THE EFFECTS OF URBANIZATION ON RIPARIAN FOREST PLANT COMMUNITIES IN THE RESEARCH TRIANGLE AREA OF NORTH CAROLINA

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ABSTRACT

Bianca E. Lopez: The effects of urbanization on riparian forest plant communities in the
Research Triangle area of North Carolina
(Under the direction of Peter S. White)

Ongoing urban development is having profound impacts on ecosystems worldwide, by reducing the amount and connectivity of natural habitat and changing the local environmental conditions. Despite the ubiquity and the continued growth of urban areas, the effects of urban development on the diversity and composition of plant communities remain poorly understood. In this dissertation, I address this issue by investigating the effects of urban development on patches of remnant riparian forest in the Research Triangle area of North Carolina. To do this, I used a rural-to-urban gradient approach, comparing the plant species and environmental conditions of sites surrounded by different amounts of urban development. I first explored the effects of different "filters" created by urban development on plant biodiversity using structural equation modeling. In this, I tested the predictions of an established conceptual framework and developed a general model that could be used to compare the effects of urbanization on plant biodiversity across cities. I then examined changes in plant species' functional traits along the rural-to-urban gradient and compared the species and traits found at these sites to high-quality riparian plant communities that represent potential targets for restoration. I found that plant traits change somewhat predictably along an urbanization gradient, particularly with regard to species' seed dispersal modes, but that traits may not be as useful for predicting which species will establish in urban restoration efforts. Finally, I assessed the ability of environmental variables and spatial variables describing habitat connectivity to explain variation in plant species composition across sites. I found that species with limited dispersal ability showed the strongest signal of dispersal limitation across sites, and that urban development between sites appears to reduce connectivity for these species. This dissertation provides insight into the ways that urban development is altering riparian forests in the Research Triangle, which may have important impacts on biodiversity and ecosystem services. My results have implications for land management, restoration, and urban planning in this landscape.

I dedicate this work to my parents, Kimberly Ann Moore and Alvaro Benito Lopez, who have supported me and inspired me with their continued excitement for learning about the world around them, and to my great friend Brendan Patrick Galvin, who has seen me through.

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CHAPTER 1: INTRODUCTION

INTRODUCTION

Over half of the people in the world live in cities (United Nations 2015) and urban areas are continuing to grow both globally (Seto et al. 2011) and across the Southeastern United States (Terando et al. 2014). Despite the ubiquity of human settlements and well-documented effects of urban development on the environment (e.g., the urban heat island effect [Oke 1995], reductions in air and water quality [Pickett et al. 2011]), the impacts of urbanization on ecosystems remain poorly understood. This is because until the 1970's, ecologists mainly chose to study relatively pristine ecosystems rather than pursue research in urban areas (McDonnell and Pickett 1990, McDonnell 2011). Since that time, the field of urban ecology has emerged to address this knowledge gap.

Early research in urban ecology focused on documenting changes in the abundance and diversity of organisms as well as ecological processes (e.g., nitrogen cycling, leaf litter decomposition) with urbanization (McDonnell et al. 1997). Although some studies have used herbarium records and other historical accounts of species occurrences to identify changes in species composition in cities over time (Van der Veken et al. 2004, Stehlik et al. 2007, Hahs et al. 2009, Duncan et al. 2011), most have used a spatial urban-to-rural gradient approach, comparing sites at different distances to the city center (McDonnell and Pickett 1990, McDonnell et al. 1997) or, later, using various measures of the amount of urban development surrounding sites (e.g., impervious surface cover, population density; McDonnell and Hahs 2008). These spatial gradients stand in as a space-for-time substitution for the process of urbanization, which is generally more difficult to study, as historical pre-urbanization records are somewhat scarce. These studies have collectively shown several general trends across cities. One is an increase in exotic species in many urban areas (Lososová et al. 2012, Aronson et al. 2015), which contribute to a global homogenization of species composition across cities (McKinney 2006, Groffman et al. 2014). Early on, some researchers recognized that different species respond to urbanization differently; some species act as “urban avoiders”, while others tend to be “urban tolerators” or “urban exploiters” (Blair 1996). Changes to the local environment, the amount and configuration of habitat, and the introductions of novel species can all have effects on natural communities within and around cities (Williams et al. 2009). Some ecologists have suggested that these changes create "novel ecosystems" that require their own theories and considerations for management (Seastedt et al. 2008, Kowarik 2011), while others have pointed out similarities between many of the effects seen in urban areas and examples in more “natural” settings, suggesting that existing ecological theories (e.g., Island Biogeography, metacommunity theory) can and should be applied to urban ecosystems (Niemelä 1999, Faeth et al. 2011).

One aspect of urban areas that makes them markedly different from many other ecosystems is the strength of the effects of human decisions, both at the individual and institutional level. This has led some urban ecologists to work collaboratively with researchers from the social sciences to treat cities as socio-ecological systems. Research of this nature has been termed “ecology *of* cities”, in contrast with “ecology *in* cities”, the single-discipline research that treats humans as a separate, outside driver of changes within the ecosystem (Pickett et al. 1997, Grimm et al. 2000). This area of research is still growing, and has mainly centered on the two urban Long Term Ecological Research centers in Baltimore, MD and Phoenix, AZ. Recently, Childers et al. (2015) proposed a third emphasis for urban ecology research, "ecology *for* cities", which attempts to make connections between ecological research, urban planning and design, and the needs of urban residents to create more sustainable, livable cities. While ecology *in* cities remains the most common type of urban ecology research being carried out today, the rise of ecology *of* and *for* cities has increased recognition of people as being an important component of urban ecosystems (Pickett et al. 2013, Wu 2014, McDonnell and MacGregor-Fors 2016, McPhearson et al. 2016, Schwarz and Herrmann 2016).

However, there is still much to learn about ecology *in* cities. In particular, since the early years of urban-to-rural gradient analysis, there has been a push towards moving past the simple documenting of patterns to understanding changes in ecosystem processes such as resource availability, disturbance, species interactions, and dispersal (Shochat et al. 2006, Faeth et al. 2011). McDonnell and Hahs (2013) have called this "moving beyond the 'low-hanging fruit'" of urban biodiversity research. They propose that in order to provide robust and useful recommendations to conservation practitioners and urban planners, it is critical to have a general, synthetic understanding of the mechanisms underlying observed responses of natural communities to urbanization. To do this, they recommend that urban biodiversity researchers adopt three best practices: 1) explicitly describing the scope of the study, in terms of the spatial and temporal scale, historical context, and definition of the urbanization gradient; 2) choosing more precise measures of drivers and community responses that help to identify mechanisms for urbanization's effects on ecological communities; and 3) contributing to synthesis by testing the generalizability of observed patterns and designing comparative studies across multiple cities.

In this dissertation, I carried out three studies based on one dataset of plant communities spanning an urban-to-rural gradient to answer the broad research question: How is urban development influencing the plant species that are found in remnant riparian forest? I emphasized the use of informative measures of ecological drivers influenced by urbanization (e.g., habitat connectivity, environmental conditions) and plant community responses. In these three studies (Chapters 2-4), I use different analytical methods and different response variables describing measures of community structure: diversity, trait composition, and beta diversity (species turnover or changes in species composition across sites). Here, I briefly summarize each of these chapters, highlighting their contributions to understanding mechanisms underlying community changes with urbanization and to promoting comparability with other urban ecology studies.

DESCRIPTION OF STUDY AREA AND RESEARCH SCOPE

I collected data for my research in the Research Triangle Area of North Carolina, a landscape comprising the state capitol, Raleigh, the smaller cities of Durham, Chapel Hill, and Cary, and a number of surrounding towns. Raleigh is the second largest city in North Carolina and one of the fastest growing cities in the United States (U.S. Census Bureau Population Division 2016). The Research Triangle area has changed substantially in the last 30 years, with the development of the Research Triangle Park and influx of new residents from other parts of the country. This landscape differs in several ways from many areas where urban ecology research has centered in terms of both city size and the amount of forest remaining (estimated to be over 50% of the current land cover). Much urban ecology research has been conducted in Europe or in major cities in the U. S. (e.g., New York City, Baltimore, Phoenix, Boston) and

Australia. Few studies have been conducted in the southeastern U.S. (but see Price et al. 2006, Burton and Samuelson 2008, Minor and Urban 2009, Nagy and Lockaby 2011), despite ongoing urban development in this region (Brown et al. 2005, Terando et al. 2014). However, in the last several years the Research Triangle has become a hotspot for new urban ecology research, specifically regarding changes to streams and insect populations (Sudduth et al. 2011, Inkilainen et al. 2013, Somers et al. 2013, Dale and Frank 2014, Youngsteadt et al. 2015, Meineke et al. 2016).

The large amount of forest in the Research Triangle area makes it an ideal study system for assessing the effects of urbanization on forests. This forest is mostly secondary, having been cleared for agriculture or grazing, or selectively harvested for timber. Much of the forest in the Triangle is found in riparian buffers that are protected from development by ordinances. Riparian forests in the North Carolina Piedmont (which includes the Research Triangle) have high plant biodiversity, particularly in the floodplains of small streams (Matthews et al. 2011), which I focused on for my dissertation. Riparian forest also provides important ecosystem services, such as maintaining water quality and moderating flooding (Peterjohn and Correl 1984, Sweeney et al. 2004, Newham et al. 2011).

I sampled sites along an urbanization gradient defined by the amount of impervious surface cover surrounding sites within a 1 km buffer. The urbanization gradient I sampled was short, with a maximum impervious surface cover of about 25%. This partially reflects the fact that all sites were located within forest on public lands (for purposes of gaining legal access), which are mostly relatively large patches compared to small forested areas on private lands. Study sites were also limited by the size of the forest plots I used (300-500 m^2), which needed to be large enough to adequately capture the composition of species present at the site. Compared to many other studies, the gradient actually captured here spans mainly from rural to suburban areas, as few sites are located close to the center of a city.

CHAPTER SUMMARIES

In Chapter 2, I use structural equation modeling to examine the effects of forest cover, forest fragmentation, environmental variables related to urbanization (temperature, soil phosphorus content, and stream incision), and human population density on plant biodiversity. This analysis tests predictions made by Williams et al. (2009) for how the "four filters" of urbanization (habitat transformation, fragmentation, the urban environment, and human preferences) influence plant taxonomic, functional, and phylogenetic diversity. I describe how this analysis can be applied in multiple different urban areas, and how I expect the results to differ in different settings.

In Chapter 3, I analyze changes in the composition of species' traits relating to environmental tolerances, habitat preferences, and dispersal abilities to describe the effects of urbanization on plant communities. I use two methods to assess the effects of urbanization: comparison of communities along the urban-to-rural gradient and comparison of species in urban communities to descriptions of reference communities matched by environmental conditions (e.g., soil nutrients and texture, elevation, stream order). In this way, I am able to use traits to describe changes in species composition with urbanization and especially which species are added to and missing from urban sites when compared to the "expected" vegetation based on reference sites. The use of species' traits helps to identify mechanisms underlying species composition patterns and enhances the potential for comparison across studies.

In Chapter 4, I assess the ability of environmental variables and spatial variables representing habitat connectivity to explain variation in plant species composition across sites. I create multiple models of habitat connectivity between sites and use these to determine whether land use between sites influences species' distributions across space. This chapter speaks to the importance of different ecological processes (environmental filtering and dispersal) for structuring plant communities in an urban landscape.

Chapter 5 serves as a conclusion to this dissertation, summarizing the results of Chapters 2-4. In this, I describe the implications of these results for conservation and restoration in the Research Triangle and point out some remaining knowledge gaps and areas for future research.

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CHAPTER 2: THE FOUR FILTERS OF URBANIZATION AND THEIR EFFECTS ON FOREST PLANT TAXONOMIC, FUNCTIONAL, AND PHYLOGENETIC DIVERSITY

INTRODUCTION

Conserving biodiversity in urban areas is important for maintaining functioning ecosystems and the services they provide, such as clean air and water, aesthetic value, and connections to nature, to the billions of people that live in cities (Dearborn and Kark 2010). However, urban development can also have major impacts on biodiversity, often limiting the suite of native species that persist in urban environments while encouraging the establishment of introduced and anthropophilic species such as ornamental plants and pigeons (Blair 1996, Zerbe et al. 2003). Over the last several decades, many studies have documented changes in species richness along urban-to-rural spatial gradients (reviewed by McKinney 2008, McDonnell and Hahs 2008). A few studies have also examined the effects of urbanization on functional or phylogenetic diversity, measures that describe the distribution of functional traits or the phylogenetic relationships between co-occurring species (Knapp et al. 2008, 2012, Nock et al. 2013, Swan et al. 2016). While this body of work has acted as an important step in the growth of the urban ecology field, its contributions to the development of tangible predictions for the effects of urbanization on biodiversity remain limited. For instance, a number of different observed species richness patterns with increasing urbanization have been found, both across and within taxonomic groups (McKinney 2008), but an understanding of the underlying drivers of these patterns is often lacking (McDonnell and Hahs 2008).

Difficulty in predicting the effects of urbanization on biodiversity arises from the variety of changes to ecosystems caused by urban development. Urbanization creates a spatially heterogeneous landscape of land cover patches and alters local climate, hydrology, and biogeochemical cycles (reviewed by Grimm et al. 2008). In recent years, research focused on the response of biodiversity to one or more of these specific drivers has increased our understanding of urban ecosystems. For example, studies have explored the effects of fine-scale land cover (Godefroid and Koedam 2007), habitat fragmentation (Angold et al. 2006, Burton and Samuelson 2008), and trampling of vegetation (Hamberg et al. 2008) on plant species richness in urban areas. Some have gone a step further, investigating the relative importance of multiple effects of urbanization on biodiversity. Many of these studies assess the relative importance of multiple environmental changes associated with urbanization, such as warmer temperatures, added soil nutrients, and higher heavy metal concentrations, on plant species richness (e.g., Godefroid et al. 2007, Albrecht and Haider 2013, Huang et al. 2013, Schmidt et al. 2014). These studies help to identify which effects of urbanization are most important for determining plant species richness and thus should be targeted in attempts to mitigate those effects. However, few studies have assessed multiple types of drivers, such as socioeconomic factors and environmental conditions (Hope et al. 2003) or habitat fragmentation and disturbance (Hamberg et al. 2008, Ramalho et al. 2014).

In 2009, Williams and colleagues published a conceptual framework for predicting how the multiple effects of urbanization influence the taxonomic (i.e., species), functional, and phylogenetic diversity of plants in cities. Their framework simplifies the complex effects of urbanization on plants to four primary "filters" of plant diversity: habitat transformation, fragmentation, the urban environment, and human preferences. Each of these prevents some species from establishing in urban areas (i.e., acts as a biodiversity filter) while encouraging colonization by other species (Williams et al. 2009). Habitat transformation reduces total remnant area, decreasing the total number of species that can inhabit remaining natural areas by causing the loss of habitat specialists, but can benefit species that thrive in edge habitat (Fahrig 2003, Godefroid and Koedam 2003). Fragmentation may inhibit species with limited dispersal ability from persisting in urban areas, but can also facilitate the spread of exotic species that are introduced in the matrix between remnant fragments (Fahrig 2003, von Der Lippe and Kowarik 2007, Vilà and Ibáñez 2011, Concepción et al. 2015). The urban environment filters species that cannot tolerate the novel environmental conditions, but also benefits species adapted to warmer temperatures, high nutrient availability, and other conditions created by urban development (Williams et al. 2015). Finally, human preferences are responsible for the removal of undesirable species from urban areas, but also the introduction of many new species such as ornamental plants sold in the horticultural industry (Reichard and White 2001). In addition to describing the positive and negative effects of these filters on plant diversity, Williams and colleagues (2009) make predictions for the net effect of each filter on taxonomic, functional, and phylogenetic diversity (Table 2.1). For example, they predict that urban environments have a net negative effect on taxonomic, functional, and phylogenetic diversity by creating novel environmental conditions where only a subset of the regional species pool with traits suited to those conditions are able to establish (as observed for phylogenetic diversity by Knapp et al. 2008).

This framework creates a conceptual model with which to evaluate the multiple effects of urbanization on plants, allowing for potential comparisons across studies and a more synthetic understanding of urban ecosystems. However, while many studies have referenced this framework, to my knowledge the predictions it provides have never been explicitly tested in any one study. Further, no study has specifically used this conceptual model to test the relative ability of the four filters of urbanization to predict plant biodiversity in urban areas. In this chapter, I use data on plant species taxonomic, functional, and phylogenetic diversity and predictor variables representing each of the four urbanization filters described by Williams et al. (2009) to test their predicted relationships between urbanization filters and diversity (Table 2.1) and evaluate the relative predictive ability of each filter. I use structural equation modeling, which allows me to assess a holistic model of the urban ecosystem, including relationships between the urbanization filters, and observe direct and indirect effects of each filter on biodiversity.

METHODS

Study area and site selection

The study was conducted in the Research Triangle area (RTA) of North Carolina, including the cities of Durham, Raleigh, Chapel Hill, and Cary. The RTA is estimated to be home to over 1.8 million people and is a rapidly growing metropolitan region (U.S. Census Bureau Population Division 2016). Urban development has been increasing in the RTA for the past several decades, particularly around the southern and central portions of the region (Cary and the Research Triangle Park), but the landscape remains highly forested (nearly 50% of land cover based on the National Land Cover Dataset [NLCD]; Homer et al. 2015). Most of the forest in this region has been exposed to prolonged human disturbance, particularly since European settlement, and much was cleared for agriculture or selectively harvested for timber.

I collected data at 52 forested sites on public lands in the RTA. In this chapter I use data from 42 of these sites where data were collected within uniformly sized plots (500 m^2). All sites were located within 20 m of a small stream (mostly first- or second-order, with a few third- and fourth-order streams). Sites were selected to span a gradient of urbanization, defined as mean impervious surface cover (%) within a 1 km buffer (calculated from 30 m-resolution land cover data from the NLCD in 2006; Fry et al. 2011). The 42-500 m^2 plots used in this study covered the entire sampled urbanization gradient (0-26% impervious surface cover within 1 km).

Plant community data

Plant species data were collected in the summers (May-September) of 2012-2014. At each site, I sampled vegetation within one randomly placed, rectangular plot. Plots were 10 m wide and 50 m long. Plots were placed roughly parallel to the stream and as close to the stream as possible. Within each plot, I identified and estimated the cover (a proxy for abundance) of all vascular plant species within three strata: the herbaceous layer (0-1m in height), shrub layer (1-4 m in height), and tree layer (4+ m in height). Species cover sampling followed the protocol laid out by the Carolina Vegetation Survey (Peet et al. 1998), with cover estimated to classes on a roughly logarithmic scale (0-1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-95%, or 95-100%). Plants were identified to the species level when possible, but some taxa were only identified to genus or were lumped with another species when the two were difficult to distinguish (e.g. *Symphiotrichum sp.*, *Vitis* [*cinerea* + *vulpina*]). Identification was based on the Flora of Virginia (Weakley et al. 2012).

For this study, I considered only species' cover estimates from the herbaceous layer, which I expected would show more significant effects of urbanization than the larger, often longer-lived overstory. This data includes low-growing vines and shrubs as well as tree seedlings but no adult trees, tall shrubs, or canopy lianas.

Trait data

I compiled data on four categorical and three continuous traits: leaf type, growth form, dispersal mode, wetland indicator status, specific leaf area, seed mass, and leaf nitrogen content (Table 2.2). I chose these traits because they are related to variation in dispersal ability (dispersal mode and seed mass); growth strategy, competitiveness, and stress tolerance (growth form, specific leaf area, and leaf nitrogen content); and habitat type (wetland indicator status). Critically, these traits were also selected because I was able to find data for many of the several hundred species in the community dataset (Table 2.2). Leaf type and growth form categorization came from Weakley (2010), and wetland indicator status data came from the U.S. Army Corps of Engineers's Wetland Plant List (Lichvar et al. 2014). Dispersal mode classification was based on a variety of published sources (but mainly from Matthews 2011 and sources within; Appendix A). Species were allowed to be categorized with more than one dispersal mode. Trait data for categorical traits can be found in Appendix A.

Continuous trait data came from the TRY database (Kattge et al. 2011), which compiles data on plant traits from many data collection efforts. For details on data selection and processing from TRY, see Appendix B. I supplemented data on seed mass and leaf nitrogen for some species missing from TRY with a dataset compiled by Coyle et al. (2014) for Eastern North American tree species. I also found data from other sources for three of several species missing from the TRY database that had high cover within plots (maximum relative cover >10%; Appendix B). I calculated mean trait values for each species and each trait across all observations. Seed mass, which ranged over several orders of magnitude, was log-transformed prior to calculation of functional diversity measures.

Phylogeny construction

I built a phylogeny using the PhytoPhylo vascular plant phylogeny (Qian and Jin 2016), an update of Zanne et al.'s (2014) phylogeny. I used the S.Phylomaker function (Qian and Jin

2016) in R (R Core Development Team 2015) to construct the phylogeny for the species in the dataset, after matching species names using the Plant List (http://www.theplantlist.org/). The S. Phylomaker function provides three options for adding missing species to the phylogeny; I used Scenario 3, which adds taxa as polytomies within parental taxa and estimates branch lengths using BLADJ (Webb and Donoghue 2005, Webb et al. 2008). This scenario is appropriate to use when calculating phylogenetic diversity to compare trends across environmental gradients (Qian and Jin 2016). After matching species names, there were several species from the community dataset still missing from the phylogeny. For those that were considered to be synonymous in the Plant List (e.g., *Acer floridanum* and *Acer leucoderme*, which are both considered subspecies of *Acer saccharum*) or were closely related and somewhat difficult to distinguish in the field (e.g., *Carex typhina*, *C. aureolensis*, and *C. squarrosa*) I lumped these combinations of species together into a single branch tip, and combined them into one species in the community data as well.

Diversity measures

Urbanization may influence plant communities by changing which species are present or absent from sites, but also by changing the relative abundance of species that are present at both rural and urban sites (Nock et al. 2013). To capture these effects, I analyzed changes in both richness measures and evenness measures, those that include information on species' relative abundances and thus capture species dominance or rarity in addition to richness. For taxonomic diversity, I calculated species richness and the Gini-Simpson index or the probability of interspecific encounter (Hurlbert 1971), a measure of evenness that gives the probability that two randomly selected individuals in a community belong to different species.

There are many ways to calculate functional and phylogenetic diversity (Petchey and

Gaston 2006, Tucker et al. 2016). I chose to include a richness and an evenness measure for each and to use measures that I could compare easily to one another. I calculated the sum of all pairwise functional trait differences between species (Functional Attribute Diversity [FAD]; Walker et al. 1999) as a measure of functional richness and the sum of all pairwise distances between species along a phylogenetic tree for phylogenetic richness. Functional differences between species were calculated as Gower's distances. Phylogenetic distances were calculated as phylogenetic branch lengths to the most recent common ancestor or each species pair. To measure functional and phylogenetic evenness, I used Rao's Quadratic Entropy, or the expected difference between any two individuals in a community, calculated as:

$$\sum_{i=1}^{S}\sum_{j=1}^{S} d_{ij}\, p_i p_j$$

where p_i is the relative abundance of species i in the community, and d_{ij} is the difference (functional or phylogenetic distance) between species i and j (Rao 1982, Botta-Dukát 2005). For taxonomic diversity, d_{ij} is equal to 0 when species are the same and 1 when species are different (i.e., all species are considered to be completely and equally distinct from one another), making it equivalent to the Gini-Simpson index (Botta-Dukát 2005). Prior to calculating functional and phylogenetic diversity measures, I scaled all functional and phylogenetic distances by the maximum distance so that all pairwise distances ranged between 0 and 1 (Botta-Dukát 2005, de Bello et al. 2010). I also calculated functional diversity for each trait separately, in order to assess which traits were driving observed trends in functional diversity.

