	N/A
BU1-T1	85	265	MU2-T4	70	N/A
BU1-T2	90	270	MU2-T5	60	N/A
BU1-T3	90	270	MU2T-6	210	N/A
BU1-T5	90	270	MU3-T1	190	340
BU1-T6	90	270	MU3-T2	220	40
BU2-T4	85	265	MU3-T3	260	80
BU2-T1	60	240	MU3-T4	165	345
BU2-T2	60	240	MU3-T5	180	360
BU2-T3	40	220	MU3-T6	180	360
BU2-T4	140	320	RC2-T1	300	120
BU2-T5	120	300	RC2-T2	270	90
CB-T1	340	160	RC2-T3	250	70
CB-T2	60	240	RC2-T4	275	95
CB-T3	10	190	RC2-T5	260	80
CB-T4	20	200	RC2-T6	260	80
CB-T5	0	180	RC-T1	95	275
CB-T6	100	280	RC-T2	95	275
FR-T4	90	N/A	RC-T3	130	310
FR-T5	320	N/A	SB1-T1	165	345
FR-T6	330	150	SB1-T2	230	50
FS2-T1	50	220	SB1-T3	160	340
FS2-T2	20	200	SB1-T4	150	330
FS2-T3	40	220	SB1-T5	165	345
FS2-T4	40	220	SB1-T6	160	340
FS2-T5	60	240	SB2-T1	160	340
FS2-T6	140	335	SB2-T2	210	30
HC2-T1	335	155	SB2-T3	180	360
HC2-T2	10	190	SB2-T4	180	360
HC2-T3	340	160	SB2-T5	160	340
HC2-T4	360	180	SB2-T6	170	320
HC2-T5	320	140	SB4-T1	156	336
HC2-T6	20	200	SB4-T2	200	20
HC-T1	290	110	SB4-T3	150	330
HC-T2	230	20	SB4-T4	180	360
HC-T3	230	50	SB4-T5	200	20
HC-T4	210	100	SB4-T6	200	20
HC-T5	210	30	SC-T1	302	122
HC-T6	220	40	SC-T2	334	154
MU1-T1	164	344	SC-T3	20	200
MU1-T2	90	270	SC-T4	312	132
MU1-T3	60	240	SC-T5	150	330
			SC-T6	234	54

APPENDIX D: Comparison of the predicted relative diameter distributions using the two-parameter Weibull-function of overstory species for all sites by land use type: a) all urban sites, b) RC1- urban site, c) agriculture, d) developing, e) managed forest and, f) unmanaged forest sites. Relative frequency represents the probability of observing a particular diameter class



APPENDIX E: Regression equations for predicting aboveground biomass (kg dry weight) for *Ligustrum sinense*

Table 1: Regression equations for predicting aboveground biomass (kg dry weight) for *Ligustrum sinense* from measured independent variables using the power equation: $y = aX^b$ (n=15)

Independent variable	Biomass component	a (± SE)	b (± SE)	R^2
Diameter at breast height (cm) (DBH)	Whole plant	0.214 (± 0.027)	2.319 (± 0.064)	0.99
	Wood	0.207 (± 0.027)	2.322 (± 0.065)	0.99
	Leaves	0.003 (± 0.003)	2.543 (± 0.414)	0.74
Basal diameter (cm)	Whole plant	0.067 (± 0.025)	2.500 (± 0.162)	0.95
	Wood	0.064 (± 0.023)	2.501 (± 0.160)	0.95
	Leaves	0.001 (± 0.001)	2.588 (± 0.541)	0.64
DBH (cm) × stem length (m)	Whole plant	0.035 (± 0.009)	1.575 (± 0.063)	0.98
	Wood	0.034 (± 0.008)	1.575 (± 0.063)	0.98
	Leaves	0.0004 (± 0.0005)	1.714 (± 0.292)	0.73