To compare across diversity measures, I transformed all diversity measures into species equivalents, or Hill's numbers. For functional and phylogenetic richness, these are effective numbers of equally distinct species; for taxonomic, functional, and phylogenetic evenness they are effective numbers of equally abundant, equally distinct species. Hill’s numbers have the advantages of being more easily interpretable than abstract measures like Rao’s Q and obey a replication principle, meaning that they scale linearly with the pooling of unique, equally abundant assemblages (Jost 2006, Chao et al. 2014). I calculated Hill’s numbers using equations provided by Chao et al. (2014) and de Bello et al. (2010).

Four filters of urbanization

I collected environmental data in the field to measure aspects of the urban environment and used publicly available remotely sensed and census data as proxies for habitat transformation, fragmentation, and human preferences. To quantify habitat transformation and fragmentation, I used land cover data from the NLCD from 2011 (Homer et al. 2015) to calculate the amount and configuration of forest surrounding sample sites. As a measure of habitat transformation, I calculated the area of forest cover present within a 1 km buffer around each site. This measure represents the amount of habitat remaining after land transformation has taken place. While it ignores past habitat area and land use legacies, which can be important for current plant diversity and species composition (Zerbe et al. 2003, Helm et al. 2006, Ramalho et al. 2014), remaining forest cover is likely an important predictor of current plant diversity based on habitat area. I calculated this measure by reclassifying 30 m-resolution land cover data into forest versus non-forest. To measure fragmentation, I defined clusters of raster cells classified as forest into patches and calculated the Landscape Division Index (LDI) of these patches. LDI is calculated as the sum of the relative size of all forest patches within the buffer, ranging from 0 to 1 and increasing with both the number of forest patches and the similarity in area between patches (i.e., equivalent to the Gini-Simpson index with the area of forest patches in the place of species' abundances; McGarigal 2015). I calculated LDI within a 1 km buffer surrounding each site, first dividing the area of each forest patch by the total forest area within the buffer.

I considered two variables as proxies of human preferences. These were human population density (hereafter “population density”) and median household income (hereafter “income”), both measured at the block group scale from the American Community Survey 2015 5-year estimates (Social Explorer 2017). I expected that the major effect of human preferences would be the introduction of ornamental species to the landscape, and that this effect would be higher in areas with both more people and higher income (Hope et al. 2003, Spear et al. 2013, Concepción et al. 2016). I expected that income alone would be a weaker predictor of plant diversity than population density. However, population density is a crude measure of overall human impacts (Thompson and Jones 1999), including inputs of nutrients via fertilizer application, trampling of vegetation, and creation of pollutants and warmer temperatures from vehicles and other forms of combustion, among other effects.

I measured three components of urban development, related to the urban heat island effect (UHI), the urban stream syndrome (USS), and additions of soil nutrients to urban areas. The UHI is the phenomenon of cities being warmer than surrounding rural areas, and is a function of waste heat from human activities such as driving and absorption of radiation by built surfaces that is released at night (Oke 1995). As a measure of the UHI, I measured air temperature at each field site for one year following data collection using one Onset HOBO data logger (Pendant UA-001-08) at each site and calculated the minimum nighttime (12am to 6am) temperature for each month. I used nighttime temperature because this is when the UHI is strongest (Coseo and Larsen 2014) and used data from August of 2014 because data from this period covered all study sites. The USS, another phenomenon ascribed to urbanization, describes a suite of characteristics of urban streams caused primarily by runoff events during storms that bring large volumes of water into streams along with fertilizer, pollutants, and other materials (Walsh et al. 2005b). One facet of the USS is stream incision, or stream channel deepening, which occurs as a result of rapid water flow in streams during and following storms, and can lead to lowered water tables and changes in flood regimes (Groffman et al. 2003). I quantified stream incision by estimating the width and depth of the stream at each sample site and calculated a depth:width ratio. Finally, I collected soil samples at each site and measured available phosphorus content as an indicator of nutrient addition from fertilizer runoff (Pouyat et al. 2010). Soil chemical analyses were performed by Brookside Labs, Ohio, USA.

Metamodel development

I constructed a meta-model based on the predictions of Williams et al. (2009) for the effects of the four urbanization filters on biodiversity (Figure 2.1A). Because the four filters of urbanization act simultaneously to influence biodiversity and are not independent of one another, I included relationships between them in the model. Specifically, I hypothesized that habitat transformation contributes to fragmentation (Stenhouse 2004), and both habitat conversion and fragmentation promote changes to environmental conditions such as warmer temperatures (Coseo and Larsen 2014; Figure 2.1A). I then made some modifications to this model to accommodate the specific data that I used to represent each filter, which I will describe below (Figure 2.1).

Williams et al. (2009) acknowledge that each urbanization filter has positive effects on some species and negative effects on others, but they also predict that each factor has either a net positive or negative effect on biodiversity (Table 2.1; Figure 2.1A). However, I expected that different aspects of the urban environment may have different, predictable net effects on diversity, as some are generally stressful for plants and thus are more likely to act as strong filters to plant biodiversity (e.g., pollutants such as heavy metals and ozone), while others may encourage plant growth and actually increase the number of species that can inhabit urban environments. Of the three aspects of the urban environment that I measured, I expected that phosphorus would have a negative effect on biodiversity but temperature and stream incision would have positive effects on biodiversity. Additions of phosphorus and other nutrients result in decreases in species richness in some systems by favoring weedy or invasive species that increase in abundance and outcompete other species (Willems et al. 1993, Lake and Leishman 2004, Ceulemans et al. 2013, Leishman et al. 2016). Warmer temperatures could increase diversity by decreasing the stress of winter frost or could decrease diversity by creating water stress in hot months. I hypothesized that the former would be more likely in my study system because high rainfall in the summer months may reduce water stress from hot summers, and warmer winters in areas affected by urban development may help explain observations of species with southern ranges (e.g., *Magnolia grandiflora)* increasing in abundance in my study system in recent years (Gruhn and White 2011). Stream incision may also lead to higher biodiversity in urban areas in the short term by allowing upland species to colonize floodplains where frequent flooding would typically prevent their successful establishment (Groffman et al. 2003, Moffatt et al. 2004). Because of these different expected effects of aspects of the urban environment on plant diversity, I included them as separate variables in analyses (Figure 2.1B). I expected that these measures of the urban environment would be differentially related to other urbanization filters as well: while all of them may be influenced by loss of forest habitat, temperature is also likely influenced by the degree of habitat fragmentation since it can be affected by tree cover, edge effects, and proximity to roads (Coseo and Larsen 2014; Figure 2.1B).

The model I tested with data was slightly different from this modified meta-model because of the proxy variables I used to represent habitat transformation, fragmentation, and human preferences. Since I used forest cover as a measure of habitat transformation, I expected that sites with higher forest cover (and thus presumably lower habitat transformation) would experience lower levels of fragmentation, temperature, phosphorus content, and stream incision (Figure 2.1C). As measures of human preferences, I expected that income and population density would both have positive effects on biodiversity; however, the effect of population density on biodiversity is less certain, since it represents not only species introductions but also other effects of people that may reduce biodiversity. I also expected that population density may have a positive effect on phosphorus via fertilizer inputs by people (Figure 2.1C).

Statistical analyses

I used the lavaan package in R (Rosseel 2012) to fit separate structural equation models (SEMs) for each diversity measure, using the structure shown in Figure 2.1C. Before fitting the models, I examined variable distributions and bivariate relationships between all variables. Population density was log-transformed prior to analysis to reduce skewness. The results of bivariate regressions caused us to make two changes to the model structure: I removed income as a variable from the analyses since it was unrelated to any other variables, and I added an estimate of the correlation between temperature and phosphorus. Prior to model construction, I scaled the range of some predictor variables by multiplying them by factors of 10 to reduce the difference in variances. (For example, forest cover, LDI, and stream incision all ranged from 0 to 1 and were multiplied by 100 prior to SEM analysis.).

Because this study used a relatively small sample size and some variables (e.g. taxonomic evenness) were non-normally distributed, I used bootstrapping to attain more accurate standard errors and p-values (Grace 2006). Census data used in this study were collected within the block group and some plots were found in the same block group unit; therefore I also used the lavaan.survey package (Oberski 2014) to adjust the standard errors and p-values of each model for the structure of census block groups using the Satorra-Bentler correction. I report the p-values from the lavaan.survey results in the few cases when bootstrapping led to the interpretation of a significant path but p-values provided by the Satorra-Bentler Robust method led to a different interpretation. I used the chi-square, RMSEA, CFI, and SRMR tests to evaluate the fit of models, as recommended by Kline (2012). I was interested in evaluating the hypothesized model rather than comparing the fits of different models. Therefore I left non-significant paths in the models (Grace 2006). I assessed the signs of significant paths ($p < 0.05$) to test hypothesized relationships between variables. I also report marginally significant paths ($p < 0.1$).

In order to help interpret the results of each SEM, I performed some additional analyses on subsets of the data, including analyzing data on species richness of native and exotic plant species separately. I also used linear regression to analyze changes in the diversity of individual traits to help interpret patterns of functional diversity.

RESULTS

I found 317 species in the herbaceous layer of the sampled plots. Of these, 265 species were native and 51 were exotic. (One species of *Allium* that was only identified to genus was not determined to be native or exotic.) Species richness in the herbaceous layer varied from 41 to 110 species, with a mean of 70 species per plot.

Bivariate relationships between variables showed that there were strong relationships between forest cover and LDI (r = -0.86), temperature (r = -0.69), population density (r = -0.84), and phosphorus (r = -0.51). Temperature was also correlated with LDI (r = 0.61), population density (r = 0.49), and phosphorus (r = 0.53). There was significant correlation between diversity measures, particularly between taxonomic and phylogenetic richness (r = 0.83). Taxonomic richness had a negative relationship with population density, as did native species richness and phylogenetic richness (Figure 2). Native species richness increased and exotic species richness decreased with increasing forest cover, while taxonomic richness overall showed no change with forest cover (Figure 3). In addition, phylogenetic richness increased and phylogenetic evenness decreased with increasing forest cover (Figure 3). Phylogenetic richness was also negatively correlated with LDI (r = -0.37) and phosphorus (r = -0.42), while phylogenetic evenness was positively correlated with LDI (r = 0.32) and temperature (r = 0.33). Functional evenness was positively correlated with stream incision (r = 0.45). Neither taxonomic evenness nor functional richness showed significant relationships with any predictors.

All SEMs fit the data (Table 2.3) and explained between 14 and 46% of the variation in diversity measures (Figure 2.4). Most of the variation in LDI was explained by forest cover (R^2 = 0.75; Figure 2.4A). The model also explained much of the variation in temperature (R^2 = 0.48), which was significantly related to forest cover (p = 0.008) but not LDI (p = 0.660). Phosphorus content was significantly explained by forest cover (R^2 = 0.29, p=0.001) but not population density (p = 0.215), and was correlated with temperature (p = 0.078). Stream incision was not explained by the other predictors in the model.

The ability of predictors to significantly explain variation in plant diversity varied strongly across diversity measures (Figure 4; effects summarized in Table 2.4). Species richness decreased with increasing population density ($R^2 = 0.27$, $p = 0.033$; Figure 2.4A), which was also true for native species richness ($R^2 = 0.32$, $p = 0.021$; Figure 2.4B). Exotic species richness decreased with increasing forest cover ($R^2 = 0.44$; $p = 0.051$; Figure 2.4C) and increased with increasing stream incision ($p = 0.096$). Species evenness was not explained by any predictor variables.

Phylogenetic richness was predicted by the three environmental variables ($R^2 = 0.46$; Figure 4D), with lower phylogenetic richness in sites with high phosphorus content ($p = 0.017$) but higher phylogenetic richness in sites with warmer temperatures ($p = 0.086$) and more incised streams ($p = 0.048$). In contrast, phylogenetic evenness decreased with increasing forest cover ($R^2 = 0.22$, $p = 0.054$; Figure 2.4E).

Functional richness was not significantly related to any predictors in the SEM, but functional evenness increased with increasing stream incision ($R^2 = 0.22$, $p = 0.004$). This trend was explained to some extent by a positive relationship between functional evenness of species' leaf nitrogen content and stream incision ($R^2 = 0.25$, $p<0.001$). Data for continuous functional traits such as leaf nitrogen content were not available for many species in the dataset, accounting for less than 50% of the cover for 8 of the 42 plots. However, when I removed these plots from functional diversity analyses, I saw no significant changes in the results.

DISCUSSION

I found that the observed effects of each urbanization filter depended on whether the biodiversity response was measured as taxonomic, functional, or phylogenetic diversity and whether richness or evenness was considered. Some of the predictors did indeed act as “filters”, limiting the diversity of plant communities, while others increased diversity. In addition, some predictors such as forest cover had both indirect and direct effects on biodiversity.

Effects of the urban environment

I included multiple measures of the urban environment in this study because I expected that many of them would be important predictors of biodiversity but that not all would act as biodiversity filters. Indeed, I found both negative and positive effects of the urban environment on diversity.

Phosphorus content appears to act as a biodiversity filter in my study system, supporting Williams and colleagues' (2009) prediction that urban environments would lead to lower plant diversity. I found that sites with high phosphorus content had lower taxonomic and phylogenetic richness. I expected that this trend would result from a loss of native plant species with phosphorus additions, as has been found in other studies (Willems et al. 1993, Ceulemans et al. 2013), but this did not appear to be the case. Although I did not see an increase in exotic species richness with increasing phosphorus, one potential mechanism for the observed decease in biodiversity is an increase in the abundance of some weedy or exotic species (Ostertag and Verwille 2002, Leishman and Thomson 2005, Fisher et al. 2008). Elevated phosphorus levels may be an important aspect of the urban environment in many cities, as a result of runoff from yards and other fertilized areas and from nearby roads (Kaye et al. 2006, Park et al. 2010). Phosphorus additions are likely coincident with additions of other nutrients such as nitrogen, which may also have a significant effect on plant diversity (Willems et al. 1993, Ostertag and Verwille 2002) but were not measured here. Phosphorus was also correlated with temperature (a marginally significant relationship), which may be due to other effects of urbanization like distance to roads that were not included in my analyses.

Unlike phosphorus, temperature and incision had positive effects on some measures of diversity in SEMs. Warmer sites had relatively high phylogenetic richness (a marginally significant relationship), suggesting that warmer temperatures may allow phylogenetically distinct species to move into urban forest patches. These may be species with southern ranges or phylogenetically conserved traits that allow them to take advantage of the warmer temperatures, such as evergreen leaves. Stream incision had a positive relationship with functional evenness, which appeared to be driven primarily by an increase in functional evenness for leaf nitrogen. This suggests that forests adjacent to incised streams may have a higher diversity of growth strategies, on the spectrum from fast growth and high resource use to slow growth and low resource use (Wright et al. 2004). This may be due in part to changes in the flooding regime associated with stream incision and the USS. Flooding acts as a strong environmental filter in floodplains, and changes to the flooding regime could allow plants with different growth strategies (i.e., upland and flood-intolerant species, including some exotic species) to establish in floodplains (Groffman et al. 2003, Sung et al. 2011, Catford and Jansson 2014, Brice et al. 2016). However, I did not see a corresponding change in the diversity of species' wetland indicator statuses with stream incision. Another potential mechanism for the change in functional diversity of leaf nitrogen content is that stream incision may be correlated with other symptoms of the USS, such as nitrogen additions from stormwater runoff.

Habitat transformation, fragmentation, and human pressure

Habitat loss and fragmentation are closely linked, and together can contribute to the loss of rare, specialist, and dispersal-limited species (Fahrig 2003). Habitat area (forest cover) was an important predictor of diversity in my analyses, with decreases in forest cover associated with increases in exotic species richness and phylogenetic evenness. I suspect that the effects on phylogenetic diversity are due to an increase in exotic, upland species in small forest patches. Although many exotic species in the study system come from the same families or even genera as native species, some are members of plant families unrepresented in the local native species pool that could increase phylogenetic diversity at these sites (e.g., Berberidaceae, Araliaceae, Elaeagnaceae). In addition to these direct effects, increasing forest cover had indirect positive effects on native species richness and phylogenetic richness via a decrease in phosphorus and increase in temperature.

I did not find any effects of fragmentation on diversity, but this may be due to the strong relationship between fragmentation and forest cover in the dataset. Indeed, some of the effects of fragmentation on dispersal may be accounted for in this study by differences in habitat area across sites. I found an increase in exotic species richness in sites with low forest cover, suggesting that exotics are better able to disperse into these sites or are facilitated by edge effects. Alternately, there may be effects of fragmentation on diversity that are not captured by the measure I used because it did not take any characteristics of the matrix between forest patches into account. Finally, it is also possible that fragmentation is truly not very important for diversity in the study landscape, where remnant forest is highly connected compared to some larger metropolitan areas. High connectivity between forest sites may make fragmentation effects less pronounced than they would be in landscapes with higher land cover heterogeneity.

Human preferences are expected to increase biodiversity primarily through introductions of novel species (Williams et al. 2009). While I expect that available data on human population density has some relationship to the strength of human preferences on plant communities, it is certainly not an ideal measure of human preferences, both because it does not adequately capture human decisions regarding plants and because it is likely correlated with many other effects of urbanization that may influence plants, including forest cover. Although population density was not a great measure of human preferences, it did have a significant negative effect on multiple measures of diversity, apparently by reducing the number of phylogenetically distinct native species from areas of high human impact. Unfortunately, the mechanisms for this loss are not clear, and may be due to unmeasured effects such as trampling, changes in herbivore densities, or environmental effects such as pollutant additions.

Implications for urban conservation

I found both positive and negative effects of urbanization on taxonomic, functional, and phylogenetic diversity. However, it is important to note that positive effects were often attributable to increases in exotic species, a response that may not be desirable for purposes of conserving biodiversity in urban areas and may create novel communities (Hobbs et al. 2006, Kowarik 2011). In addition, decreases in taxonomic and phylogenetic diversity in response to increased human impact and altered urban environments are concerning. These effects may mean that urban forests will be less able than rural forests to respond to changing environmental conditions in the future (Knapp et al. 2008). Considering measures of diversity other than species richness and looking at patterns for both native and exotic species help to illuminate these different effects.

My results point to the importance of setting aside large patches of remnant habitat in order to maintain diversity in urban areas. Sites with higher forest cover in this study had higher connectivity between forested areas, fewer exotic species, and lower phosphorus content, thus strongly contributing to overall diversity patterns. These findings support those of other studies, which have found that remnant habitat patch size and connectivity are important indicators of species richness (Ramalho et al. 2014, Beninde et al. 2015), either directly or through indirect effects on herbivore density and environmental conditions (Ramalho et al. 2014). However, conservation of large areas is not often feasible, particular in urban areas where land prices are high. Thus it is also important to consider ways to manage smaller habitat patches to improve their ability to harbor biodiversity.

I also found that environmental conditions associated with urbanization can have significant impacts on biodiversity. Therefore attempting to mitigate some of the environmental impacts of urbanization could be another important strategy for conservation, particularly in small forest patches. Of the environmental variables I considered in this study, soil phosphorus availability is the clearest target for mitigation because of its negative effects on taxonomic and phylogenetic richness. Stream incision may also be a good target for mitigation since it is associated with increased exotic species richness. Both stream incision and nutrient additions are related to the USS, resulting from stormwater runoff (Walsh et al. 2005b). Local stream restoration, a common practice in urban areas, can reduce stream incision, but restoring flooding regimes and reducing nutrient inputs may require watershed-scale efforts (Walsh et al. 2005a, Bernhardt and Palmer 2007). Plans to maintain riparian buffers and increase green infrastructure may help to reduce the impacts of the USS.

Although I did not see clear effects of human preferences in this study, there were prominent effects of urbanization on exotic species richness. Exotic species may impact local environmental conditions and recruitment of native species (Richardson et al. 2007). Because of this, exotic species removal is common in restoration projects and management of conservation lands. However, removal of exotic species can be expensive or simply infeasible (Simmons et al. 2015). I found some indications that exotic species contribute to phylogenetic diversity in the study system, which may have some positive effects on ecosystem functioning or resilience to environmental change (Cadotte et al. 2012, Srivastava et al. 2012). Thus the question of how much emphasis should be placed on exotic species management remains open. If exotic species in urban forests is a concern, education about the potential negative effects of exotic species may be a useful strategy for changing the effects of human preferences on plant communities. Future work to identify the contribution of people's choices of what plants to keep in their yards could provide further insight into opportunities to mitigate the effects of urbanization on biodiversity.

The four filters of urbanization and comparative urban ecology

The utility of the conceptual framework developed by Williams ans colleagues (2009) is that it can apply to many urban ecosystems and allow for comparison between them. In this paper, I used this framework to develop a meta-model that can be tested in multiple cities to gain a more synthetic understanding of the effects of urbanization on biodiversity. I expect that other cities will show different trends that will improve our understanding of contingencies on the effects of urbanization on ecosystems. My system is somewhat unique in that it has lots of remnant forest and high baseline plant biodiversity. I would expect that the effects of fragmentation are higher in cities with less connected remnant vegetation and that the effects of individual environmental factors and environmental filtering as a whole will be different in cities with different background environments, such as in different climates. Human preferences are likely more important in actively managed sites and in studies where the focus is an entire urban flora or non-remnant habitat patches.

Future studies may improve upon this method by identifying alternate proxy measures for urbanization filters. As with all landscape-scale studies investigating multiple drivers, I was limited in my inference by the appropriateness of available data to quantify the drivers of interest. I used mostly publicly available data as proxies of different urbanization filters. This maximizes the applicability of my methodology to other study systems, at least in places like the United States where remotely sensed data products and census data have comprehensive coverage. However, I also relied on environmental data that was collected in the field, which could limit comparison to some studies that lack access to such data. Finally, I lacked a good measure of human preferences, which I expect will be difficult to quantify in other studies as well. Ecologists are more frequently engaging in collaborations with social scientists to collect survey data to address some of these important factors (e.g., Avolio et al. 2014), which I expect will lead to greater ability to quantify human influences on biodiversity in the future.

Table 2.1. Predictions of the net effects of the four filters of urbanization on plant biodiversity (modified from Williams et al. 2009).

	Predicted effects on diversity			
Filter	**Taxonomic**	**Functional**	**Phylogenetic**	**Explanation**
Habitat transformation	decrease	decrease		Loss of specialist species from the most frequently converted habitats (e.g. wetlands). Loss of sink species.
Fragmentation	decrease	decrease	decrease	Loss of species with limited dispersal or reproductive output and species with specialist mutualists. Gain of exotic species.
Urban environment	decrease	decrease	decrease	Loss of species that cannot tolerate novel environmental conditions.
Human preferences	increase		increase	Gain of ornamental and other exotic species.

Table 2.2. Information on traits used in analyses of functional diversity.

Trait	Type	Categories or Units	% of species with data
Categorical			
Leaf type	Categorical	Evergreen Deciduous	100
Growth form	Categorical	Tree Shrub Subshrub Vine Forb Graminoid	100
Dispersal mode	Categorical	Wind Water Vertebrate Unassisted	91
Wetland indicator status	Ordinal	1: Upland 2: Facultative upland 3: Facultative 4: Facultative wetland 5: Obligate wetland	97
Continuous			
Specific leaf area	Numeric	mm^2/mg	53
Seed mass	Numeric	mg	71
Leaf nitrogen content	Numeric	mg/g	51

Table 2.3. Model fit statistics for structural equation models.

	χ^2	df	Bollen-Stine bootstrap p	RMSEA	CFI	SRMR
Taxonomic Richness	4.395	7	0.72	1	0	0.034
Taxonomic Evenness	4.395	7	0.71	1	0	0.031
Phylogenetic Richness	4.395	7	0.721	1	0	0.035
Phylogenetic Evenness	4.395	7	0.705	1	0	0.032
Functional Richness	4.395	7	0.723	1	0	0.032
Functional Evenness	4.395	7	0.676	1	0	0.032
Native Species Richness	4.395	7	0.688	1	0	0.033
Exotic Species Richness	4.395	7	0.716	1	0	0.032

Table 2.4. Overview of observed effects of biodiversity “filters” on measures of biodiversity.

			Taxonomic Diversity		**Functional Diversity**		**Phylogenetic Diversity**	
Filter	**Variable**	**Predicted effect**	**Richness**	**Evenness**	**Richness**	**Evenness**	**Richness**	**Evenness**
Habitat transformation	Forest cover (note: opposite sign of relationships shown)	–						+
Fragmentation	LDI	–						
Urban environment	Temperature	+					+	
	Phosphorus	–	–				–	
	Stream incision	+				+	+	
Human preferences	Population density	+	–					–

Figure 2.1. Meta-model diagram of relationships between predictor variables (urbanization filters) and plant biodiversity. Conceptual variables are outlined in dashed boxes and measured variables are outlined in solid boxes. Black arrows represent negative hypothesized relationships and red arrows represent positive hypothesized relationships. I hypothesized that habitat transformation would influence fragmentation and both variables would affect the urban environment (**A**), but different measures of the urban environment would have positive or negative effects on biodiversity (**B**). Expected relationships between all observed variables are shown in **C**.

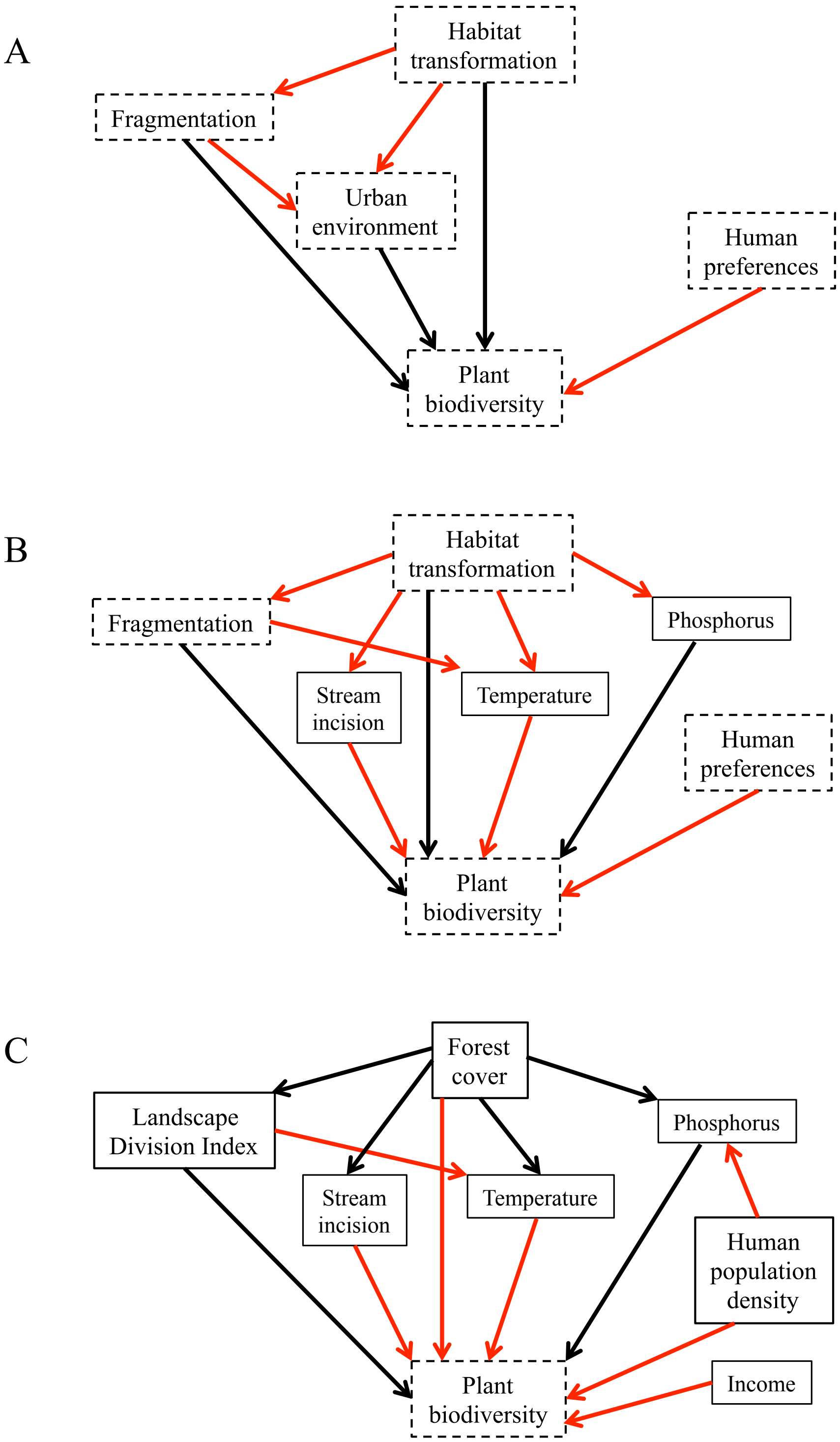

A
Habitat transformation
Fragmentation
Urban environment
Human preferences
Plant biodiversity
B
Habitat transformation
Fragmentation
Phosphorus
Stream incision
Temperature
Human preferences
Plant biodiversity
C
Forest cover
Landscape Division Index
Phosphorus
Stream incision
Temperature
Human population density
Income
Plant biodiversity

Figure 2.2. Bivariate relationships between diversity measures and population density with standard errors. Relationships with population density depend on whether analyzing data on richness for all species (**A**), native species (**B**), or exotic species (**C**) and whether using presence/absence (**A**, **E**) or abundance (**D**, **F**) data. Phylogenetic richness shows a similar pattern with population density to that shown by taxonomic richness, but the relationship is slightly stronger. Linear relationships and R^2 are shown only when relationship was significant ($p < 0.05$).

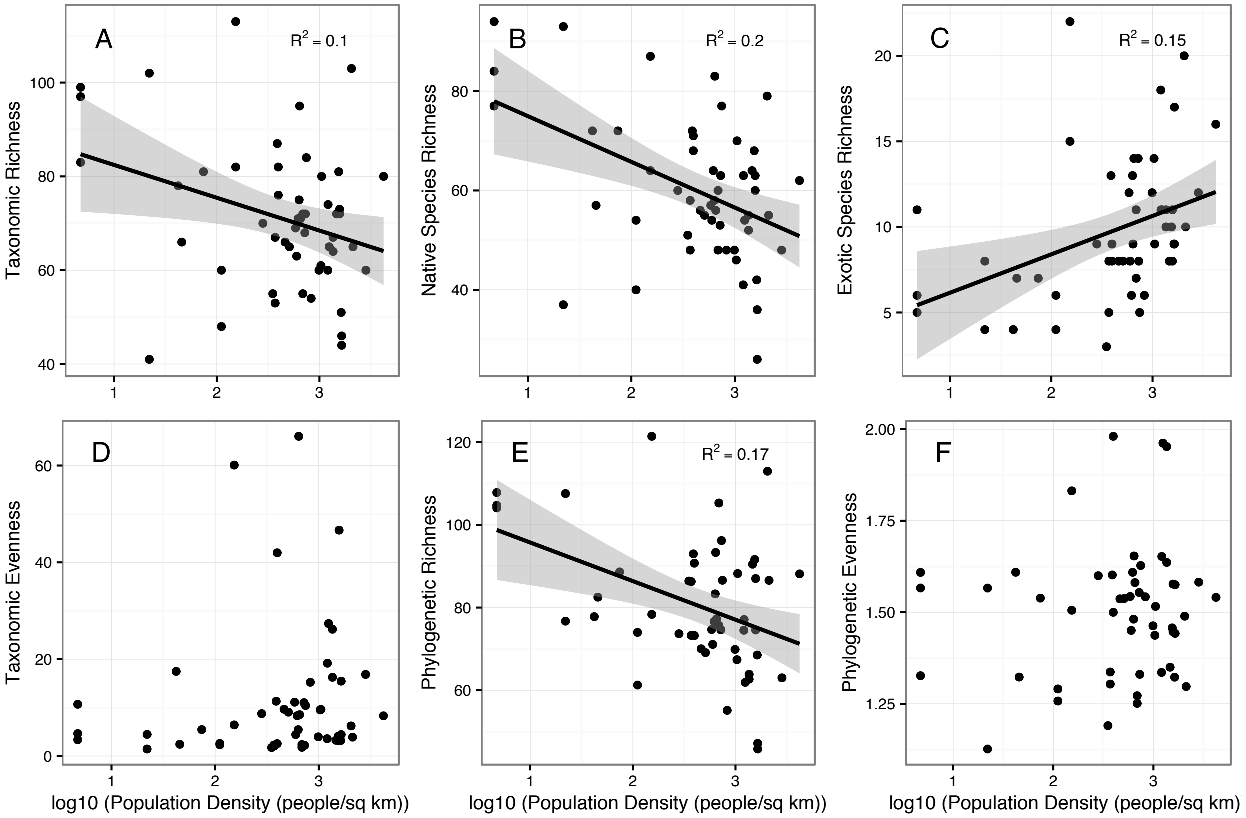


Figure 2.3. Bivariate relationships between diversity measures and forest cover, with standard errors. This figure demonstrates the differences between relationships depending on whether abundance data (richness vs. evenness) and phylogenetic information (taxonomic vs. phylogenetic diversity) is used. Taxonomic richness shows no relationship with forest cover (**A**), due to an increase in native species richness (**B**) and decrease in exotic species richness with forest cover (**C**). Linear relationships and R^2 are shown only when relationship was significant ($p < 0.05$).

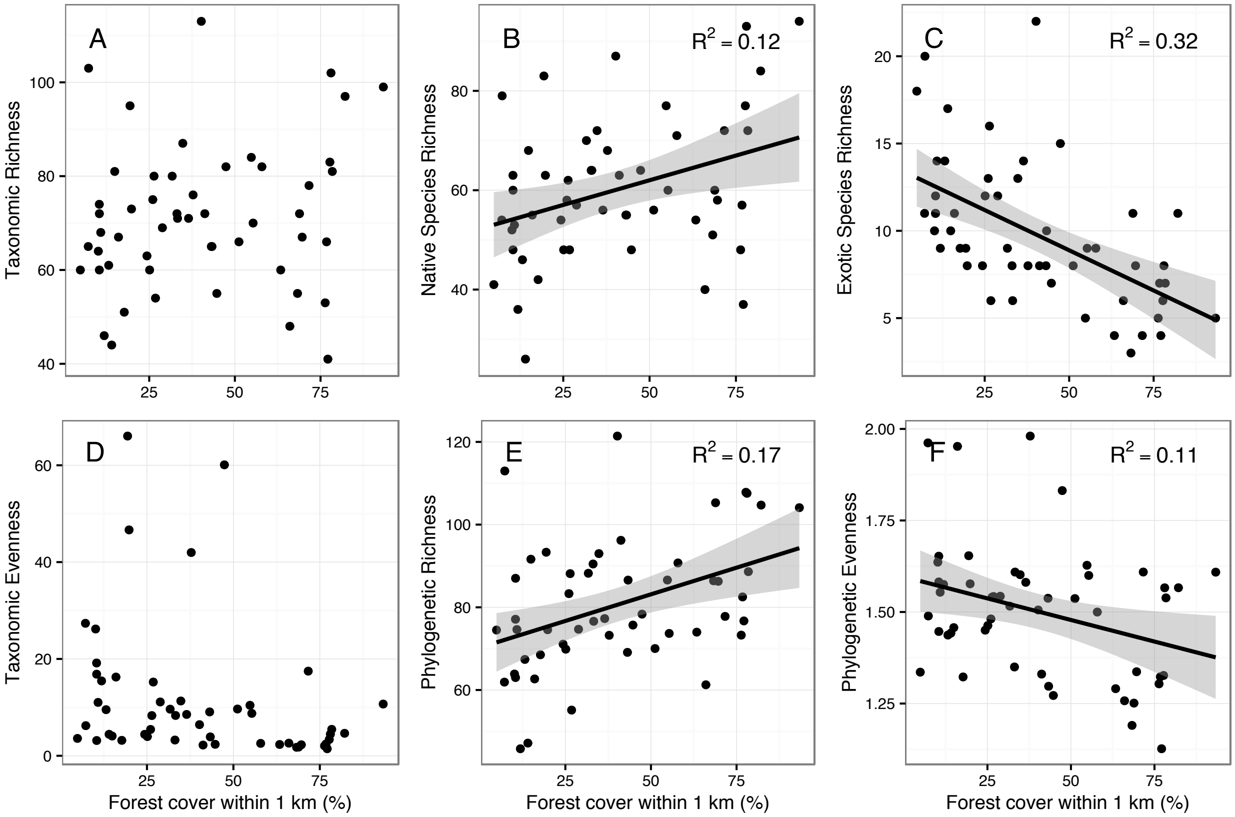
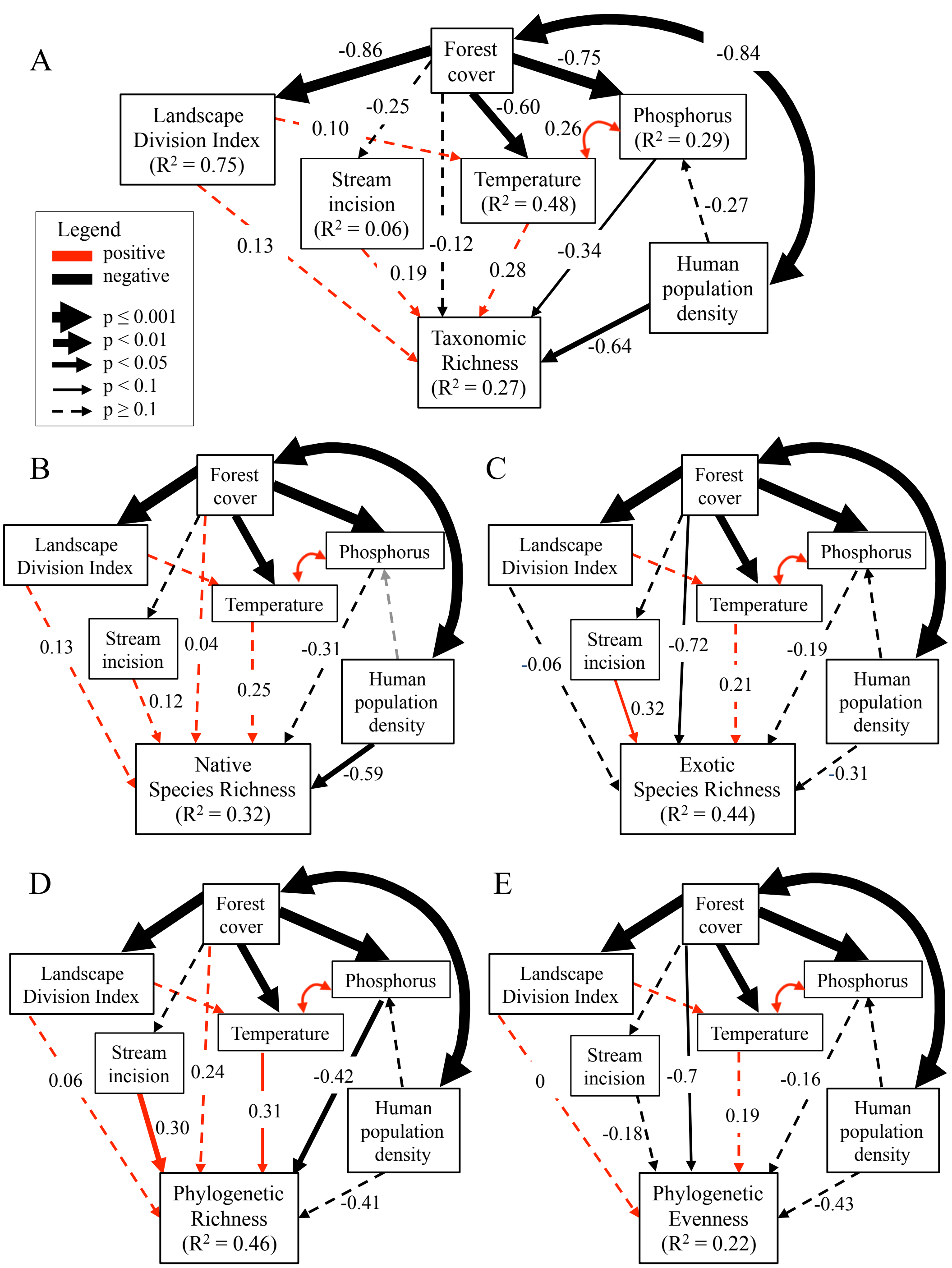


Figure 2.4. Results of structural equation models predicting taxonomic richness (**A**), native (**B**) and exotic (**C**) species richness, phylogenetic richness (**D**), and phylogenetic evenness (**E**). Relationships between predictors are only shown in **A**, and relationships between predictors and diversity measures are shown in all panels. Standardized effect sizes are shown. Arrow size reflects the level of significance, and non-significant paths ($p > 0.1$) are shown with dashed lines. Fit measures for all models suggest an adequate fit to the data (see Table 2.3).



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CHAPTER 3: USING PLANT TRAITS TO DETERMINE THE OPPORTUNITIES AND LIMITATIONS OF RIPARIAN FOREST RESTORATION IN URBAN AREAS

INTRODUCTION

With the growth of urban areas worldwide (Seto et al. 2011), it is increasingly important to understand how urban development influences ecosystems. In the last several decades a growing body of research has addressed this knowledge gap, including a number of studies examining changes in plant species diversity and composition in response to urbanization. Some researchers have made use of historical records such as herbarium specimens to track changes in species composition over time as urbanization has progressed (e.g., Stehlik et al. 2007, Hahs et al. 2009, Duncan et al. 2011). More commonly, urban ecologists take a space-for-time substitution approach, comparing plant communities sampled along gradients spanning from rural to urban areas (Williams et al. 2005, Burton and Samuelson 2008, Pennington et al. 2010, Trammell and Carreiro 2011, Aronson et al. 2015). Documenting the effects of urbanization can inform urban conservation and restoration efforts by identifying species of concern and species that persist in urban areas.

Restoration of degraded lands is a common strategy for combating biodiversity loss and environmental changes caused by human activities. Many restoration projects involve re-establishing native plant species (Stanturf et al. 2014), often with the selection of a target species list to guide initial planting and/or assess project success (Brinson and Rheinhardt 1996, Harris 1999, Rheinhardt et al. 1999). Target species lists are sometimes based on descriptions of high quality reference communities or plant community types, the result of regional (e.g., the Carolina Vegetation Survey) and national (e.g., the National Vegetation Classification) efforts to sample and describe natural variation in plant community composition. The benefit of using reference communities to define restoration targets is that they identify a set of species that typically co-occur and are often linked to a particular geographic and environmental conditions (Lane and Texler 2009, Matthews et al. 2011). Matching the target species list to the setting of the restoration site may produce more historically realistic restored communities and a higher likelihood of project success (White and Walker 1997, Lane and Texler 2009).

A potential problem with using reference communities to define target species lists for urban restoration is that some of the species present in reference sites may fail to establish or persist in urban areas. Urbanization has several different effects that can negatively affect some plant species. Urban development changes local environmental conditions, including warmer temperatures (the urban heat island effect; Oke 1995), altered hydrology (the urban stream syndrome; Walsh et al. 2005), and higher concentrations of nutrients and pollutants (Lovett et al. 2000, Pouyat et al. 2008). In addition, urbanization reduces the size and connectivity of vegetated areas (Stenhouse 2004), which can lead to a decline in habitat specialists and rare species (Van der Veken et al. 2004), as well as reducing the ability of some species to disperse between isolated habitat patches (Knapp et al. 2009, Concepción et al. 2015). Identifying which species tolerate urban environments and which do not can inform modification of target species lists based on reference sites to make them more appropriate for restoration in urban areas.

Considering species' traits can aid in developing predictions for which species will respond to urbanization in different ways (Duncan et al. 2011, Williams et al. 2015). Data on traits relating to species' environmental tolerances, habitat preferences, dispersal ability, and growth strategy are increasingly used in studies of the effects of urbanization on plant communities (Williams et al. 2005, Burton et al. 2009, Knapp et al. 2009, Palma et al. 2016, Brice et al. 2016, Kalusová et al. 2017). This approach has several benefits. One is that it allows for comparison across studies with different species pools, thus enabling prediction and promoting synthesis across studies (Williams et al. 2015). Additionally, when traits are linked to particular environmental gradients or community assembly processes such as dispersal, can provide more insight into the mechanisms driving changes in species composition (Lavorel and Garnier 2002, McGill et al. 2006, Lopez et al. 2016).

In this chapter, I used information on species' traits to assess the effects of urbanization on riparian forest plant communities in the Research Triangle area of North Carolina. Urban streams and adjacent riparian forests are common targets of urban restoration, particularly in North Carolina (Sudduth et al. 2007), because they are often highly modified by the movement of stormwater over impervious surfaces and through pipes (Walsh et al. 2005b, Bernhardt and Palmer 2007). I used two approaches to assess the effects of urbanization on plant communities: analyzing changes in species' traits in communities spanning an urban-to-rural gradient and comparing the species- and trait composition of these communities to reference community types with similar environmental conditions. These approaches allowed me to ask the following questions: 1) Are there predictable changes in plant species' functional traits along the urbanization gradient? and 2) How are plant communities in urban sites different from reference plant communities in terms of species' traits? I made predictions for how the composition of traits related to species' provenance, growth strategy, habitat, and dispersal ability would change with urbanization (summarized in Table 3.1). I expected that more urban sites would be more different from reference community types and that this effect might be explained by the traits of species missing from urban sites and those added to urban sites.

METHODS

Plant community data

I collected data on plant species composition at 52 riparian forest sites in the Research Triangle area, located within the Piedmont region of North Carolina. The Research Triangle area has a population of over 1.8 million people (U.S. Census Bureau Population Division 2016) and includes the cities of Durham, Raleigh, Chapel Hill, and Cary. All sample sites were located on public lands within the floodplains of small streams (first- to fourth order) of the Neuse and Cape Fear River watersheds. Sites were chosen to span a gradient of urbanization, defined as mean impervious surface cover (%) within a 1 km buffer (calculated from 30 m-resolution land cover data from the National Land Cover Dataset [NLCD] in 2006; Fry et al. 2011). Data were collected in the summers (May-September) of 2012-2014.