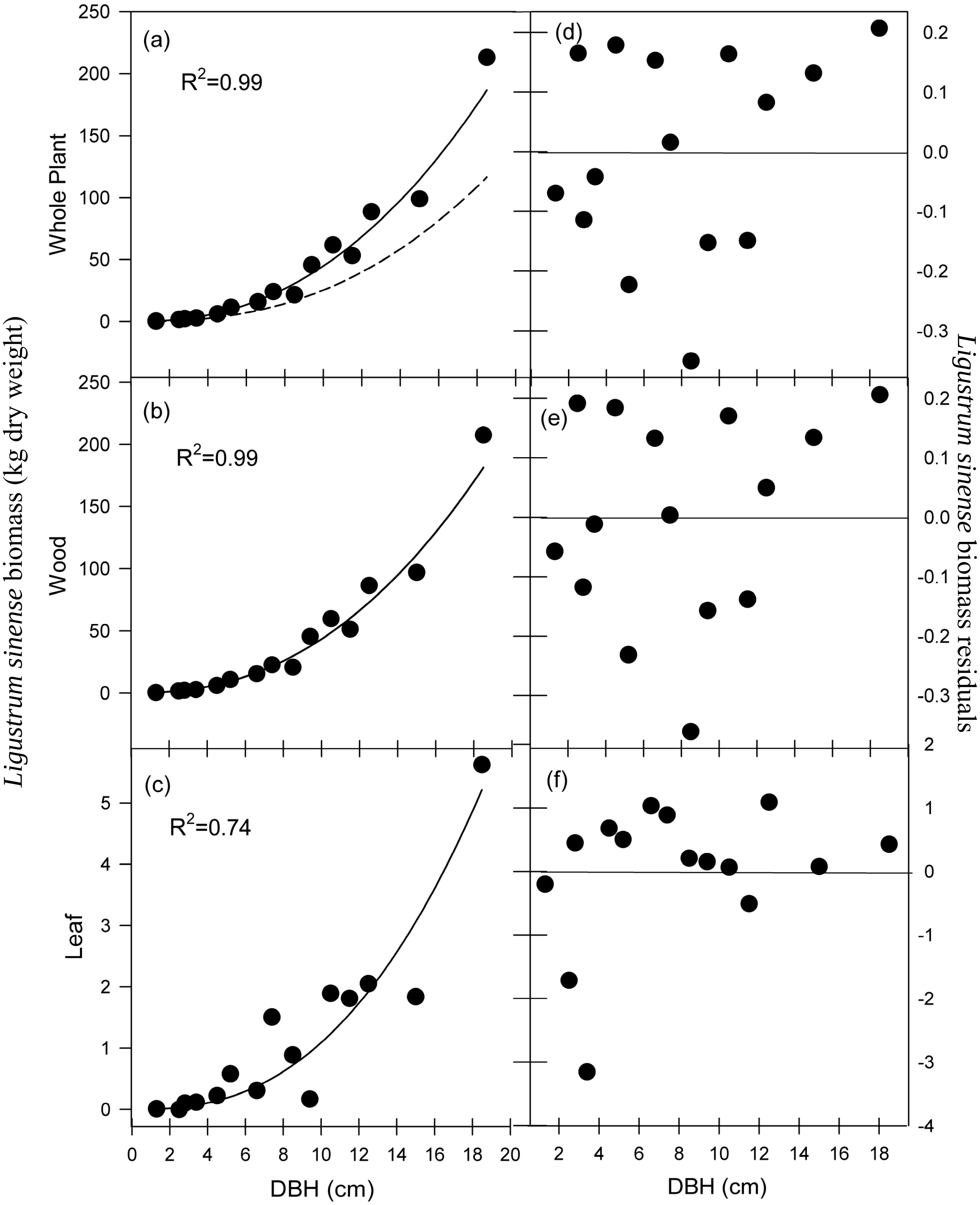


Figure 1: Allometric relationships for predicting (a) whole plant, (b) wood, and (c) leaf biomass from DBH (cm) of *Ligustrum sinense*. Figures (d-f) show the biomass residual plots for whole plant, wood, and leaves, respectively. The dashed line in (a) shows the general equation for estimating aboveground biomass for mixed understory hardwoods in the United States (Jenkins et al. 2003).