At each site, I sampled vegetation within one randomly placed, rectangular plot. Plots were 10 m wide and 30, 40, or 50 m long, depending on the size of the forest patch, width of the floodplain, and sinuosity of the stream. Plots were placed roughly parallel to the stream with the length of the plot adjacent to the stream, as close to the stream as possible. Within each plot, I identified and estimated the cover (a proxy for abundance) of every vascular plant species I could find. Species cover sampling followed the protocol laid out by the Carolina Vegetation Survey (Peet et al. 1998), with cover estimated to classes on a roughly logarithmic scale (0-1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-95%, or 95-100%). Plants were identified to the species level when possible, but some taxa were only identified to genus or were lumped with another species when the two were difficult to distinguish (e.g. *Symphiotrichum sp*., *Vitis* [*cinerea* + *vulpina*]). Identification was based on the Flora of Virginia (Weakley et al. 2012).

Reference community data

I used descriptions of riparian forest community types as potential restoration target species lists against which to compare sampled plant communities. These twelve reference community types were described by Matthews et al. (2011) as a proposed update to the National Vegetation Classification (Table 3.2). Matthews et al. (2011) defined the community types using a community classification analysis performed on 182 high quality riparian plant communities in the North Carolina Piedmont that were sampled using the Carolina Vegetation Survey protocol. Descriptions of reference community types consist of a list of species found in at least one third of the vegetation plots classified into that community type, along with the mean cover value of that species within plots classified into that community type. One of the goals of the community classification and description was to provide restoration targets for riparian forests in this region based on quantitative vegetation data and matched to geographic and environmental specifications of restoration sites (Matthews et al. 2011). Thus it was appropriate to use these reference community type species lists as plausible examples of restoration targets.

I also accessed data from a set of the high quality sites that had been used to perform the original community classification by Matthews et al. (2011) from the Carolina Vegetation Survey database. I did this in order to quantify typical variation across communities classified into the same community type, so that I could evaluate whether the sampled communities were more different from reference community types than would be expected from natural variation in species composition across communities. For this, I chose the 45 sites that are located within the Cape Fear and Neuse watersheds and have a similar range of stream order and floodplain width as the sampled sites.

I created a single site-by-species matrix using all three datasets (reference community types, high quality sites, and communities sampled along the urbanization gradient) to be able to compare species composition between them. It was necessary to reconcile differences in species names and identification between the datasets, which all differed somewhat in their taxonomic resolution and naming conventions. In cases where species were only identified to the genus level in one dataset, I lumped the species in that genus to the genus level across datasets, with the exception of unique, easily identifiable species. I used my botanical knowledge and best judgment to decide which species to lump and which to keep separate. I also removed all species that were found in less than 10% of either the high quality sites or our sampled sites, retaining all species that were included in the reference community type descriptions. Matching species names and removing rare species from the dataset allowed me to make more conservative estimates of differences in species composition between sampled sites and restoration targets.

Trait data

I compiled data on a number of traits related to species' provenance (native vs. exotic), growth strategy (woody vs. herbaceous, evergreen vs. deciduous, specific leaf area, and leaf nitrogen content), habitat (wetland indicator status, range orientation [northern, southern, both, or neither]), and dispersal ability (dispersal mode, seed mass; Table 3.1). Information on leaf type, woodiness, range orientation, and growth form categorization came from Weakley (2010), and wetland indicator status data came from the U.S. Army Corps of Engineers's Wetland Plant List (Lichvar et al. 2014). Dispersal mode classification was based on a variety of published sources (but mainly from Matthews 2011 and sources within; Appendix A). Species were allowed to be categorized with more than one dispersal mode. Continuous trait data came from the TRY database (Kattge et al. 2011), which compiles data on plant traits from many data collection efforts. Details on trait data acquisition and processing can be found in Appendix B. I supplemented data on seed mass and leaf nitrogen for some species missing from TRY with a dataset compiled by Coyle et al. (2014) for Eastern North American tree species. I also found data from other sources for three of several species missing from the TRY database that had high cover within plots (maximum relative cover >10%; Appendix B). I calculated mean trait values for each species and each trait across all observations. Seed mass, which ranged over several orders of magnitude, was log-transformed prior to calculation of functional diversity measures.

Environmental and land cover data

I collected environmental data at each of our 52 field sites at the time of plant community sampling. Environmental variables measured in the field included geomorphic position, slope (measured using a clinometer), geographic coordinates, distance to the stream channel, and soil nutrient and texture variables (analyzed by Brookside Labs in Ohio from soil samples collected from the A layer [top 10 cm of mineral soil]). As a measure of the urban heat island effect, I measured air temperature at each field site for one year following data collection using one Onset HOBO data logger (Pendant UA-001-08) at each site, and calculated the minimum nighttime (12am to 6am) temperature for each month. I used nighttime temperature because this is when the urban heat island effect is strongest (Coseo and Larsen 2014) and used data from August of 2014 because data from this period covered all study sites. I also quantified stream incision, or stream channel deepening, by estimating the width and depth of the stream at each sample site and calculated a depth:width ratio.

I used a GIS to acquire data on other environmental variables from publicly available datasets: elevation from the USGS National Elevation Dataset (http://ned.usgs.gov/), stream order and cumulative upstream area drained (watershed area) determined from surface water themes from the USGS National Hydrography Dataset (http://nhd.usgs.gov/) using the FLoWS and STARS toolboxes in ArcGIS (Theobald et al. 2005, Peterson and Ver Hoef 2014), width of the 100-year floodplain determined from North Carolina digital floodplain maps (http://www.ncfloodmaps.com/), mean annual temperature and precipitation from PRISM (PRISM Climate Group; http://prism.oregonstate.edu), and mapped soil unit and bedrock formation from the USDA-NRCS Soil Survey Geographic Database (SSURGO; http://soildatamart.nrcs.usda.gov/). These data were used to match sample sites to reference community types with similar environmental conditions (see below). I also calculated impervious surface cover and forest cover (using NLCD data from 2011; Homer et al. 2015) within a 1 km buffer surrounding each site. To calculate the amount of forest cover for each site, I first classified land cover data into either forest (including Deciduous Forest, Evergreen Forest, Mixed Forest, and Woody Wetlands) or non-forest.

Data analysis: Comparison to restoration targets

To determine how the sampled plant communities differ from restoration targets, I matched each sampled community to reference community types with similar environmental conditions. As part of their community classification analysis to define riparian forest community types, Matthews et al. (2011) determined the environmental variables that were related to differences between community types. Matthews (2011) and colleagues then created a database tool that matches restoration sites to reference community types based on these environmental variables. To use this tool, users input data on the environmental conditions of the restoration site, including geomorphic position, mapped soil series, floodplain width, stream order, and mean annual temperature and precipitation (i.e., variables that are usually easily determined on-site or available from existing datasets). There is also an option to include data on soil nutrients and texture, which I chose to do since we had collected soil data at the sample sites. The tool then calculates dissimilarity between the input environmental data and the mean values for high quality sites classified into each of the twelve reference community types in the original community classification (Matthews et al. 2011). Environmental dissimilarity is calculated as

$$\frac{\sum |N_i - G_i| * w_i}{\sum |N_i + G_i| * w_i}$$

where N_i = i^{th} environmental variable at the new site, G_i = group average for i^{th} environmental variable, w_i = weight for i^{th} environmental variable. The user can then select the reference community type with the most similar environmental conditions to the new (restoration) site and receive a list of the species that are associated with that community type (i.e., those found in at least one third of the plots classified into that community type in the original dataset) and their mean cover.

I used this tool to match each of the sampled plots to reference community types with similar environmental conditions, and then compared the species lists for the sampled plots and the restoration targets. I used equal weights for all environmental variables. Most of the sampled plots were reported by the database tool to be similar to multiple reference community types (difference in dissimilarity metric of environmental conditions <0.02). I therefore compared each sampled plot to two reference community types: the one with the most similar environmental conditions, and the one of the top three most environmentally similar community types that had the most similar species composition to the sampled plot. The latter was determined by calculating the Bray-Curtis dissimilarity between each plot and the three most environmentally similar reference community types to find the most compositionally similar of these options. I used presence-absence data to calculate dissimilarity because of possible differences in species' cover estimation that could exaggerate species composition dissimilarity between the two datasets.

I used linear regression to examine changes in the Bray-Curtis dissimilarity between each plot and its matched restoration target in response to impervious surface cover and forest cover, to see if communities located in more urban or less forested sites were more different from reference communities. I also used analysis of variance to compare the dissimilarity between sampled plots and reference community types to the dissimilarity between the high quality reference sites and reference community type descriptions. To do this, I compared the minimum dissimilarity between each sampled plot and any reference community type (whether or not it was matched to the environmental conditions) and the minimum dissimilarity between each high quality reference sites and any reference community type.

I used two methods to explore how the species and traits of sampled sites were different from environmentally similar reference community types. For both methods, I compared the species composition of each site to the most compositionally similar of the top three most environmentally similar reference community types, in order to make sure that differences were not simply due to considering the wrong reference community type. First I identified missing and added species for each plot, to look at how the traits of these species groups changed with urbanization. Missing species were those that were expected to occur at the site based on the restoration target species list but were not found there, and added species were those found at the site that were not included on the restoration target species list. I calculated the proportion of all species from each restoration target species list that were missing from the site and the proportion of species found in the plot that were added (i.e., not included in the restoration target species list). To determine how species' traits influenced which species were missing from or added to sites, I calculated the proportion of missing and added species for each plot that fell into the different trait categories described above. For numeric traits I calculated a community-weighted mean, treating all species as equally abundant. I used linear regression to look at changes in these trait measures for missing and added species in response to the impervious surface cover surrounding sites.

Second, I identified species that were frequently added to or missing from the most urban sites within the dataset and used traits to describe these species groups (Kirkman et al. 2004). I selected the 14 plots (about one quarter of the sampled plots) with the highest third of impervious surface cover and lowest third of forest cover within a 1 km buffer (>14% impervious surface and lower than 40% forest cover). For each species in these plots, I calculated the number of sites where that species was predicted to occur based on its inclusion in the matching reference community type, and the proportion of these plots where the species was indeed present. Of species that were expected to occur in at least 5 plots, I categorized those present in less than 30% of the plots where they were expected to occur as “missing”. I also defined those species present in at least 40% of the plots where they were not included in the description of the matching reference community type as “added”.

I then compared traits of the species classified into each of these groups to those of the larger species pool, in order to identify individual species that may be at risk from urbanization. In addition to the traits described above, I also calculated the number of reference community types that a species was included in, as a measure of habitat specificity or generality (i.e., species included in many different community types could be considered generalists). For categorical traits (e.g., nativity, woodiness, and dispersal type), I used two-tailed Fisher's exact tests to compare the proportion of species in each group to the set of species it was pulled from (Fischer et al. 2013). For missing species, I used the set of predicted species (those expected to occur in at least 5 plots) as the species pool, and for added species I used all of the species in the dataset (species included in reference community type descriptions or found in at least 10% of sampled plots). To examine differences in continuous traits (e.g., wetland indicator status, habitat specificity), I compared the means for each group to the mean of a random set of the same number of species sampled from the larger species pool. Species groups whose means fell outside of 95% of the distribution of 5000 randomly sampled means from the species pool were considered to be significantly different for that characteristic (Fischer et al. 2013). I did not use seed mass, specific leaf area, or leaf nitrogen content in these analyses because the number of species with missing data was too large to obtain meaningful results.

Data analysis: Changes in traits with urbanization

For each trait, I calculated a community-weighted mean for each community using species' relative cover estimates, and the mean of all species within the community weighted equally. For most of the categorical traits (nativity, woodiness, leaf type, range orientation, and dispersal mode) I treated the trait as binary and thus calculated the proportion of species and the relative cover of species falling within a particular category (e.g., northern species, exotic species, vertebrate-dispersed species, etc.; Table 3.1). Wetland indicator status was treated as a numeric variable since it was coded as an integer ranging from 1 to 5, with 1 representing species that generally occur only in uplands and 5 representing obligate wetland species. I also calculated community-weighted means and proportions using only native species to see if observed changes in traits with urbanization were accounted for by the introduction of exotic species, since many of the ornamental exotic species within the dataset had similar traits (e.g., woody, vertebrate-dispersed, and evergreen).

I then used linear regression to test for changes in the community-weighted means and proportions for each trait (for all species and only native species) with increasing impervious surface cover surrounding sites. Since I expected some traits to show stronger changes with variables other than impervious surface (e.g., dispersal traits with forest cover, leaf type and range orientation with temperature, wetland indicator status with stream incision; Table 3.1), I also performed multiple regressions for each trait, including impervious surface, forest cover, temperature, and stream incision as predictors. I interpreted a significant effect of a predictor other than impervious surface in a multiple regression as an indication that it explained variation in the trait pattern beyond that explained by impervious surface. Because several of the predictor variables were highly correlated (e.g., forest cover and impervious surface cover; $r = -0.83$), I used the variance inflation factor to determine whether multiple regression coefficients were interpretable ($VIF < 4$).

RESULTS

I found 370 species in plots spanning the urbanization gradient, with the number of species per plot ranging from 45 to 115. Of these, 314 species were native and 56 were exotic. (One species of *Allium* that was only identified to genus was not determined to be native or exotic.)

Dissimilarity between sample sites and reference community types

The dataset matching species from sampled plots, reference community types, and high quality riparian forest sites from the study area contained a total of 474 species. Only 270 of these were included in restoration target species lists and/or found in at least 10% of the sampled plots or high quality sites. These 270 species were included in calculations of dissimilarity between communities and reference community types.

The mean Bray-Curtis dissimilarity between each sampled plot and its most environmentally similar reference community type was 0.53, but this decreased to 0.47 when I matched each plot to the most compositionally similar of its three most environmentally similar community types. Still, half of all plots were most compositionally similar to a community type other than the three most environmentally similar types. Dissimilarity between each plot and its most environmentally similar community type increased weakly but significantly with increased impervious surface ($R^2 = 0.08$, $p = 0.02$) and more strongly with decreasing forest cover ($R^2 = 0.22$, $p<0.001$). This trend did not hold for impervious surface when each plot was compared to the most compositionally similar of the three community types with the most similar environmental conditions, but still showed a weak but significant increase with decreasing forest cover ($R^2 = 0.14$, $p = 0.003$).

When I compared the similarity of plots from urbanization gradient dataset and the subset of high quality sites from the study region to reference community types, plots along the urbanization gradient were significantly more different from any reference community types than were reference sites, even when urbanization gradient plots were compared to their most similar community type regardless of environmental conditions ($p<0.001$, mean for reference plots = 0.37, mean for urbanization gradient plots = 0.44).

Differences in species composition between urban sites and restoration targets

When I compared the species present in each plot to the species expected to occur there based on the most compositionally similar of the three community types with matching environmental conditions, I found that on average 47% of the expected species were missing from plots and 49% of the species present in plots were not expected to occur there. The proportion of missing species was unrelated to impervious surface cover but increased with decreasing forest cover ($R^2 = 0.16$, $p = 0.002$). The proportion of added species (i.e., those present but not expected based on community type) did not change with either impervious surface cover or forest cover.

There were significant changes in the traits of missing and added species in relation to urbanization, consistent with some of the changes in traits observed across plots with increasing urbanization (Figure 3.1). With increasing impervious surface cover, there was an increase in the proportion of added species that were exotic, evergreen, and vertebrate-dispersed and a decrease in the proportion of added species that were herbaceous and had unassisted dispersal. There were also decreases in the wetland indicator status (towards more upland species) and specific leaf area of added species with impervious surface. Along the same gradient, the proportion of missing species that were herbaceous and had unassisted dispersal increased.

There were 39 species that were consistently missing from urban plots and 47 species that were consistently added to urban plots (Appendix C). Three species, *Phryma leptostachya*, *Thalictrum thalictroides*, and *Diospyros virginiana,* were included in both the missing and added species grups, meaning that they were found in several urban plots but not in the ones where they were expected to occur based on the sites' environmental conditions. In contrast, 24 of the added species were also found in at least 40% of the sites where they were expected to occur based on matching reference community types. None of the missing species were evergreen, and compared to a random distribution of species included in community type descriptions, missing species were included in the descriptions of significantly fewer community types (i.e., they are relative specialists in a few community types). Added species had a significantly higher proportion of exotic species and fewer herbaceous species than the full set of species in the dataset (Table 3.3), and had a slightly lower wetland indicator status (i.e., more upland species) than a random distribution of species in the dataset.

Changes in traits with urbanization

I found statistically significant changes in several traits along the urbanization gradient. There was an increase in the proportion of exotic species (but not percent cover) with increasing impervious surface (Figure 3.2). Multiple regression using forest cover, temperature, and stream incision as predictors along with impervious surface showed that forest cover was the strongest predictor of the proportion of exotic species (Table 3.4). The proportion of herbaceous species and herbaceous native species decreased with increasing impervious surface (Figure 3.2). Herbaceous cover also decreased with urbanization, but this trend was not seen for native species alone, suggesting it is due to an increase in woody exotic species in urban sites.

The proportion and cover of evergreen species increase with increasing urbanization, but these patterns did not hold for native species alone (Figure 3.2). There was no change in the proportion or cover of northern species along the gradient. However, in the multiple regression analysis temperature was a significant predictor of northern species, with a decrease in northern species in warmer sites (Table 3.4). Wetland indicator status decreased slightly along the urbanization gradient, meaning that urban sites had species more adapted to upland habitats, but this effect was not related to stream incision as expected. When only native species were included in the analysis, there was no change in wetland indicator status with urbanization, suggesting that colonization of exotic upland species, not native species, caused the effect. SLA and leaf nitrogen did not change significantly with urbanization.

There were significant changes in the representation of dispersal modes along the urbanization gradient. More urban sites had a higher proportion of vertebrate-dispersed species and a lower proportion of wind-dispersed and unassisted species (Figure 3.2). Among native species, there was an increase in the proportion of vertebrate-dispersed species and a decrease in the proportion of unassisted species along the urbanization gradient as well. Cover of vertebrate species increased and the cover of other dispersal modes decreased with increasing urbanization, but these trends were not reflected in native species alone. In multiple regressions, the proportion of unassisted species and the cover of wind-dispersed species were significantly related to forest cover, but there were no significant relationships for the other two dispersal modes (Table 3.4). There was no change in seed mass along the urbanization gradient.

DISCUSSION

I found support for seven out of twelve hypothesized relationships between plant species' traits and urbanization, including some results that are consistent with those of other studies. These findings demonstrate the utility of considering information on species traits and suggest that there are some predictable effects of urbanization on species composition. However, several of the patterns in traits I observed appear to be driven mostly or entirely by the additions of exotic species to urban sites, rather than explaining changes in native species composition. Similarly, when I compared observed species composition in sites along the urbanization gradient to reference community types that could be used to define restoration targets, it was easier to describe species added to urban sites in terms of their traits than to predict which species are missing from urban sites. These results have implications for restoration and conservation of forests in urban areas.

Changes in traits with urbanization

I found that forest plant communities in more urban areas have more exotic, vertebrate-dispersed, woody, evergreen, and upland species. In addition, I observed a decrease in species with northern ranges in sites with warmer summer temperatures. These results are consistent with other studies that have found increases in vertebrate-dispersed or declines in wind-dispersed and unassisted species in urban areas (Williams et al. 2005, Sodhi et al. 2008, Knapp et al. 2009, Concepción et al. 2015) and an increase in exotic species (Schmidt et al. 2014, Aronson et al. 2015) and those adapted to warmer temperatures (Knapp et al. 2009). Like some other studies, I did not see strong responses of physiological and morphological traits (seed mass, specific leaf area, or leaf nitrogen content) with urbanization (Williams et al. 2015), although in this study this may be because data was missing for so many species. Another possible explanation is that for some traits like leaf nitrogen content, measurements can vary strongly across individuals within a species depending on local environmental conditions; therefore using a species-level mean value as an indicator of traits at a local site is often far less informative than measuring traits on individuals within study sites (i.e., accounting for intraspecific trait variation in analyses; Jung et al. 2010). With the number of species within the study plots, measuring trait data on-site was infeasible, but this may afford further insight in future studies. While it would be useful to be able to relate these types of traits to urbanization, it may be the case that easily interpretable categorical traits, such as those related to dispersal mode and habitat type, have clearer responses to urbanization. These traits may also be more useful for practitioners making decisions about which species to include in conservation and restoration plans.

Notably, many of the trait patterns with urbanization that I observed were accounted for entirely by additions of exotic species to urban sites. This finding shows that in the study area, exotic species (many of which were introduced through the horticultural industry) are changing the fundamental composition and structure of forests. Exotic species account for shifts towards more woody and evergreen vegetation, primarily through the introduction of ornamental broad-leaved evergreen shrubs and woody vines such as *Hedera helix*, *Ligustrum sinense*, *Mahonia bealei*, *Nandina domestica*, *Ilex cornuta*, and *Euonymus fortunei*. Some of these, such as *Hedera helix*, are likely present as legacies of past landscaping, as they cover much of the understory. Others, like *Mahonia bealei* and *Nandina domestica*, are currently frequently used as ornamentals in parking lots and on college campuses in the Research Triangle area and may be only beginning to spread into forests in the region. Many of these exotic, woody, evergreen plants are dispersed by birds, which helps to explain their escapes into forested areas (Aronson et al. 2007, McCay et al. 2009). I expected that warmer temperatures would favor these species in urban areas, since their thick leaves can reduce evapotranspiration and they may be able to take advantage of photosynthesis during warm periods during winter months, but this hypothesis was not supported by the data. Nevertheless, the increase in evergreen, vertebrate-dispersed species in urban forests may have strong effects on resource availability for birds and other animals (Reichard et al. 2001). In addition, the change in forest structure, phenology, and leaf litter quality associated with these changes in plant species composition are unknown and could be substantial (Rodewald et al. 2009, Shustack et al. 2009).

Comparison of urban sites to reference community types

When I compared plant communities sampled along the urbanization gradient to restoration targets, I saw some of these same trait patterns reflected in the species that were added to urban sites that were not expected to occur there (i.e. exotic, evergreen, and vertebrate-dispersed species). It is clear from my results that exotic species additions will be an important factor that will need to be considered in restoration efforts. Indeed, some have suggested that in highly urban areas, attempting to exclude non-native species from restored sites may be a futile gesture, or at least will require a long-term commitment to attempt (Simmons et al. 2015). However, there are also several native plant species that appear to be frequently found in urban sites, including those sites where they are expected to occur and sites where they are not expected to occur based on matching reference community types. These species, which include trees (e.g., *Ilex decidua*, *Nyssa sylvatica*, *Morus rubra*, and several oaks), grasses and sedges (e.g., *Carex amphibola* and *C. oxylepis*, *Leersia virginica*), shrubs (*Rubus* sp. and *Viburnum prunifolium*), and ferns (e.g., *Botrypus virginianus* and *Sceptridium* sp.) may make good options for replacing exotic species in restoration sites. Compared to the species that were commonly missing from urban sites, these species tend to be habitat generalists, which others have found to be less threatened by urbanization than specialist species (Van der Veken et al. 2004, Concepción et al. 2016).

Predicting which species will go missing from urban sites might be more difficult than predicting which species colonize urban areas (Palma et al. 2016). Analysis of the identities of missing species along the urbanization gradient showed a loss of herbaceous species and those with unassisted dispersal in more urban areas, but the individual species that were commonly missing from urban sites did not have significantly different traits than a random subset of species, except that they tended to be relatively specialized to certain community types. Species may be missing from urban sites for a number of different reasons, including dispersal limitation, local factors such as environmental conditions or negative interspecific interactions, or, if the species are typically rare, simply because of stochasticity and ecological drift. Our results suggest that dispersal limitation may be an important factor limiting the species that persist in urban forest patches, and thus efforts to reintroduce dispersal-limited species should be emphasized in urban restoration projects when possible. However, dispersal-limited species may also be more likely to go locally extinct if they have negative responses to environmental conditions or are vulnerable to drift, so just because missing species tend to have unassisted dispersal does not necessarily mean that reintroducing them will lead to population persistence over time. One positive result is that some specialist, herbaceous species with unassisted dispersal are indeed found where they are predicted to occur, even in urban sites, and there is the potential that these species will persist in urban environments (Lawson et al. 2008). Of course it is also possible that some of these species are in decline and will contribute to an extinction debt in the future (Honnay et al. 2005, Ramalho et al. 2014).

Compared to traits related to dispersal, I did not see clear patterns in traits I expected to respond to environmental effects of urbanization such as temperature and stream incision. One exception was the negative response of northern species to warmer temperatures. I did see that species that were frequently added to urban sites were slightly more affiliated with upland habitats, although this relationship was weak. These were likely exotic species, and so the question remains whether the increase in upland species is due simply to propagule pressure of exotics allowing them to colonize uplands or whether the effects of urbanization on stream morphology and hydrology facilitates their colonization (as was shown in Sung et al. 2011, Ho and Richardson 2013, Catford and Jansson 2014). This would influence whether restoring the stream channel is likely to have an impact on exotic species invasion. I saw no other effects of stream incision on community composition.

Implications for restoration

Some common restoration practices, such as increasing tree canopy cover (and therefore likely lowering air temperature) and removing invasive species, may have strong effects on the changes in plant species composition I saw here (Richardson et al. 2007, Wallace et al. 2017). I also found that the amount of forest cover at a large spatial scale (1 km radius) was a significant predictor of the distributions of several traits, particularly dispersal mode. Thus connectivity of forest in the surrounding landscape is potentially an important factor determining the persistence of some species (e.g., those with limited dispersal) in urban areas (Kimberley et al. 2014). Indeed, loss of forest cover is often correlated with increases in forest fragmentation and edge effects, as well as warmer air temperatures, and has also been found to be a useful predictor of changes in species composition in other studies (Douda 2010). In addition, forest buffer width may also be important for invasion of riparian areas (Ives et al. 2011, Vilà and Ibáñez 2011). This demonstrates one way in which the surrounding landscape may have strong effects on the success of species in restoration projects that are not mitigated by on-site activities. Maintaining forest cover and connectivity at a larger spatial scale may increase the success of local-scale restoration projects and efforts to conserve native plant diversity in urban areas.

Table 3.1. Traits used in analyses with predicted responses to urbanization and hypothesized mechanisms.

Trait	**Type**	**Units or categories**	**Predicted urbanization response**	**Predictor (other than impervious surface)**	**Explanation**
Nativity	Binary	1: Nonnative 0: Native	Increase		Introductions of ornamental and other nonnative species by humans.
Herbaceousness	Binary	1: Herbaceous 0: Woody	Decrease		Local extinction of herbaceous species in response to urban environments on relatively short time scales.
Leaf type	Binary	1: Evergreen 0: Deciduous	Increase	Temperature	Evergreen species that may lose less water through evapotranspiration in hot summers and be able to take advantage of photosynthesis in warm winters.
Range orientation	Binary	1: Northern 0: Not	Decrease	Temperature	Warmer temperatures favor species with southern ranges over those with northern ranges.
Wetland indicator status	Ordinal	1: Upland 2: Facultative Upland 3: Facultative 4: Facultative Wetland 5: Obligate Wetland	Decrease	Stream incision	Riparian forests with incised streams will have more upland species colonize the floodplain.
Specific leaf area	Numeric	mm^2/mg	Increase		Urbanization may favor fast-growing, competitive species that can take advantage of nutrient inputs.
Leaf nitrogen content	Numeric	mg/g	Increase		Urbanization may favor fast-growing, competitive species that can take advantage of nutrient inputs.
Vertebrate-dispersed	Binary	1: Vertebrate-dispersed 0: Not	Increase	Forest cover	Habitat fragmentation favors species with high dispersal ability over those with low dispersal ability.

Wind-dispersed	Binary	1: Wind-dispersed 0: Not	Increase	Forest cover	Habitat fragmentation favors species with high dispersal ability over those with low dispersal ability.
Unassisted	Binary	1: Unassisted 0: Not	Decrease	Forest cover	Habitat fragmentation favors species with high dispersal ability over those with low dispersal ability.
Water-dispersed	Binary	1: Water-dispersed 0: Not	Decrease	Stream incision	Changes to flooding regimes associated with washed-out stream would decrease seed deposition on stream banks.
Seed mass	Numeric	mg	Increase	Forest cover	Habitat fragmentation favors species with facilitated dispersal (usually large-seeded species).

Table 3.2. Descriptions of reference community types (from Matthews et al. 2011) with number of plots matched with each.

Broad vegetation group	Reference community type	Description	# plots in original dataset	# reference plots in study area	# sampled plots (matched by environment)	# sampled plots (most similar of 3 matched by environment)
I. Small streams and narrow floodplains	Ia	*Liriodendron tulipifera – Liquidambar styraciflua/Lindera benzoin/Amphicarpaea bracteata* forest	18	9	3	17
	Ib	*Liriodendron tulipifera – Betula nigra/Cornus florida/Sanicula canadensis var. canadensis* forest	6	4	20	5
II. Oak–hickory flats	IIa	*Liquidambar styraciflua – Quercus nigra/Carpinus caroliniana/Mitchella repens* forest	32	7	0	8
	IIb	*Liquidambar styraciflua – Quercus pagoda – Carya cordiformis/Asimina triloba/Arundinaria tecta* forest	3	0	2	0
	IIc	*Carya carolinae-septentrionalis – Acer floridanum/Aesculus sylvatica/Zizia aurea* forest	8	1	0	2
III. Large river levee forests	IIIa	*Ulmus americana – Celtis laevigata/Lindera benzoin/Osmorhiza longistylis* levee forest	33	7	21	6
	IIIb	*Fraxinus pennsylvanica – Platanus occidentalis/Acer negundo/Chasmanthium latifolium* levee forest	30	5	3	8

IV. Bottomland and swamp forests	IVa	*Quercus (phellos – pagoda – michauxii) – Ulmus americana*/*Ilex decidua*/*Arisaema triphyllum* bottomland forest	17	4	2	5
	IVb	*Fraxinus pennsylvanica – Acer rubrum – Ulmus americana*/*Ilex decidua*/*Saururus cernuus* swamp forest	24	3	0	1
	IVc	*Fraxinus pennsylvanica – Betula nigra – Platanus occidentalis*/*Alnus serrulata*/*Boehmaria cylindrica* swamp forest	6	2	0	0
	IVd	*Quercus lyrata – Fraxinus pennsylvanica*/*Saururus cernuus* swamp forest	3	3	1	0
	IVe	*Carya aquatica – Nyssa aquatica* swamp forest	2	0	0	0

Table 3.3. Results of Fisher's exact test comparing the ratio of species in each trait category between missing or added species and a larger species group. Traits of missing species are compared to predicted species, those expected to occur in at least 5 plots, and traits of added species are compared to all species in the dataset.

Species Group	**Trait**											
	Nativity (%)				**Woodiness (%)**				**Leaf Type (%)**			
	n	Exotic	Native	p	n	Herbaceous	Woody	p	n	Evergreen	Deciduous	p
Missing	39	3	97	0.673	39	62	38	0.183	39	0	100	-
Predicted	93	6	94		93	47	53		93	8	92	
Added	47	23	77	0.016*	47	45	55	0.054 .	47	15	85	0.157
All	265	10	90		265	60	40		266	8	92	

Species Group	**Trait**											
	Range orientation %)				**Vertebrate-Dispersed (%)**				**Unassisted (%)**			
	n	Northern	not Northern	p	n	Vertebrate-Dispersed	not Vertebrate-Dispersed	p	n	Unassisted	not Unassisted	p
Missing	38	37	63	0.403	37	38	62	0.172	37	27	73	0.489
Predicted	93	28	72		91	53	47		91	21	79	
Added	47	23	77	0.387	46	61	39	0.025*	46	17	83	0.053 .
All	263	31	69		244	43	57		244	32	68	

Table 3.4. Results of multiple regression analyses of the prevalence of species' traits in communities in response to urbanization measures. Significant estimates for predictors other than impervious surface are bolded.

Response variable			**Multiple regression model estimates**				
Proportion of species	**Intercept**	**Impervious surface**	**Forest cover**	**Temperature**	**Stream incision**	**R^2**	**p-value**
Exotic	0.140	-0.013	**-0.047*** **	0.007	0.005	0.45	<0.001***
Herbaceous	0.479	0.002	0.031	-0.026 .	-0.007	0.31	0.001**
Evergreen	0.125	0.001	-0.017 .	0.012	0.005	0.399	<0.001***
Northern	0.262	0.013	0.008	**-0.024***	0.001	0.15	0.089 .
Wetland Indicator Status	2.789	-0.062	-0.041	-0.044	-0.007	0.12	0.201
Specific leaf area	13.968	-0.145	-0.403	**-0.571***	0.323	0.14	0.123
Leaf nitrogen content	11.395	-0.027	-0.543	-0.285	**0.430***	0.20	0.034*
Vertebrate-dispersed	0.496	0	-0.035 .	0.014	0.004	0.34	<0.001***
Wind-dispersed	0.252	-0.005	0.007	0.002	0	0.10	0.284
Unassisted	0.233	0.003	**0.030***	-0.008	-0.004	0.40	<0.001***
Water-dispersed	0.106	0.001	0.002	-0.008	0.001	0.07	0.520
Seed mass	261.0	-15.59	-12.82	-21.53	10.74	0.04	0.719
Relative cover	**Intercept**	**Impervious surface**	**Forest cover**	**Temperature**	**Stream incision**	**R^2**	**p-value**
Exotic	0.244	-0.024	-0.031	-0.021	0.026	0.04	0.707
Herbaceous	0.228	0.023	0.064 .	-0.031	0.016	0.22	0.017*
Evergreen	0.086	-0.014	-0.039 .	0.026	-0.001	0.26	0.007**
Northern	0.194	-0.021	-0.009	-0.021	0.015	0.11	0.236
Wetland Indicator Status	2.854	-0.020	-0.006	-0.054	0.009	0.05	0.621

Specific leaf area	21.413	0.187	1.562	-0.271	0.686	0.14	0.118
Leaf nitrogen content	14.449	-0.428	-1.163	0.186	-0.151	0.13	0.161
Vertebrate-dispersed	0.511	-0.049	-0.065 .	-0.029	0.039 .	0.12	0.189
Wind-dispersed	0.576	0.016	**0.110****	0.025	0.001	0.25	0.008**
Unassisted	0.075	0.044 **	0.016	-0.007	-0.014	0.20	0.029*
Water-dispersed	0.246	-0.023	0.030	-0.022	0.020	0.19	0.041*
Seed mass	305.84	-46.94	-40.32	-68.93	-48.53	0.05	0.694

Figure 3.1. Changes in the proportions of traits of added and missing species with increasing urbanization. Regression lines and R^2 values are only shown for significant relationships ($p < 0.05$).

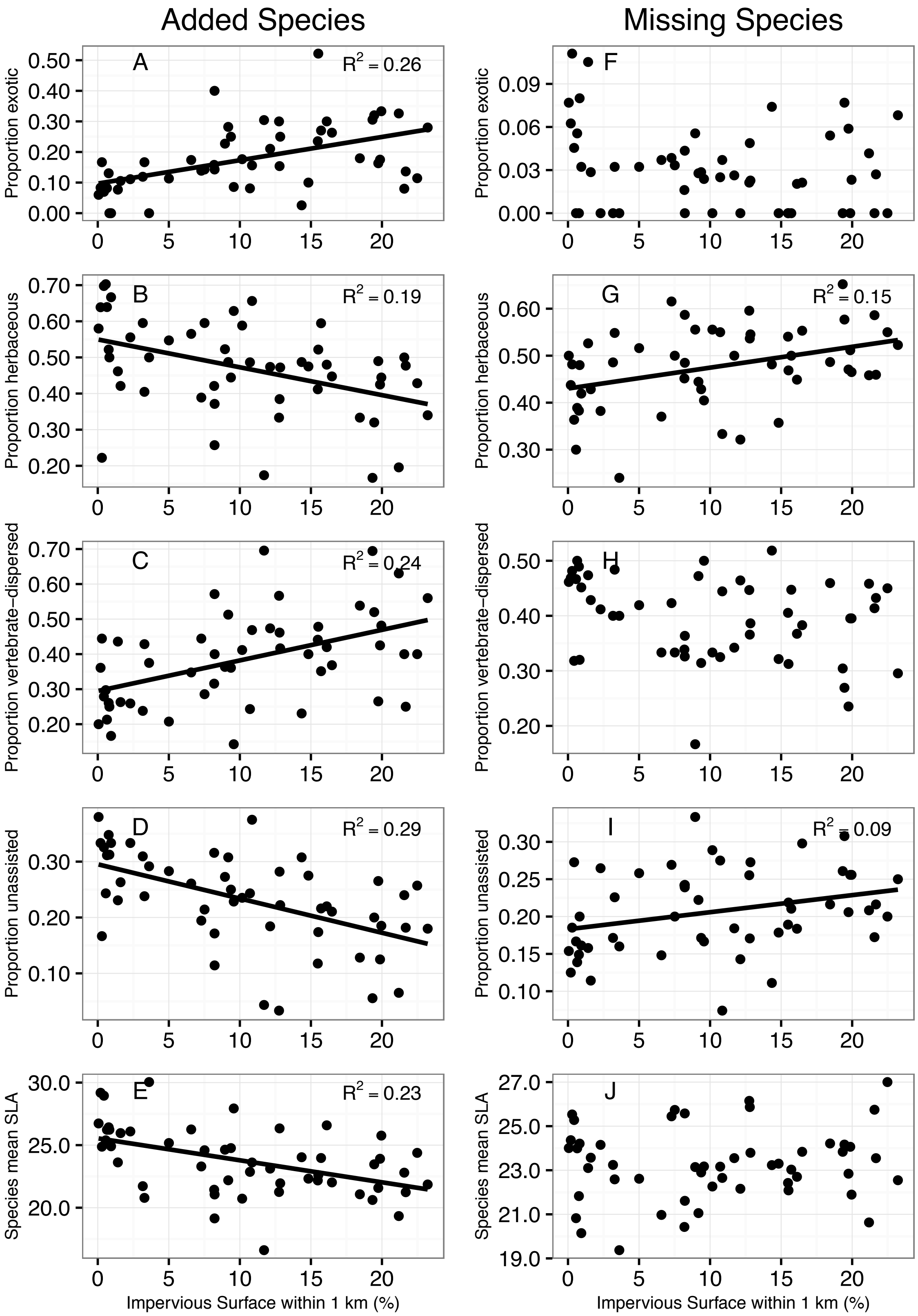
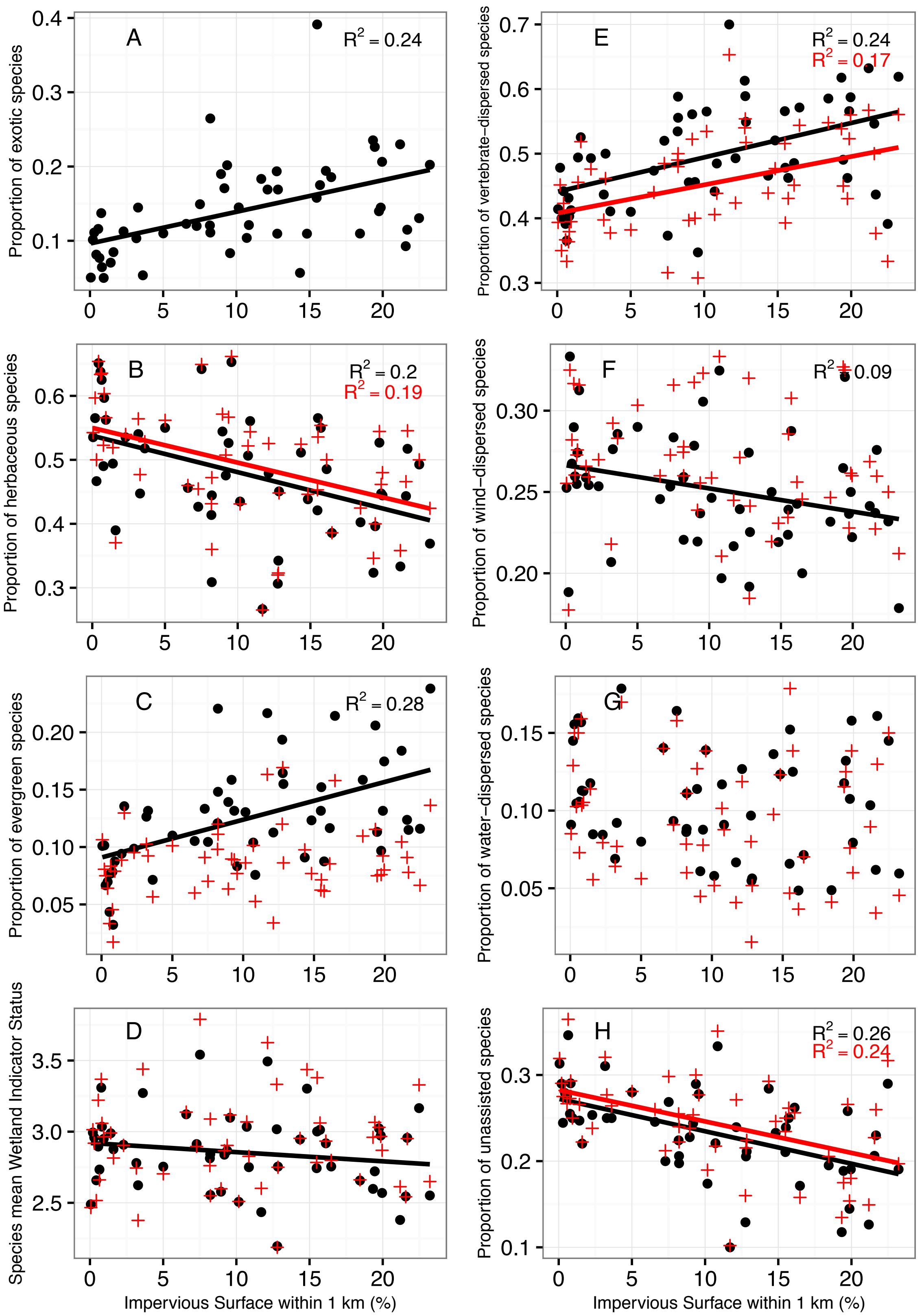

Added Species
Missing Species
A
R² = 0.26
Proportion exotic
0.00
0.10
0.20
0.30
0.40
0.50
F
0.00
0.03
0.06
0.09
B
R² = 0.19
Proportion herbaceous
0.20
0.30
0.40
0.50
0.60
0.70
G
R² = 0.15
0.30
0.40
0.50
0.60
C
R² = 0.24
Proportion vertebrate–dispersed
0.20
0.30
0.40
0.50
0.60
0.70
H
0.20
0.30
0.40
0.50
D
R² = 0.29
Proportion unassisted
0.10
0.20
0.30
I
R² = 0.09
0.10
0.15
0.20
0.25
0.30
E
R² = 0.23
Species mean SLA
20.0
25.0
30.0
J
19.0
21.0
23.0
25.0
27.0
0
5
10
15
20
Impervious Surface within 1 km (%)

Figure 3.2. Changes in the proportions of categorical traits of all species with increasing urbanization. Black points and regression lines show results for all species, and red points and regression lines show results for only native species. Regression lines and R^2 values are only shown for significant relationships ($p < 0.05$).


A
$R^2 = 0.24$
Proportion of exotic species
0.4
0.3
0.2
0.1
B
$R^2 = 0.2$
$R^2 = 0.19$
Proportion of herbaceous species
0.6
0.5
0.4
0.3
C
$R^2 = 0.28$
Proportion of evergreen species
0.20
0.15
0.10
0.05
D
Species mean Wetland Indicator Status
3.5
3.0
2.5
Impervious Surface within 1 km (%)
E
$R^2 = 0.24$
$R^2 = 0.17$
Proportion of vertebrate–dispersed species
0.7
0.6
0.5
0.4
0.3
F
$R^2 = 0.09$
Proportion of wind–dispersed species
0.30
0.25
0.20
G
Proportion of water–dispersed species
0.15
0.10
0.05
H
$R^2 = 0.26$
$R^2 = 0.24$
Proportion of unassisted species
0.3
0.2
0.1
Impervious Surface within 1 km (%)
0
5
10
15
20

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CHAPTER 4: PLANT SPECIES' RESPONSES TO HABITAT CONNECTIVITY AND URBAN ENVIRONMENTS DEPEND ON NATIVITY AND SEED DISPERSAL MODE

INTRODUCTION

Ongoing urban development is having profound effects on plant communities in and around cities (Hahs et al. 2009, Williams et al. 2015). With urbanization come the loss of natural habitat and habitat fragmentation (Stenhouse 2004), which can reduce the ability of some species to disperse between remnant habitat patches (Schleicher et al. 2011, McConkey et al. 2012). Urbanization also changes local environmental conditions, creating warmer temperatures (the urban heat island effect; Oke 1995), inputs of nutrients and pollutants (Lovett et al. 2000, Pouyat et al. 2008), and incised streams (deeper stream channels) caused by large runoff events during storms (part of the urban stream syndrome; Walsh et al. 2005). These environmental changes affect plant growth (Gregg et al. 2003), recruitment (Trammell and Carreiro 2011), and survival (Broshot 2011), and thus can act as filters limiting the plant species that persist in urban environments (Williams et al. 2005, 2009, Knapp et al. 2008). Few studies have assessed the relative importance of dispersal versus environmental conditions for structuring plant communities in urban systems (but see Lososová et al. 2012, Rouquette et al. 2013, Brice et al. 2016). This question is important for biodiversity conservation in urban landscapes, since it will determine how much emphasis should be placed on maintaining or creating connectivity between protected habitat patches (e.g., by creating corridors; Hobbs 1992) versus prioritizing patches based on their environmental conditions (Fahrig and Merriam 1994, Kang et al. 2015).

The strengths of local environmental conditions and dispersal for determining plant species composition vary with species' dispersal abilities (Flinn et al. 2010). Plant species tend to track environmental gradients (Cottenie 2005, Matthews 2011, Beaudrot et al. 2013, Rouquette et al. 2013, Brice et al. 2016), but species with limited dispersal ability may not spread to all sites with favorable environmental conditions, weakening species-environment relationships (Ozinga et al. 2005, Flinn et al. 2010, Brice et al. 2016). Dispersal limitation is most often seen in plants whose seeds move only short distances, such as those dispersed by invertebrates, thrown by explosive dehiscence, or moved by gravity (here collectively termed “unassisted” species). Species whose dispersal is facilitated by wind, water, or vertebrates tend to show less dispersal limitation (Flinn et al. 2010, Aiba et al. 2012). Instead, species with high dispersal ability are sometimes able to colonize and persist in sites with suboptimal environmental conditions (“mass effects”; Shmida and Wilson 1985, Leibold et al. 2004).

Dispersal is important for determining the distributions of exotic species. Recently introduced species may experience dispersal limitation as they spread across the landscape (Minor and Gardner 2011). In addition, these species can show mass effects in areas near introductions, especially as many species purposefully introduced by people have high investment in seed production (Murray and Phillips 2010). Together, dispersal and mass effects often lead to patterns of higher abundance or diversity of exotic species near places where they have been introduced, such residential areas or natural areas surrounded by higher levels of human land use (Borgmann and Rodewald 2005, Bartuszevige et al. 2006, Ohlemüller et al. 2006).