APPENDIX F: Species × trait matrix

	EVER LEAF	DECID LEAF	SEED WIND	SEED WATER/GRAVITY	SEED VERT	FORM SHRUB	FORM MID	FORM OVERST	SHADE TOL	SHADE INTER	SHADE INTOL	POLL WIND	POLL ANI
ACBA	0	1	1	0	0	0	1	0	1	0	0	1	0
ACNE	0	1	1	0	0	0	0	1	0	0	1	1	0
ACRU	0	1	1	0	0	0	0	1	1	0	0	1	0
AEPA	0	1	0	1	0	1	0	0	1	0	0	0	1
AEPA2	0	1	0	1	0	1	0	0	1	0	0	0	1
ALJU	0	1	1	0	0	0	0	1	0	0	1	1	0
ALSE	0	1	0	1	0	1	0	0	0	0	1	1	0
ASTR	0	1	0	0	1	1	0	0	1	0	0	0	1
BENI	0	1	1	0	0	0	0	1	0	0	1	1	0
CAAM	0	1	0	0	1	1	0	0	0	1	0	0	1
CABI	0	1	0	1	0	0	0	1	0	0	1	0	1
CACA	0	1	0	0	1	0	1	0	1	0	0	1	0
CACO	0	1	0	1	0	0	0	1	0	0	1	1	0
CAGL	0	1	0	1	0	0	0	1	0	1	0	1	0
CAOV	0	1	0	1	0	0	0	1	0	1	0	1	0
CAOV2	0	1	0	1	0	0	0	1	0	1	0	1	0
CATO	0	1	0	1	0	0	0	1	0	0	1	1	0
CECA	0	1	0	0	1	0	1	0	1	0	0	0	1
CETE	0	1	0	0	1	0	1	0	1	0	0	1	0
CHVI	0	1	0	0	1	0	1	0	1	0	0	0	1
COFL	0	1	0	0	1	0	1	0	1	0	0	0	1
COST	0	1	0	0	1	1	0	0	1	0	0	0	1
CRSP	0	1	0	0	1	1	0	0	1	0	0	0	1

	EVER LEAF	DECID LEAF	SEED WIND	SEED WATER/GRAVITY	SEED VERT	FORM SHRUB	FORM MID	FORM OVERST	SHADE TOL	SHADE INTER	SHADE INTOL	POLL WIND	POLL ANI
DIVI	0	1	0	0	1	0	0	1	1	0	0	1	0
ELPU	1	0	0	0	1	1	0	0	0	1	0	0	1
FAGR	0	1	0	1	0	0	0	1	1	0	0	1	0
FRAM	0	1	1	0	0	0	0	1	0	0	1	1	0
FRPE	0	1	1	0	0	0	0	1	0	0	1	1	0
GLTR	0	1	0	0	1	0	0	1	0	0	1	1	0
HATE	0	1	0	1	0	0	1	0	1	0	0	0	1
HAVI	0	1	1	0	0	1	0	0	1	0	0	1	0
HYQU	0	1	1	0	0	1	0	0	1	0	0	0	1
ILDE	0	1	0	0	1	1	0	0	1	0	0	0	1
ILOP	1	0	0	0	1	0	1	0	1	0	0	0	1
JUNI	0	1	0	1	0	0	0	1	0	0	1	1	0
JUVI	0	1	1	0	0	0	0	1	0	0	1	1	0
KALA	1	0	1	0	0	1	0	0	1	0	0	0	1
LIBE	0	1	0	0	1	1	0	0	0	1	0	0	1
LIJA	1	0	0	0	1	1	0	0	0	1	0	1	0
LISI	1	0	0	0	1	1	0	0	0	1	0	1	0
LIST	0	1	0	1	0	0	0	1	0	0	1	1	0
LITU	0	1	1	0	0	0	0	1	0	0	1	0	1
MAAC	0	1	0	0	1	0	0	1	0	1	0	0	1
MAGR	1	0	0	0	1	0	0	1	1	0	0	0	1
MAMA	0	1	0	0	1	0	0	1	0	1	0	0	1
MAVI	1	0	0	0	1	0	0	1	0	1	0	0	1
MEAZ	0	1	0	0	1	0	0	1	0	0	1	0	1
MORU	0	1	0	0	1	0	1	0	1	0	0	1	0
MYCE	1	0	0	0	1	1	0	0	0	1	0	1	0
NYSY	0	1	0	0	1	0	0	1	1	0	0	0	1
OSVI	0	1	1	0	0	0	1	0	1	0	0	1	0
OXAR	0	1	1	0	0	0	1	0	1	0	0	0	1
PITA	1	0	1	0	0	0	0	1	0	0	1	1	0
PLOC	0	1	0	1	0	0	0	1	0	0	1	1	0