Fragmentation caused by urbanization may increase the likelihood of dispersal limitation for native species (Cottenie and De Meester 2004). Fragmentation may affect unassisted species most, as they are least able to cross farther distances between remnant habitat patches; indeed, some studies have found a decrease in species with limited dispersal abilities in urban areas (Knapp et al. 2009, Concepción et al. 2015). However, urbanization may also impede dispersal for plants with facilitated dispersal by changing qualities of the matrix between habitat patches. For example, some vertebrate dispersers may avoid urban areas (Tremblay and St. Clair 2009, Hale et al. 2012, Munshi-South 2012), and deposition of water-dispersed seeds on stream banks can decrease with altered flooding regimes caused by urban development upstream (Groffman et al. 2003, Araujo Calçada et al. 2015). In contrast, urban development may facilitate the spread of exotic species from areas where they have been purposefully planted or accidentally introduced by humans (Knapp et al. 2008, Vidra and Shear 2008, Minor et al. 2009).

Because dispersal is difficult to measure, it is common to infer the effects of dispersal by analyzing spatial patterns of species composition across a landscape (Urban et al. 2006, Flinn et al. 2010, Sattler et al. 2010, Braaker et al. 2014). When species show strong spatial patterns that are not explained by environmental variation, this is often interpreted as a signal of dispersal limitation. These spatial patterns may be evident in relation to the connectivity between sites; for instance, the species composition of aquatic organisms and water-dispersed plants often tracks stream networks (Brown and Swan 2010, Rouquette et al. 2013, Warfe et al. 2013). Least-cost paths, routes that follow the path of least resistance through a landscape, can also be used to model habitat connectivity between sites (Adriaensen et al. 2003). For example, resistance based on land use or land cover data can be used to model the "effective distance" (Adriaensen et al. 2003) between habitat patches for species that avoid urban areas. Comparing the ability of different measures of habitat connectivity to explain patterns of species composition can help to understand how features of the landscape influence dispersal (Cañedo-Argüelles et al. 2015).

I investigated the roles of habitat connectivity, environmental conditions, and surrounding land use (a proxy for exotic species introductions) for structuring riparian forest plant communities in an urban landscape. I first compared the explanatory power of different models of habitat connectivity, in order to determine whether spatial patterns of plant species composition match a model with greater movement around, rather than through, urban areas. I constructed least-cost path models with high resistance in urban areas and low resistance through forest, and compared them to habitat connectivity models that ignored land use between sites (i.e., Euclidean distance and distance along streams). I constructed least-cost paths using land cover data from two different time periods (2011 and 1992) because I expected that species composition might show a time-lagged response to changes in habitat connectivity (Honnay et al. 2005, Helm et al. 2006, Ramalho et al. 2014). I addressed the following questions:

1. Which model of habitat connectivity is best at predicting differences in species composition across sites?
2. What is the relative importance of habitat connectivity, environmental conditions, and surrounding land use for predicting plant species composition?

I expected that the answers to these questions would differ depending on species' dispersal modes and between native and exotic species. Specifically, I hypothesized that least-cost paths would explain patterns of native species composition better than other connectivity measures, particularly for vertebrate-dispersed species that would show resistance to movement across areas of urban development. I also hypothesized that the importance of dispersal (and thus measures of habitat connectivity) would vary across dispersal mode for native species, with unassisted species showing the strongest signature of dispersal limitation. I expected that environmental variables would be stronger predictors of species composition for native than for exotic species, and that exotic species composition would be explained by measures of urbanization surrounding sites (e.g., impervious surface cover, housing density).

METHODS

Study system

This study was carried out in the Research Triangle area (RTA) in the Piedmont region of North Carolina, including the cities of Durham, Raleigh, Chapel Hill, and Cary. The RTA is estimated to be home to over 1.8 million people and is one of the faster growing metropolitan regions in the United States (U.S. Census Bureau Population Division 2016). There are two watersheds that drain the RTA, the Neuse River and Cape Fear River basins, which form two stream networks along which we sampled riparian forest vegetation. Urban development has been increasing in the RTA for the past several decades, particularly around the southern and central portions of the region (Cary and the Research Triangle Park), but the area remains highly forested (nearly 50% of land cover based on the National Land Cover Dataset [NLCD, Homer et al. 2015]). Most of the forest in this region has been exposed to prolonged human disturbance, particularly since European settlement, and much was cleared for agriculture or selectively harvested for timber.

Site selection

I collected data at 52 forested sites on public lands in the RTA (Figure 4.1). All sites were located within 20 m of a small stream (mostly first- or second-order, with a few third- and fourth-order streams). Sites were selected to span a gradient of urbanization, defined as mean impervious surface cover (%) within a 1 km buffer (calculated from 30 m-resolution land cover data from the NLCD, 2006; Fry et al. 2011). I identified sites using ArcGIS version 10.0, then visited them to ensure that they were: a) remnant forest, defined as having trees larger than 30 cm diameter at breast height and not solely consisting of early-successional tree species such as Loblolly pine (*Pinus taeda*), Sweetgum (*Liquidambar styraciflua*), and Tuliptree (*Liriodendron tulipifera*); and b) located within the floodplain, determined by presence of riparian species, flat topography, and signs of recent flooding. Sites were nearly evenly represented in the two watersheds, with 24 sites in the Cape Fear watershed and 28 sites in the Neuse watershed.

Plant community data

Plant species data were collected in the summers (May-September) of 2012-2014. At each site, we sampled vegetation within one randomly placed, rectangular plot. Plots were 10 m wide and 30, 40, or 50 m long, depending on the size of the forest patch, width of the floodplain, and sinuosity of the stream. Plots were placed roughly parallel to the stream with the length of the plot adjacent to the stream, as close to the stream as possible. Within each plot, I identified and estimated the cover (a proxy for abundance) of every vascular plant species I could find. Species cover sampling followed the protocol laid out by the Carolina Vegetation Survey (Peet et al. 1998), with cover estimated to classes on a roughly logarithmic scale (0-1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-95%, or 95-100%). Plants were identified to the species level when possible, but some taxa were only identified to genus or were lumped with another species when the two were difficult to distinguish (e.g. *Symphiotrichum sp*., *Vitis* [*cinerea* + *vulpina*]). Identification was based on the Flora of Virginia (Weakley et al. 2012).

I assigned plant species to one or more of four dispersal modes: unassisted, vertebrate-dispersed, wind-dispersed, and water-dispersed, using a variety of published sources (but mainly from Matthews 2011 and sources within; Appendix A). Here, exotic species are defined as those that are not native to the Southeastern U.S.

Environmental and landscape data

I collected field data on several environmental variables that have been found to be important for riparian vegetation in other studies (e.g., Matthews et al. 2011) or are associated with urbanization (i.e., measures of the urban heat island effect and urban stream syndrome). To assess the magnitude of the urban heat island effect across sites, I installed one Onset HOBO data logger (Pendant UA-001-08) at each site, which recorded continuous air temperature for one year. I used nighttime temperature because this is when the UHI is strongest (Coseo and Larsen 2014) and used data from August of 2014 because data from this period covered all study sites. At the time of sampling I measured slope, aspect, and light penetration through the forest canopy, recorded an index of the amount of trash found within the vegetation plot (a proxy for human activity onsite and upstream), measured distance to the nearest edge of the forest, and quantified stream incision by estimating the width and the depth from the bank to the thalweg (deepest point) of the stream. I also collected soil samples from the A layer (top 10 cm of mineral soil), which were subsequently analyzed for nutrients and texture. For definitions and ranges of variables, see Table 4.1.

Other data for predictor variables was downloaded from existing remotely sensed or modeled datasets: a digital elevation model from the USGS National Elevation Dataset (NED; http://ned.usgs.gov/), surface water themes from the USGS National Hydrography Dataset (NHD; http://nhd.usgs.gov/), primary and secondary roads from the North Carolina Department of Transportation (DOT; https://connect.ncdot.gov/), housing density from the American Community Survey 2015 5-year estimates (Social Explorer 2017), and impervious surface cover and land cover data from the NLCD (http://www.mrlc.gov/; Vogelmann et al. 2001, Homer et al. 2015). Raster datasets were downloaded at a 30 m-resolution and NHD data were downloaded at the medium resolution (1:100,000-scale). Impervious surface cover, roads, and census data were used to calculate landscape-level measures of urbanization surrounding sites ("landscape variables"), including distance to the nearest road and impervious surface cover at multiple spatial grains (Table 4.1).

In order to limit the environmental and landscape variables to an ecologically meaningful subset of unique predictors, I performed a Pearson correlation test on the available variables and removed several (some soil measurements and impervious surface cover at several scales) that were conceptually redundant and colinear ($\varrho \geq 0.6$). Variables with strongly skewed distributions (phosphorus, distance to the forest edge, distance to the nearest road, and housing density) were log-transformed prior to data analysis.

Statistical analyses: Habitat connectivity models

I used several different models of habitat connectivity between sites to predict patterns in species composition across the landscape. To do this, I first defined stream networks and created least-cost paths based on land cover data, and then calculated pairwise distances between sites along each of the different habitat connectivity networks (including simple Euclidean distance) to create distance matrices. From each pairwise distance matrix I created Moran's Eigenvector Maps, variables that describe spatial structure at multiple scales (Borcard and Legendre 2002, Legendre and Legendre 2012). I used the spatial variables associated with each connectivity model as predictors of species composition. To assess which habitat connectivity model best predicts functional connectivity for plant species, I compared the ability of spatial variables for each connectivity model to explain species composition patterns. I then controlled for the effects of environmental and landscape variables on species composition to determine whether spatial variables explained a significant pure fraction of variation in species composition, an indication of dispersal effects. I explain each of these steps in more detail below.

Distance matrices: I constructed four distance matrices to represent alternative models of connectivity between sites (paths depicted in Figure 4.2A-D). For the Euclidean distance matrix, I calculated distances between sites using their UTM coordinates (Figure 4.2A). For the along-stream distance matrix, I used the FLoWS toolbox (Theobald et al. 2005) in ArcGIS 10.3.1 (ESRI 2015) to create stream networks for the Cape Fear and Neuse watersheds and calculate distances between sites within each watershed (Figure 4.2D). Although downstream distance between sites may be a more accurate model of seed movement between sites (Rouquette et al. 2013), the small stream orders of my field sites meant that few sites were connected to one another using this network definition. Therefore I considered distances along streams without consideration of flow direction.

I also created two least-cost path models, one based on current land cover data (2011, the approximate time of plant community sampling; Homer et al. 2015) and one using data from about twenty years prior (1992; Vogelmann et al. 2001). This was because I expected that changes in species composition in response to changes in habitat connectivity would take time to manifest, especially for long-lived species like trees. To create these models, I used 30 m-resolution land cover data from the two time periods (Figure 4.2B-C). This required several steps. First I created a resistance raster map for each time period by assigning each land cover category a resistance value between 1 and 100. The aim was to create a simple model that might be an improvement over Euclidean distance as a measure of connectivity for seed dispersal vectors, particularly vertebrates. I assumed that for vertebrates that transport the seeds of forest plants, movement would be easiest through forest (as Carlo and colleagues [2013] have shown for birds), and so gave forest a resistance value of 1. Highly developed (urban) grid cells and those occupied by water were given the highest resistance values (100), with less developed and agricultural land cover types assigned lower resistance values (either 25, 50, or 75) and vegetation types other than forest given yet lower values (10). Because the land cover data were categorized differently for the two time periods (Fry et al. 2009), I used simplified categories to which I assigned resistance classes. (For details on resistance raster creation for the two time periods, see Appendix D.) I then used Linkage Mapper (McRae and Kavanagh 2011) in ArcGIS 10.3.1 to create least-cost paths from the two resistance raster maps and calculate the pairwise distances between sites along those paths.

Moran's Eigenvector Maps: I created Moran's Eigenvector Maps (MEMs) from each of the distance matrices described above to act as spatial variables representing each connectivity model in analyses of community composition. MEMs are statistical models of spatial structure, comprised of orthogonal predictor variables that describe spatial variation between sample sites at different scales (Borcard and Legendre 2002, Legendre and Legendre 2012). These models are often used in analyses of variance partitioning to separate the effects of environmental and spatial processes on species composition (Legendre et al. 2005, Urban et al. 2006, Sattler et al. 2010, Braaker et al. 2014). All MEMs were created in R using the spacemakeR package (Dray 2010).

I used two different kinds of MEMs. For the Euclidean distance model, I used a specialized version called principal coordinates of neighborhood matrices (PCNM; Borcard and Legendre 2002), a type of distance-based Moran's eigenvector map where distances between sites are scaled to 4 times a threshold distance, defined as the longest edge of a minimum spanning tree connecting all sites (Dray et al. 2006; Figure 4.2E). For the least-cost path and along-stream distance models, we used a generalized version of MEMs, which requires two steps: first creating a network where each pair of sites is either connected or not, and then weighing the connections between sites by the distance between them (i.e., along-stream or least-cost path distance). To enable comparison across spatial models, I created MEMs that matched the PCNM formulation as closely as possible, by using minimum spanning trees to define connections between sites (Figure 4.2F-H) and using a threshold distance to scale distances between sites (Dray et al. 2006).

For all MEMs, I included only eigenvectors with significant positive spatial autocorrelation (Moran's I, with a cutoff of $p<0.05$; Dray et al. 2006) in analyses relating these variables to species composition data. This is because eigenvectors with positive eigenvalues are more consistent with the patterns expected as a result of dispersal limitation and mass effects (i.e., sites that are closer together are more similar), whereas negative spatial correlations imply negative interactions between species (Legendre and Legendre 2012). I mapped the fitted site scores of the positive eigenvectors to identify the relative spatial scales they represent (eigenvectors 1–4 are large, 5–8 are medium, and 9-11 are small scale; Figure 4.2I-L). MEMs of along-stream distance were created for each watershed separately, since sites in the two watersheds are not connected along streams.

Statistical analyses: Redundancy analysis

I performed redundancy analysis (RDA) using the R package vegan (Oksanen et al. 2015) to test relationships between predictor variables and community composition for each group of species (native vs. exotic and unassisted, vertebrate-dispersed, wind-dispersed, and water-dispersed; see Figure 4.3). Redundancy analysis is a type of constrained ordination, similar to linear regression with multivariate response data (Legendre and Legendre 2012). The response matrix in each analysis was Hellinger-transformed species cover data for a species group (here, square-root of the percent cover of each species within a plot; Legendre and Gallagher 2001), only including species that were found in at least 3 plots (5% of sampled plots). I used a forward-selection approach (Blanchet et al. 2008) using Akaike's Information Criterion (AIC; Burnham and Anderson 2002) to choose the variables to include in each predictor variable category by selecting the model with the lowest AIC for each category (AIC_c for MEMs, as recommended by Godinez-Dominguez and Freire 2003, Blanchet et al. 2008). For each group of species, I first identified the connectivity model that best explained species composition for that group (based on R^2_{adj}), which was used for subsequent analysis. To compare the explanatory power of the model based on along-stream distance to other connectivity models, I correlated forward-selected variables from each of these models to species composition in the two watersheds separately. The selection of the best connectivity model for each group of species was used to answer my first question, whether functional connectivity is reduced by urbanization, since the least-cost path connectivity models represent lower connectivity across urban areas than across other land cover types. To answer my second question, I performed variance partitioning on a RDA model using all forward-selected predictors grouped into environmental, landscape, and spatial variables, to find the variation in species composition explained uniquely and jointly by each set of predictors (Figure 4.3).

RESULTS

Across the 52 plots included in this study, I identified 355 vascular plant species; 244 of these were found in at least 3 plots. These included 209 native species and 34 exotic species, plus one (*Allium* sp.) that I was unable to confidently identify to species and so was not classified as native or exotic (Appendix A). Fifty-one of the native species (25%) were classified as wind-dispersed, 20 (10%) as water-dispersed, 82 (39%) as vertebrate-dispersed, and 62 (30%) as unassisted (Table 4.2). Of the exotic species, 5 (15%) were classified as wind-dispersed, 6 (18%)

as water-dispersed, 7 (21%) as unassisted, and 23 (68%) as vertebrate-dispersed (Table 4.2). There were also 14 native species and 1 exotic species for which I was unable to find information on dispersal mode.

Comparing the least-cost path models from the two time periods, effective distance between sites increased substantially between most sites from 1992 to 2011 (Figure 4.4).

Connectivity model- and variable selection

The best connectivity model for predicting species composition varied across nativity and dispersal mode. For native species, the Euclidean distance model was best at explaining variation in all native and vertebrate-dispersed species composition (Figure 4.5), capturing spatial variation at a large scale (Table 4.2). Variation in native wind-dispersed, water-dispersed, and unassisted species composition was best explained by the 1992 least-cost path model, with large- and medium-scale spatial variables forward-selected for each group, as well as a small-scale spatial variable for unassisted and water-dispersed species (Table 4.2). Along-stream distance was not significantly correlated with species composition for any group of native species.

For exotic species, the along-stream distance connectivity model was best at explaining species composition for all groups except for unassisted species, which were best explained by the 1992 least-cost path model (Figure 4.5). Unassisted exotic species composition was significantly related to spatial variables at large-, medium-, and small scales (Table 4.2). For all other exotic species groups, the same two large-scale MEM variables from the along-stream connectivity model were forward-selected for predicting species composition of each group: MEM 2 in the Cape Fear watershed and MEM 3 in the Neuse watershed (Figure 4.2L).

Environmental and landscape variable selection

Soil texture (percent sand) and minimum air temperature in August were important predictors of most species groups (Table 4.2). Elevation was also forward-selected for several groups of native species (all native, wind-dispersed, and vertebrate-dispersed). Among exotic species, canopy openness was forward-selected for most species groups (all exotic and wind-, water-, and vertebrate-dispersed), but only within the Neuse watershed, while temperature was selected in the Cape Fear watershed but not in the Neuse (Table 4.2). Variables related to soil fertility were only related to species composition for a few groups: wind-dispersed native species (pH), water-dispersed native species (phosphorus), and unassisted exotic species (phosphorus). The only other environmental variables that were selected as significant predictors of species composition were trash for unassisted native species and stream incision for water-dispersed native species.

Of the landscape variables, housing density and impervious surface cover were the only variables related to species composition, and these were forward-selected for different species groups. Housing density and large-scale impervious surface cover (10 km radius) were significant predictors of species composition for different native species groups, but unassisted native species composition was not significantly correlated with any landscape variables. As with the environmental variables, different landscape variables were selected in each of the two watersheds for exotic species; for most species groups, housing density was selected in the Cape Fear watershed and small-scale impervious surface cover (1 km radius) was selected in the Neuse watershed (Table 4.2).

Variance partitioning

The variance in species composition explained by all variables ranged from about 11-40%, depending on the species group (Figure 4.5). While this is low, it is similar to what has been found in other studies in urban systems (Sattler et al. 2010, Braaker et al. 2014) and of plant communities (Douda 2010, Arellano et al. 2016).

Spatial variables explained 19-86% of the total explained variation in species composition across groups (Figure 4.6), with the highest proportion of variation explained for unassisted exotic species (77% of the explained variation attributed to spatial variables alone; see Table 4.3 for variance partitioning results and tests of significance for unique fractions). Spatial variables explained a significant fraction of the variation in species composition for all groups of native species except for vertebrate-dispersed species, as well as unassisted exotic species and wind- and water-dispersed exotic species (in the Cape Fear watershed only).

Environmental variables generally explained more variation in species composition than did spatial or landscape variables, accounting for 25-92% of the total explained variation across groups (Figure 4.6). Environmental variables also uniquely explained a significant fraction of the total explained variation in all groups except for water-dispersed native species and unassisted exotic species (although only in the Neuse watershed for wind- and water-dispersed exotic species; Table 4.3). For each dispersal mode, environmental variables usually explained more variation in native species composition than exotic species composition (Figure 4.6). Landscape variables generally explained the lowest amount of variation in species composition across groups, but explained more variation in exotic species composition (18-63% of total explained variation) than in native species groups (0-20% of total explained variation). Landscape variables uniquely explained a significant fraction of the variation in unassisted exotic species, as well as all exotic and vertebrate-dispersed exotic species in the Cape Fear watershed (Table 4.3).

For every group of species, some of the variation in species composition that was explained by spatial variables was also explained by either environmental or landscape variables or both (Figure 4.6). Most of this variation was jointly explained by spatial and environmental variables (for native species) or all three variable categories (for both native and exotic species). A high proportion of the variation in species composition for exotic species groups (except for unassisted species) was jointly explained by environmental and landscape variables, but not by spatial variables (Figure 4.6). Overlap in variation explained by spatial and landscape variables was high in the Cape Fear watershed for exotic species groups (Table 4.3).

DISCUSSION

I found that connectivity models based on least-cost paths that avoided urban land cover outperformed other connectivity models for several groups of species, lending support to the hypothesis that urban development impedes dispersal for some species. In addition, the least-cost path model using older land-cover data always predicted more variation in species composition than did the model using contemporary data, suggesting that species show a time-lagged response to changes in connectivity caused by urban development. I found that urbanization influences plant species composition through its effects on both habitat connectivity and local environmental conditions, and that the relative importance of these factors for species composition depends on dispersal mode. These results provide insight into the ways that urbanization differentially affects species according to their nativity and dispersal mode and point to important considerations for conservation and management of natural vegetation within an urban landscape.

Effects of land use on habitat connectivity and dispersal limitation

Most groups of native species I examined (wind- and water-dispersed and unassisted species), as well as unassisted exotic species, had stronger relationships with the 1992 least-cost path model than any other connectivity model. This suggests that, as hypothesized, dispersal is facilitated within forests compared to across areas of urban development for many native species. Urbanization may reduce rates of seed dispersal between forest patches through several different mechanisms. While I am unable to distinguish between these with the analyses used here, I expect that these mechanisms vary for species with different dispersal modes. Buildings and other built structures may deflect seed dispersal by wind, while changes to the flood regime and stream bank erosion (Groffman et al. 2003, Walsh et al. 2005b) can decrease the deposition of water-dispersed seeds on stream banks (Araujo Calçada et al. 2015). All of these plant species could experience population sinks in urban areas if seeds land there but fail to establish due to concrete barriers or harsh environmental conditions; however, unassisted species, which disperse only small distances, may show stronger impacts of these effects (Penone et al. 2012).

Another possible interpretation for the importance of least-cost path models for explaining species composition is that sites within a contiguous forest patch have similar species composition because of homogeneous environmental conditions or shared land-use or disturbance history within a forest patch. For some species such as unassisted exotics, current distributions may reflect historical introductions of these species into some forested areas and not others. However, other results from this study are consistent with the interpretation of least-cost path connectivity models representing the effects of urban development on seed dispersal. I found that all of the species groups that were most closely related to least-cost path connectivity models also showed strong variation in species composition across space, consistent with the effects of dispersal limitation between sites, rather than differences in environmental conditions.

This was shown by significant relationships between the composition of these species groups and spatial variables even when controlling for environmental and landscape variables. Furthermore, species composition of those groups that I would expect to show dispersal limitation at small scales along least-cost paths (i.e., unassisted and water-dispersed species) was predicted by small-scale spatial variables in addition to the larger-scale variables that explained variation in other species groups. Together, these results demonstrate that the importance of least-cost paths for explaining species composition is at least partly attributable to the effects of urbanization on functional connectivity.

The effects of changing connectivity take time to manifest in species composition, with potential for extinction debts lasting for decades after initial habitat fragmentation (Honnay et al. 2005, Helm et al. 2006, Ramalho et al. 2014). I found results consistent with a time-lagged response of species composition to loss of connectivity from urban development in the study landscape, with the 1992 least-cost path model almost always outperforming the 2011 model at explaining species composition. Since urban development has been occurring in the RTA for longer than 20 years, is it possible that current species composition more closely reflects connectivity between forest patches at an even earlier date, as well as environmental conditions from earlier time periods. Community composition at any time point should reflect the conditions that were present when seeds arrived at the site, when individual plants established, and throughout the period of growth; for long-lived species such as trees, this time period of influence could go back up to hundreds of years, even in this secondary forest study system. What I am able to show in this study with available data is that past connectivity levels appear to be better predictors of species composition than current connectivity levels, which suggests that as urban development continues in this landscape, future community composition of forest patches in the RTA will likely reflect lower connectivity between sites.

The importance of spatial variables for species composition was somewhat predictable based on nativity and dispersal mode. Native species generally showed stronger relationships with spatial variables than did exotic species. Furthermore, as hypothesized, species with the lowest dispersal ability (unassisted species, both native and exotic) showed the strongest signature of dispersal limitation. Native wind- and water-dispersed species also showed signs of dispersal limitation, as has been found in other studies (Matthews 2011, Beaudrot et al. 2013, Rouquette et al. 2013). Contrary to my hypothesis, I found no evidence that vertebrate-dispersed species have higher rates of dispersal within forests than across urban areas. Indeed, this species group showed no sign of dispersal limitation across the landscape. Instead the results suggest that, on the whole, vertebrate dispersers are not constricted to movement within forest corridors in the RTA (a finding that is consistent with some studies of birds in urban landscapes: e.g., Buckley et al. 2006, Aronson et al. 2007, Minor et al. 2009, Gilbert-Norton et al. 2010), or at least that distances between forest patches are small enough for the landscape to be relatively well connected for vertebrate dispersers such as songbirds (Minor and Urban 2008). In addition, some vertebrates that carry seeds may be more frequently found at forest edges than within core forest habitat.

Among exotic species, only wind- and water-dispersed species showed spatial patterns consistent with dispersal limitation, and then only in one of the two watersheds. The importance of connectivity along streams for these species may reflect the use of riparian corridors for movement of exotic plant species in the Cape Fear watershed (Brown and Peet 2003, Säumel and Kowarik 2010, Rouquette et al. 2013). However, interpreting results for these two groups is somewhat tenuous because they consist of the same few species, with Japanese stiltgrass (*Microstegium vimineum*) driving most of the trend in species composition for both groups due to its strong variation in abundance across sites. Indeed, the small number of exotic species classified as unassisted, wind-dispersed, and water-dispersed in this study means that the results for these groups should be interpreted with caution.

Environmental effects on species composition

Except for those species groups that showed the strongest signs of dispersal limitation (i.e., unassisted species), environmental variables were almost always the strongest predictors of species composition across groups. This finding was consistent with other studies of plant metacommunities that have shown that species sorting is the general paradigm for plants (Cottenie 2005, Matthews 2011, Rouquette et al. 2013). Contrary to my hypothesis, environmental variables explained more variation in species composition for some groups of exotic species than for native species.

Many of the environmental variables that explained variation in species composition were related to urbanization. These included August minimum (nighttime) air temperature, a measure of the urban heat island effect (Oke 1995) which was one of the most commonly selected environmental variables; the degree of stream incision, a component of the urban stream syndrome (Walsh et al. 2005b) that likely reflects lowered water tables (Groffman et al. 2003); soil fertility measures that are often correlated with urbanization (pH and phosphorus; Godefroid et al. 2007, Pouyat et al. 2010, Pickett et al. 2011); and the amount of trash at a site, a proxy for human disturbance. This finding supports other studies that have shown that urban environments often strongly influence plant species composition (Williams et al. 2005, Knapp et al. 2008).

Effects of urban land cover surrounding sites

Landscape variables uniquely explained a significant fraction of variation in species composition for a few groups of exotic species. I interpret this result as a signature of dispersal limitation and/or mass effects for these groups, where housing density and impervious surface cover act as proxies for species introductions by humans in urban areas. However, many exotic plant species have been present in the landscape for many decades and were probably introduced to areas that are currently farmland or forest as well as urban areas. Thus it is also possible that the importance of landscape variables for predicting species composition reflects some other effect of urbanization such as carbon dioxide concentrations or nitrogen additions that could differentially affect exotic plant species but was not measured in this study. Landscape variables were generally less important than other predictors, explaining variation in species composition that was almost entirely also explained by environmental variables, spatial variables, or both for most groups. Thus I conclude that urbanization mainly influences plant species composition in the RTA through its effects on habitat connectivity and environmental conditions.

Implications for conservation in urban areas

My results suggest that both environmental conditions and habitat connectivity are important determinants of species composition in our study area. This finding leads me to recommend that both factors receive consideration in selecting conservation priorities for riparian forest patches in the study landscape. Environmental variables are generally strong predictors of species’ distributions in this system and important environmental variables were remarkably similar across most species groups, with species composition generally predicted by soil texture, air temperature, and elevation. This suggests that protecting riparian forests with varying levels of these variables would promote beta diversity, and thus gamma diversity, across the landscape. Additionally, reducing the urban heat island effect on forest patches may mitigate some of the effects of urbanization on plant community composition. Setting aside larger contiguous forest patches and increasing canopy cover within the urban matrix are two potential strategies for reducing warming within forests (Coseo and Larsen 2014) that could also increase habitat connectivity and seed dispersal between forested sites.

Forest patches in the RTA are already relatively well connected, particularly for vertebrate-dispersed species. However, even in this highly forested landscape, I found indications that human land use increases dispersal limitation between remnant forest patches. This is particularly true for unassisted species, which means that the species that are already most likely to be limited by dispersal may experience further dispersal limitation as a result of urbanization. My results also suggest that human-built structures may inhibit movement for wind-dispersed seeds and that urbanization's effects on flood regimes may reduce deposition of water-dispersed seeds, although future work is needed to explicitly test these effects. Also concerning is the fact that most groups of species were better explained by past levels of habitat connectivity, suggesting a time lag for the effects of reduced connectivity (and possibly other effects of urbanization) to be seen in species composition patterns, particularly for long-lived species. Thus the effects of connectivity loss will likely become more pronounced over time.

This study takes place in a landscape with remarkably high cover of remnant forest and focuses on riparian areas, which tend to be a highly connected subset of forested lands. Thus this landscape is one in which there appears to be potential for maintaining connectivity among forest patches for many plant species into the future, provided that ongoing development does not continue to make forest patches smaller and the matrix between them more impregnable. More studies in other systems are needed to gain a broader understanding of the importance of dispersal and environmental conditions for plant community composition in urban areas.

Table 4.1. Description of variables used in redundancy analyses.

Variables	Range	Description and data source
Environment		
Elevation (m)	51.8 - 125.5	30 m-resolution Digital Elevation Model (NED)
Temperature (°C)	18.6 - 20.5	Mean daily minimum air temperature during August, 2014, measured using HOBO data logger
Stream incision	0.1 - 1	Maximum stream depth : mean stream width ratio, estimated in the field
Openness	9.2 - 36.5	Forest canopy openness index, measured using a densiometer
Sand (%)	44.1 - 87.8	Mean sand content of soil samples in the A horizon
pH	3.8 - 5.5	Mean pH of soil samples in the A horizon
Organic matter (%)	3.5 - 11.8	Mean organic matter content of soil samples in the A horizon
Phosphorus* (mg/kg)	10 - 48	Mean available phosphorus of soil samples in the A horizon
Trash	0 - 3	Index of the amount of trash in the plot
Slope (°)	-8 - 10	Slope, facing stream bank, measured using a clinometer
Aspect	-1 - 1	Transformed aspect: cosine(45 - *A*) + 1, where *A* is aspect in degrees (Beers et al. 1966)
Landscape		
Impervious surface (%)		Average impervious surface cover (30 m-resolution data from 2011; NLCD) within a given radius
1 km radius	0.2 - 26.0	
10 km radius	0.7 - 19.1	
Edge distance* (m)	1.0 - 1037.9	Distance to the nearest edge of the forest, calculated from GPS coordinates
Road distance* (m)	25.1 - 1047.3	Distance to the nearest primary or secondary road, measured in ArcGIS using road maps from the North Carolina DOT
Housing density* (units/km^2)	0 - 1143.4	Density of housing units within the block group, from the North Carolina census, 2010
Spatial		
MEMs calculated from the following connectivity models (see Methods and Figure 4.2)		
Euclidean		Geographic distance between sites
Along-stream		Distance between sites along stream channels, calculated in ArcGIS using the FLoWS toolbox and data from the NHD
Least-cost paths		Distance between sites along least-cost paths calculated using land cover classifications at 30 m-resolution (NLCD) from 1992 and 2011 (see Appendix D)

NED = National Elevation Dataset; NLCD = National Land Cover Dataset
DOT = Department of Transportation; NHD = National Hydrography Dataset
* Log-transformed in data analysis to approach a normal distribution.

Table 4.2. Forward-selected spatial, environmental, and landscape variables predicting species composition of species groups in redundancy analysis.

	Group of native species					*Group of exotic species*								
	All	**Wind**	**Water**	**Vertebrate**	**Unassisted**	**All**		**Wind**		**Water**		**Vertebrate**		**Unassisted**
						CF	*N*	*CF*	*N*	*CF*	*N*	*CF*	*N*	
Number of species	209	51	20	82	62	26	29	4	4	4	5	18	21	7
Predictors														
Spatial														
Connectivity model selected:	Euc	LCP'92	LCP'92	Euc	LCP'92	Stream		Stream		Stream		Stream		LCP'92
MEM variables:	1, 4	1, 4, 6	1, 6, 9	4	1, 5, 9	2	3	2	3	2	3	2	3	2, 6, 7, 10, 11
Environment														
Elevation	X	X		X										
Temperature	X	X		X				X		X		X		X
Stream incision			X											
Openness							X		X		X		X	
Sand	X	X		X		X			X					X
pH		X												
Organic matter														
Phosphorus			X											X
Trash					X									
Slope														
Aspect														
Landscape														
Impervious surface														
1km radius							X		X		X		X	X
10km radius			X	X										X
Road distance														
Housing density	X	X				X		X		X		X		

Table 4.3. Results of variance partitioning with tests of significance for pure fractions of variation in species composition explained by spatial, environmental, and landscape variables.

	Group of native species				
Fraction	**All**	**Wind**	**Water**	**Vertebrate**	**Unassisted**
Connectivity [a]	0.019 *	0.051 **	0.064 **	0.007	0.059 **
Environment [b]	0.062 **	0.082 **	0.017	0.073 **	0.027 **
Landscape [c]	-	0.002	0.006	0.004	-
[a + b]	0.019	0.029	0.031	0.012	0.069
[b + c]	0.003	0.014	-	0.003	-
[a + c]	0.004	0.003	0.011	-	-
[a + b + c]	0.014	0.014	0.013	0.017	-
Total explained	0.122	0.195	0.143	0.114	0.154
Unexplained	0.878	0.805	0.857	0.886	0.846

	Group of exotic species								
	All		**Wind**		**Water**		**Vertebrate**		**Unassisted**
Fraction	*Cape Fear*	*Neuse*	*Cape Fear*	*Neuse*	*Cape Fear*	*Neuse*	*Cape Fear*	*Neuse*	
Connectivity [a]	0.042	0.012	0.135 *	0.023	0.136 *	0.024	0.051	0.012	0.322 **
Environment [b]	0.074 *	0.135 **	-	0.240 **	-	0.239 **	0.077 *	0.142 **	0.005
Landscape [c]	0.047 *	0.006	0.071	-	0.071	-	0.067 *	0.005	0.048 *
[a + b]	0.033	0.021	-	0.048	-	0.047	0.036	0.021	0.013
[b + c]	-	0.035	-	0.051	-	0.052	-	0.034	0.005
[a + c]	0.049	0.006	0.113	0.010	0.113	0.010	0.057	0.007	0.008
[a + b + c]	-	0.077	-	0.128	-	0.128	-	0.080	0.012
Total explained	0.236	0.293	0.319	0.480	0.320	0.479	0.278	0.302	0.412
Unexplained	0.764	0.707	0.681	0.520	0.680	0.521	0.722	0.698	0.589

Figure 4.1. Map of impervious surface cover in the Research Triangle area (30 m-resolution data from the National Land Cover Dataset) and sample sites. Sample sites are shown as black circles.

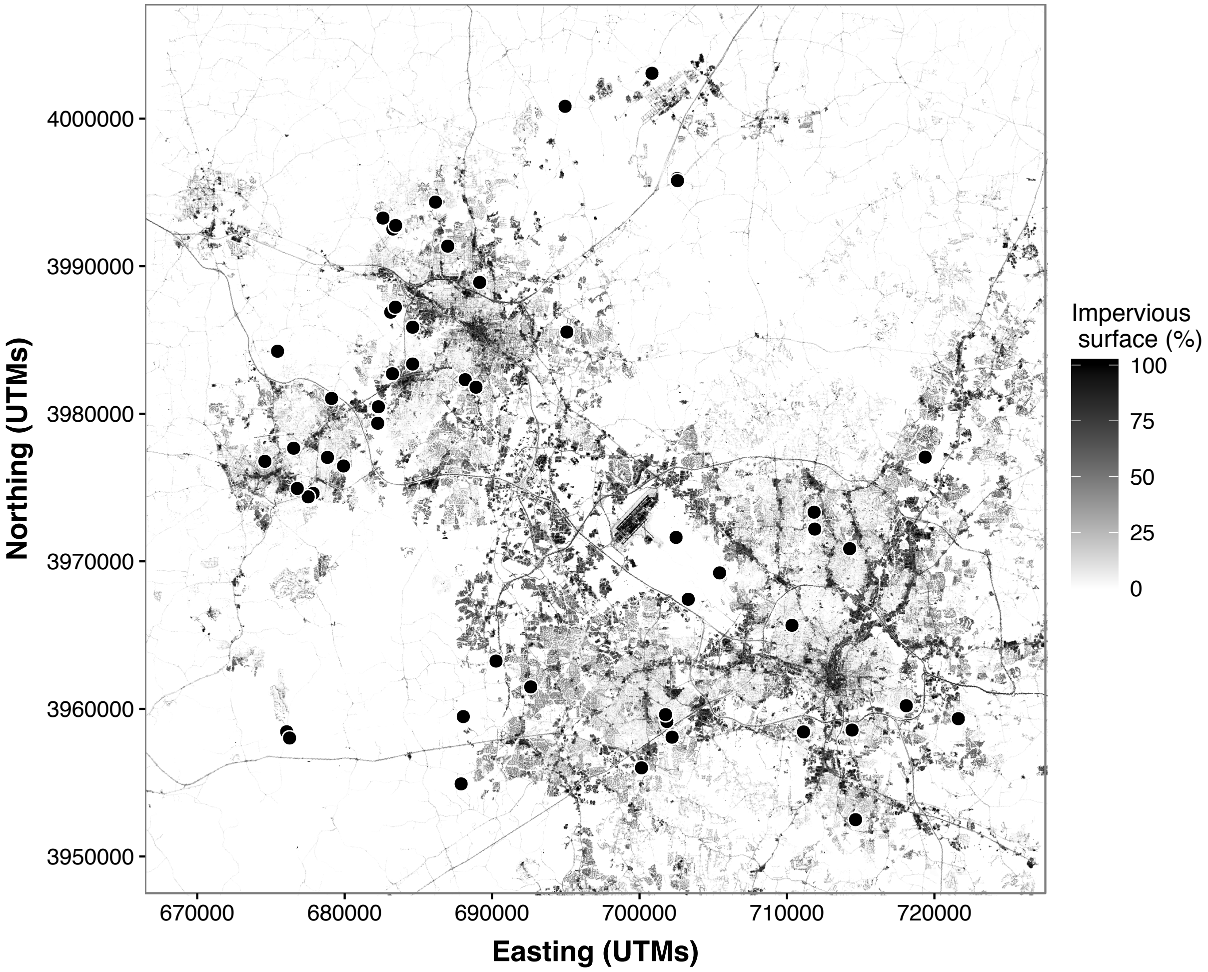


Figure 4.2. Maps depicting connectivity networks (A-D), minimum spanning trees connecting sites (E-H), and graphed MEM eigenvectors (I-L) for Euclidean distance (1st row, with large-scale MEM 4), 1992 least-cost paths (2nd row, with medium-scale MEM 6), 2011 least-cost paths (3rd row, with small-scale MEM 9), and along-stream distance (4th row, with large-scale MEMs 2 from Cape Fear and 3 from Neuse watershed models). MEM eigenvector values are shown by square symbols. Larger squares correspond to higher positive values in black and more negative values in white (adapted from Hawkins et al. 2007, Braaker et al. 2014). In panels depicting along-stream distance (D, H, and L), the Neuse river watershed and associated sites are shown in light grey and the Cape Fear river watershed and associated sites are shown in dark grey.

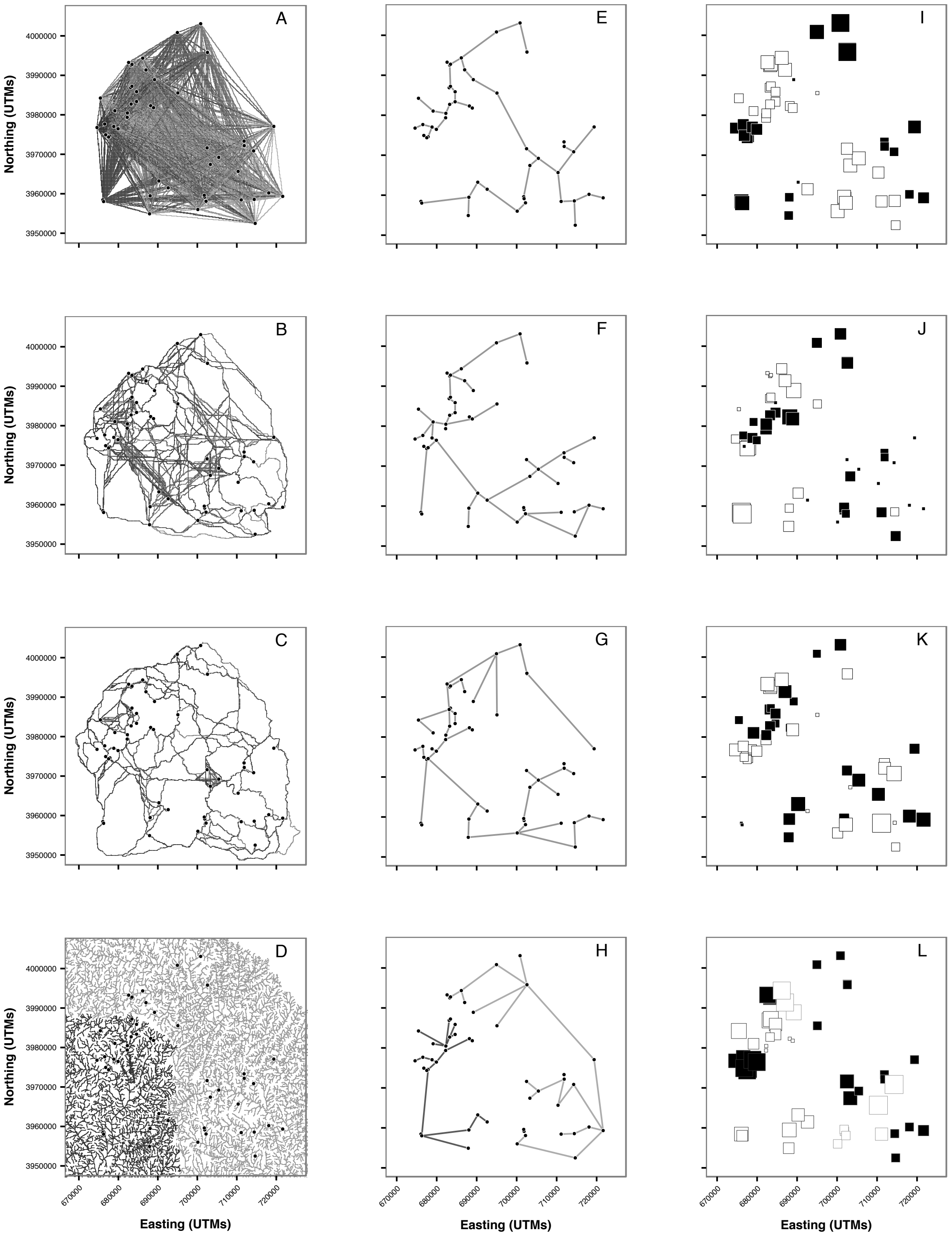

A
B
C
D
E
F
G
H
I
J
K
L
Northing (UTMs)
4000000
3990000
3980000
3970000
3960000
3950000
670000
680000
690000
700000
710000
720000
Easting (UTMs)

Figure 4.3. Conceptual flow diagram of data analysis steps. For spatial variables, the different connectivity models are abbreviated as "Euc" (Euclidean distance), "LCP'92" (least-cost paths from 1992 land cover data), "LCP'11" (least-cost paths from 2011 land cover data), and "Stream" (along-stream distance). See Methods for details on analysis steps.

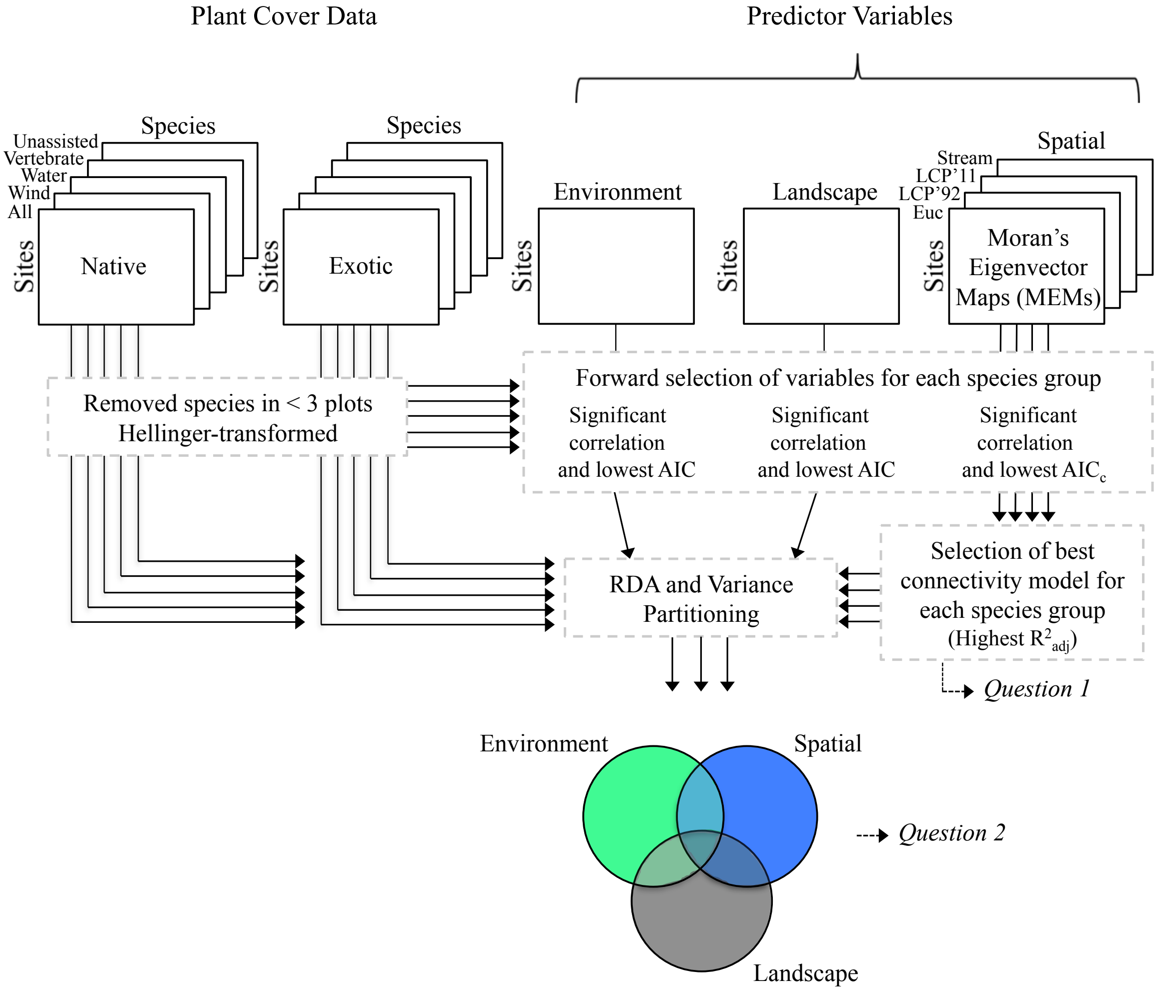


Figure 4.4. Effective distance along least-cost paths was generally higher using 2011 land use data than using 1992 data. This is shown by points located above the 1:1 line.