	EVER LEAF	DECID LEAF	SEED WIND	SEED WATER/GRAVITY	SEED VERT	FORM SHRUB	FORM MID	FORM OVERST	SHADE TOL	SHADE INTER	SHADE INTOL	POLL WIND	POLL ANI
PRCA	1	0	0	0	1	0	0	0	1	0	0	0	1
PRSE	0	1	0	0	1	0	0	1	0	0	1	0	1
PSSI	0	1	0	1	0	1	0	0	0	0	1	1	0
QUAL	0	1	0	0	1	0	0	1	0	0	1	1	0
QUFA	0	1	0	0	1	0	0	1	0	0	1	1	0
QULY	0	1	0	0	1	0	0	1	0	1	0	1	0
QUMI	0	1	0	0	1	0	0	1	0	0	1	1	0
QUNI	0	1	0	0	1	0	0	1	0	0	1	1	0
QUPA	0	1	0	0	1	0	0	1	0	0	1	1	0
QUPH	0	1	0	0	1	0	0	1	0	0	1	1	0
QURU	0	1	0	0	1	0	0	1	0	1	0	1	0
QUSH	0	1	0	0	1	0	0	1	0	0	1	1	0
QUVE	0	1	0	0	1	0	0	1	0	0	1	1	0
RHSP	0	1	1	0	0	1	0	0	0	1	0	0	1
RHCO	0	1	0	0	1	1	0	0	0	0	1	1	0
SAAL	0	1	0	0	1	0	1	0	0	0	1	0	1
SACA	0	1	0	0	1	1	0	0	0	0	1	0	1
SANI	0	1	1	0	0	0	0	1	0	0	1	1	0
SASE	0	1	0	0	1	0	0	1	0	0	1	1	0
TIAM	0	1	1	0	0	0	0	1	1	0	0	0	1
ULAL	0	1	1	0	0	0	0	0	1	0	0	1	0
ULAM	0	1	1	0	0	0	0	1	0	1	0	1	0
ULRU	0	1	1	0	0	0	0	1	1	0	0	1	0
VAAR	1	0	0	0	1	0	0	0	1	0	0	0	1
VAEL	0	1	0	0	1	1	0	0	0	1	0	0	1
VIRU	0	1	0	0	1	1	0	0	0	1	0	0	1
WIRO	0	1	0	0	1	1	0	0	0	0	1	0	1

	GROWTH SLOW	GROWTH MED	GROWTH FAST	ROOT SHALL	ROOTS DEEP	FLOOD TOL	FLOOD INTER	FLOOD INTOL	LSSHORT	LSMED	LSLONG
ACBA	0	1	0	1	0	0	1	0	0	1	0
ACNE	0	0	1	1	0	1	0	0	1	0	0
ACRU	0	0	1	1	0	1	0	0	1	0	0
AEPA	0	1	0	0	1	0	1	0	0	0	1
AEPA2	0	1	0	1	0	0	1	0	0	0	1
ALJU	0	0	1	1	0	0	0	1	0	1	0
ALSE	0	1	0	1	0	1	0	0	0	1	0
ASTR	0	1	0	0	1	0	0	1	1	0	1
BENI	0	0	1	1	0	1	0	0	0	1	0
CAAM	0	0	1	1	0	0	1	0	0	1	0
CABI	0	0	1	1	0	1	0	0	0	0	1
CACA	0	1	0	0	1	0	1	0	0	1	0
CACO	1	0	0	0	1	1	0	0	0	1	0
CAGL	1	0	0	0	1	0	0	1	0	1	0
CAOV	1	0	0	0	1	0	0	1	0	1	0
CAOV2	1	0	0	0	1	0	0	1	0	0	1
CATO	1	0	0	0	1	0	0	1	0	0	1
CECA	0	0	1	0	1	0	0	1	1	0	0
CETE	0	1	0	1	0	0	1	0	0	1	0
CHVI	1	0	0	0	1	0	1	0	1	0	0
COFL	0	1	0	1	0	0	0	1	1	0	0
COST	0	1	0	1	0	1	0	0	0	1	0
CRSP	1	0	0	1	0	0	0	1	0	1	0

	GROWTH SLOW	GROWTH MED	GROWTH FAST	ROOT SHALL	ROOTS DEEP	FLOOD TOL	FLOOD INTER	FLOOD INTOL	LSSHORT	LSMED	LSLONG
DIVI	1	0	0	0	1	1	0	0	0	0	1
ELPU	0	0	1	1	0	1	0	0	1	0	0
FAGR	0	1	0	1	0	1	0	0	0	0	1
FRAM	0	1	0	0	1	0	1	0	0	1	0
FRPE	0	1	0	0	1	0	0	0	1	0	0
GLTR	0	0	1	1	0	0	1	0	0	1	0
HATE	1	0	0	0	1	0	0	1	0	1	0
HAVI	1	0	0	0	1	0	0	1	0	0	1
HYQU	0	1	0	1	0	0	0	1	0	1	0
ILDE	1	0	0	0	1	0	1	0	0	1	0
ILOP	1	0	0	0	1	0	1	0	0	1	0
JUNI	1	0	0	0	1	0	1	0	0	1	0
JUVI	1	0	0	0	1	0	1	0	0	1	0
KALA	1	0	0	1	0	0	1	0	0	0	1
LIBE	1	0	0	0	1	0	1	0	0	0	1
LIJA	0	0	1	1	0	0	0	1	0	1	0
LISI	0	0	1	1	0	0	0	1	0	1	0
LIST	0	0	1	0	1	1	0	0	0	0	1
LITU	0	0	1	0	1	0	0	1	0	1	0
MAAC	0	0	1	0	1	0	0	1	0	1	0
MAGR	0	0	1	0	1	0	0	1	0	0	1
MAMA	0	0	1	0	1	0	0	1	0	1	0
MAVI	0	1	0	0	1	1	0	0	0	1	0
MEAZ	0	0	1	1	0	0	1	0	0	1	0
MORU	0	1	0	1	0	0	0	1	0	1	0
MYCE	0	1	0	1	0	1	0	0	0	0	1
NYSY	0	1	0	0	1	1	0	0	0	1	0
OSVI	0	1	0	0	1	0	1	0	1	0	0
OXAR	0	1	0	0	1	0	0	1	0	1	0
PITA	0	0	1	1	0	0	1	0	0	1	0
PLOC	0	1	0	0	1	1	0	0	0	0	1

	GROWTH SLOW	GROWTH MED	GROWTH FAST	ROOT SHALL	ROOTS DEEP	FLOOD TOL	FLOOD INTER	FLOOD INTOL	LSSHORT	LSMED	LSLONG
PRCA	0	0	1	1	0	0	0	1	1	0	0
PRSE	0	0	1	1	0	0	0	1	0	1	0
PSSI	1	0	0	1	0	0	1	0	0	1	0
QUAL	1	0	0	0	1	0	0	1	0	0	1
QUFA	0	1	0	0	1	0	0	1	0	0	1
QULY	1	0	0	1	0	1	0	0	0	0	1
QUMI	0	1	0	0	1	0	1	0	0	1	0
QUNI	0	0	1	0	1	1	0	0	0	1	0
QUPA	0	1	0	0	1	0	1	0	0	1	0
QUPH	0	0	1	1	0	1	0	0	0	0	1
QURU	0	1	0	0	1	1	0	0	0	0	1
QUSH	0	1	0	0	1	0	1	0	0	0	1
QUVE	1	0	0	0	1	0	0	1	0	1	0
RHSP	1	0	0	0	1	0	0	1	0	0	1
RHCO	1	0	0	1	0	0	1	0	0	1	0
SAAL	0	1	0	1	0	0	0	1	0	1	0
SACA	0	0	1	1	0	1	0	0	0	1	0
SANI	0	1	0	1	0	1	0	0	1	0	0
SASE	0	0	1	1	0	1	0	0	0	1	0
TIAM	0	0	1	1	0	0	1	0	0	1	0
ULAL	0	0	1	1	0	0	0	0	1	0	0
ULAM	0	1	0	1	0	1	0	0	0	1	0
ULRU	0	1	0	1	0	1	0	0	0	1	0
VAAR	1	0	0	1	0	0	0	1	0	0	1
VAEL	1	0	0	1	0	0	0	1	0	1	0
VIRU	1	0	0	0	1	0	1	0	0	1	0
WIRO	0	0	1	1	0	0	0	1	0	1	0

Leaf
- Ever = Evergreen leaf
- Decid = Deciduos leaf

Seed
- Wind = Wind dispersed
- Water/gravity = Water or gravity dispersed
- Vert = Animal dispersed

Form
- Shrub = Shrub
- Mid = Mistory
- Overst = Overstory

Shade
- Tol = Shade tolerant
- Inter = Shade intermediate
- Intol = shade intolerant

Pollination (Poll)
- Wind = Wind pollination
- Ani = Animal pollination

Growth
- Slow = Slow growth rate
- Med = Medium growth rate
- Fast = Fast growth rate

Root
- Shall = Shallow rooting depth
- Deep = Deep rooting depth

Flood
- Tol = Flood tolerant
- Inter = Intermediate flood tolerance
- Intol = Flood intolerant

Life span (LS)
- LSshort = Short life span
- LSmed = Medium life span
- LSlong = Long life span