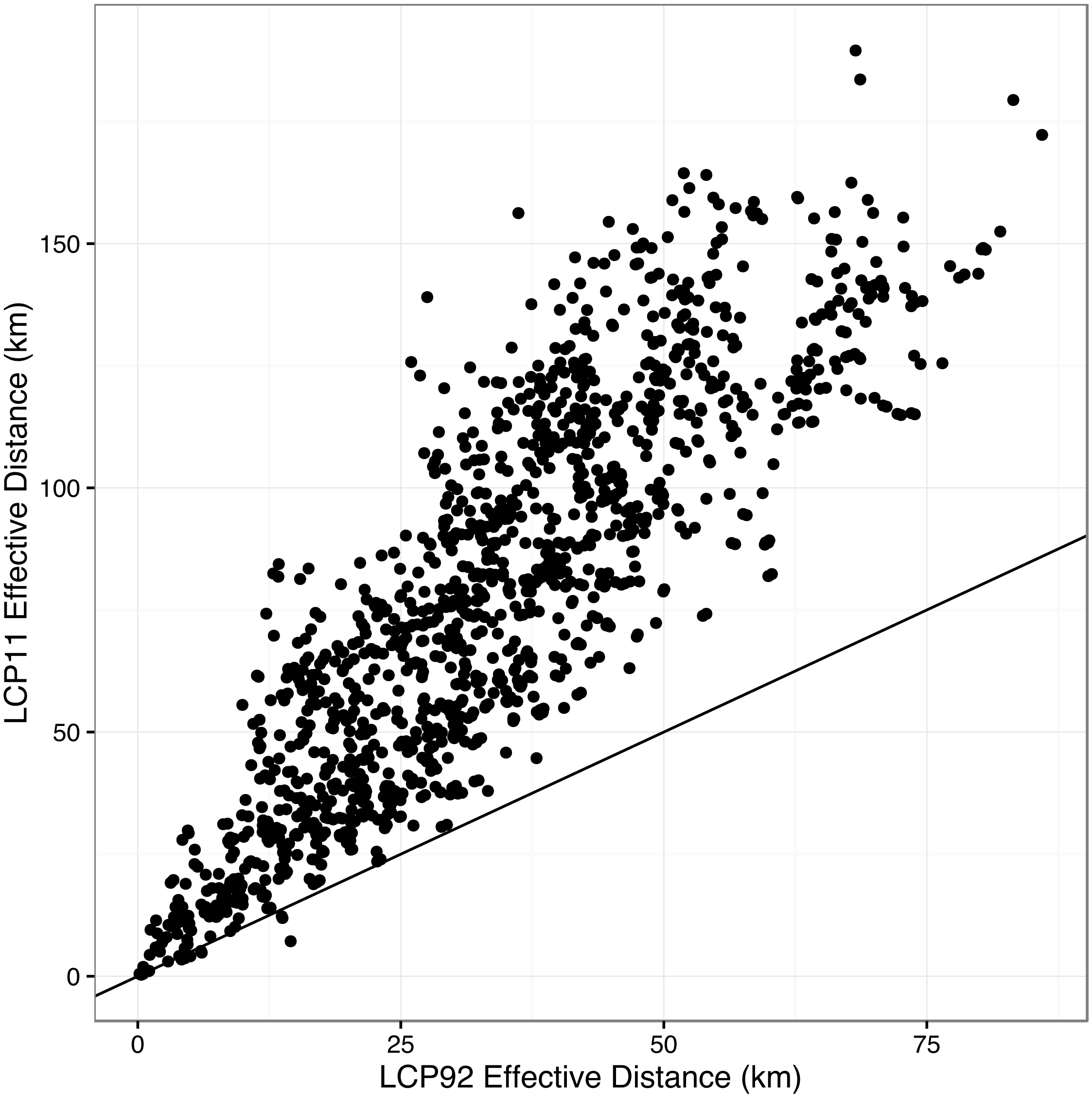


Figure 4.5. Variation in species composition of each species group explained by spatial variables for different connectivity models.

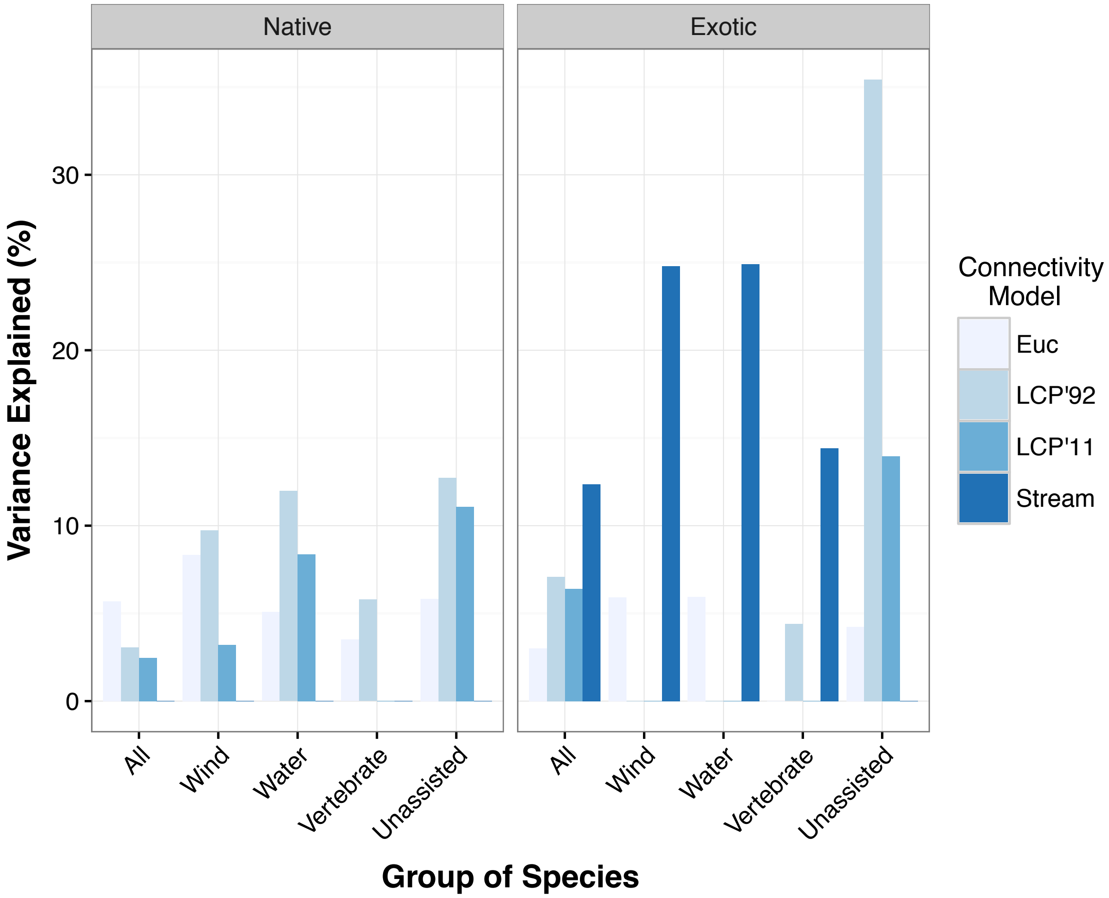
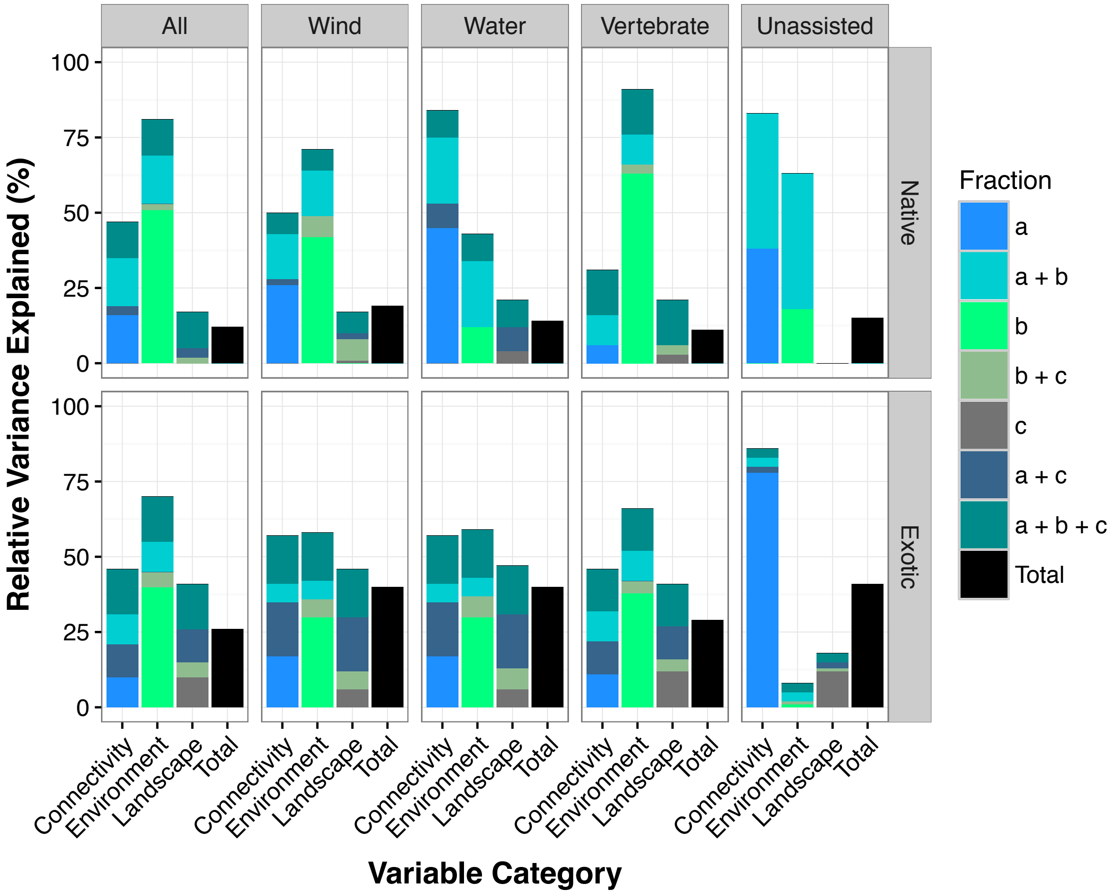


Figure 4.6. Results of variance partitioning of species composition explained by spatial, environmental, and landscape variables. Fraction *a* is variation uniquely explained by spatial variables representing the selected connectivity model for each group (labeled "connectivity"), fraction *b* by only environmental variables, and fraction *c* by only landscape variables. Other fractions (e.g., *a* + *b*) represent variation that is jointly explained by two or more variable types. All fractions (colored bars) are plotted as proportions of the total explained variation. Black bars on the right of each figure show the total variation explained for each species group.



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CHAPTER 5: CONCLUSION

In this dissertation, I used three complementary approaches to address the question of how urban development influences forest plant communities. In this work, I documented changes in several different measures of plant community composition: taxonomic, functional, and phylogenetic diversity, trait composition, and species composition. Together these approaches provide a more nuanced picture of the ways in which habitat loss, fragmentation, altered environmental conditions, and introductions of new species influence forests. Understanding the response of plant communities to these different components of urbanization can help to predict the effects of future development on ecosystems and inform conservation planning and management to create more sustainable cities.

In this chapter, I briefly describe some of the predictions for how habitat loss, fragmentation, environmental conditions, and species introductions affect urban plant communities, and highlight conclusions of my dissertation regarding these topics, bringing together results from the different chapters and summarizing implications of each topic for conservation and restoration in the Research Triangle. I then discuss some of the limitations of this study and considerations for future research directions.

Habitat area

The first and simplest way that urbanization affects ecosystems is by reducing the amount of vegetated area by replacing it with buildings, parking lots, and roads. The reduction of total habitat area is expected to decrease the total number of species through a sampling effect because there will be fewer individuals, extirpation of species with small populations, and a loss of “core” species that are sensitive to edge effects (Fahrig 2003). Increased edge habitat is expected to favor other species, including exotic species that inhabit the urban matrix (McDonald and Urban 2004, 2006, Vilà and Ibáñez 2011). In addition, the loss of other organisms from urban areas, such as herbivores or pollinators, could have strong effects on plant community composition (Christie and Hochuli 2005, Pauw 2007, Faeth et al. 2011).

I found no change in species richness with the amount of habitat surrounding sites (measured as forest cover within a 1 km radius). However, areas with lower forest cover had more exotic species and higher phylogenetic evenness. Habitat loss had effects on species composition as well. Sites with low forest cover were more different from reference sites, and tended to be missing habitat specialists that were expected to occur in those sites based on their soil and stream properties. The number of species with low dispersal ability also declined with decreasing forest cover, perhaps because sites with lower forest cover were also less connected to other forested sites. Indeed, structural equation modeling showed that sites with lower forest cover in the surrounding area were more fragmented, warmer, and had higher soil phosphorus concentrations. Thus loss of habitat also has indirect effects on plant species diversity and composition via its effects on habitat connectivity and environmental conditions (described below).

These results suggest that, as has been recommended by others, protecting large remnant forest areas is a good strategy for conserving native species diversity and maintaining forests that resemble high-quality, reference sites. This is important not only for maintaining forest specialist species but also is likely to be effective for reducing the effects of environmental changes (e.g., warmer temperatures, additions of soil nutrients) within forest patches. Conservation organizations in the Research Triangle area such as the Triangle Land Conservancy attempt to preserve land adjacent to large parcels, such as the Johnston Mill Nature Preserve, which is adjacent to the larger Duke Forest. However, purchasing (or donation) of land is often opportunistic and large swaths are not readily available in land where urban development is already present and increasing. Efforts to maintain large forested areas that may be at risk for development may be important. In addition, other smaller forest patches could also have conservation value, as I will discuss below.

Habitat fragmentation

Loss of habitat connectivity, like habitat loss, can lead to the loss of species with small populations while benefiting "edge species" and facilitating colonization by species found within the matrix (Fahrig 2003). In addition, fragmentation can prevent species with limited dispersal ability and those with specialist mutualism requirements, such as specialist pollinators, from persisting in urban areas (Pauw 2007, Knapp et al. 2009, Concepción et al. 2015).

I found no effects of fragmentation on diversity in my study, but connectivity between sites through forest was a significant predictor of species composition for native species with unassisted, wind-dispersed, and water-dispersed seeds. Although the Research Triangle area has such a high amount of apparently well-connected forest (Minor and Urban 2008), for some species, especially those that already are likely to experience dispersal limitation (i.e., unassisted species), loss of forest connectivity and replacement of forest with urban development seem to contribute to dispersal limitation, with the ultimate result of fewer unassisted species in urban areas. Emphasizing species with limited dispersal ability in restoration and conservation efforts may help to maintain these species in urban areas.

Plans to prevent further losses in connectivity and to even try to increase connectivity between forest patches could also help to maintain native species composition. Efforts to restore connectivity may be most effective in areas where forest patches are not very small and highly isolated, but rather in places where the connectivity is intermediate, as small patches are more likely to have highly altered environmental conditions and be more invaded. Current policies that protect riparian buffers create linear elements connecting riparian forest in much of the Triangle, although small streams (and, of course, those that are channelized and go under roads) sometimes have very narrow or nonexistent buffers.

Loss of hydrologic connectivity in floodplains with changes to the flooding regime may have influenced the changes in water-dispersed species composition across sites and their relationship to stream incision. Thus increasing hydrologic connectivity may also be important for maintaining native plant communities in floodplains. Restoring regular flooding will require a large-scale planning effort to manage stormwater flow and imperviousness upstream from protected areas (Bernhardt and Palmer 2011).

Environmental effects

Environmental conditions are generally important predictors of the number, identity, and traits of species found at different sites. Changes to the urban environment may limit the persistence of some species in urban areas, particularly when these environmental changes cause stressful conditions such as drought or toxicity (Williams et al. 2005, Knapp et al. 2009, Broshot 2011). Many of the environmental changes in urban environments may have some generally positive effects on plant growth and survival, however, by creating warmer winters and adding nutrients such as nitrogen and phosphorus (Gregg et al. 2003). However, these changes may favor some species over others, and may particularly facilitate the spread of non-native or weedy species into urban forest patches (Ostertag and Verwille 2002).

Environmental variables had strong effects on species composition in my study, particularly for species with high dispersal ability (i.e., vertebrate- and wind-dispersed species). Soil texture and elevation were important predictors of species composition across sites, as they are for high-quality riparian sites within the North Carolina Piedmont (Matthews et al. 2011). However, the species composition of more urban sites was not as well predicted by these variables (using descriptions of reference community types with similar environmental conditions) than more rural sites. I found that environmental conditions altered by urbanization (e.g., warmer air temperatures, higher soil phosphorus content, and more incised streams) were important predictors of diversity, composition, and traits of riparian forest plant species.

Temperature was an important variable for explaining changes in plant species composition across sites, particularly for native species. I found no changes in species richness with warmer temperatures, but there was an increase in phylogenetic richness in warmer sites. Warmer temperatures were also associated with a decrease in the proportion of northern species and species with high specific leaf area. These changes in traits may reflect stressful conditions that warmer temperatures put on species with large, thin leaves that tend to have higher evapotranspiration rates and species adapted to cooler temperatures. Warmer temperatures may also facilitate colonization by species with southern ranges, as has been suggested for Southern Magnolia (*Magnolia grandiflora*; Gruhn and White 2011); I did not observed this in my data, however, as there were only eight species in the dataset with strictly southern ranges.

Sites with greater stream incision had a higher number of exotic species, which may contribute to an increase in phylogenetic richness and functional evenness at these sites. Stream incision was also associated with a higher proportion of species with high leaf nitrogen content and an increase in the diversity of leaf nitrogen content of species within the community (functional evenness). These patterns could be explained by increases in nitrogen availability (which I did not measure in the field) in sites affected by the urban stream syndrome (Walsh et al. 2005b) favoring species with fast growth that are able to take advantage of these conditions. I did not see a change in wetland indicator status with increasing stream incision, which has also been found in other studies on the effects of urbanization on riparian plant communities (Von Behren et al. 2013). There was some indication that stream incision influences the composition, if not the diversity, of water-dispersed species, likely through decreasing flooding frequency. A direct measure of flooding may have been more informative than stream incision, which is a rough proxy and can also be strongly influenced by past land use (Allan and Arbor 2004).

Soil phosphorus content was the only environmental variable that appeared to have a negative effect on plant species richness, as well as a negative effect on phylogenetic richness. I had expected that this would occur because of a decrease in native species and potentially an increase in exotic species, but I found no change in the diversity or cover of either group in response to changes in phosphorus content.

Attempting to mitigate environmental effects may increase the conservation value of forest patches in the Research Triangle area. Restoration of streams and increasing canopy cover of riparian buffers will help with some of the environmental changes by increasing shade and reducing stream incision. However, for small forest patches that are most affected by surrounding urban land use, larger-scale efforts beyond the forest patch may be required to mitigate environmental impacts. Increasing vegetative cover outside of forests by planting street trees and other plants could help to reduce the magnitude of the urban heat island effect (Coseo and Larsen 2014). Interventions at the watershed scale may be necessary to reduce nutrient additions and urbanization's effects on stream morphology (Sudduth et al. 2007). Increasing green infrastructure projects and pervious surfaces, and prioritizing protection of headwater areas could help to mitigate the urban stream syndrome. Education about the effects of nutrient additions on forests and encouraging people to use less fertilizer could help to reduce nutrient inputs to urban forests as well.

Species introductions

Increases in exotic species richness and abundance in urban areas are one of the most often documented effects of urbanization on natural communities (e.g., Pennington et al. 2010, Knapp et al. 2012, Aronson et al. 2015). Nevertheless, one of the most striking results of my dissertation research was the number of exotic species present at my study sites (up to 23 species, almost 40% of the total species richness at that site, and sometimes more than half of the cover of the plot). Piedmont riparian forests in general are highly invaded by exotic species, including many of the high-quality reference sites used by Matthews et al. (2011) to describe community types for the National Vegetation Classification. Many of these sites have high cover of Japanese Stiltgrass (*Microstegium vimineum*) and Japanese honeysuckle (*Lonicera japonica*), which tend to cover much of the understory, as well as frequent occurrence of Chinese Privet (*Ligustrum sinense*). Interestingly, *Microstegium vimineum* was one exotic species that tended to have higher cover in more rural sites in my dataset, whereas the opposite was true for exotic ornamental species.

Ornamental species accounted for more than half of the exotic species in my dataset, and some sites had as many as 17 horticultural species, which could cover up to 42% of a plot. As in Matthews and colleagues' (2011) sites, *Lonicera japonica* and *Ligustrum sinense* were among the most abundant ornamental species, as were Autumn Olive (*Elaeagnus umbellata*), English Ivy (*Hedera helix*), Multiflora Rose (*Rosa multiflora*), and Chinese Wisteria (*Wisteria sinensis*). Some of these, such as *Hedera helix* and *Rosa multiflora*, were likely introduced to this region many decades ago and have been spreading since that time, having particularly high abundances in forests that were once private homes or gardens. Other species that have low abundances and occur infrequently in forests in this area, such as Oregon Grape (*Mahonia bealei*) and Nandina (*Nandina domestica*) are currently used in landscaping in the area and may be only just beginning to spread into forests.

Many of the ornamental species commonly used for landscaping in the Research Triangle area are woody, evergreen species with red fruits that attract birds to disperse their seeds. I saw signatures of these nonrandom trait distributions in urban sites, where the proportion of species with evergreen leaves, wood, and vertebrate-dispersed seeds increased significantly. As these species spread into forests, they may create additional sources of resources for birds, change the quality of leaf litter and its decomposition rate, and increase shade in the understory in early spring. Another effect of the spread of ornamental and other exotic species into urban forest patches may be a decline in native species. In my data, sites with higher cover of exotic species have lower native species richness, including sites dominated by *Microstegium vimineum* and those with a diversity of ornamental species.

The extent to which exotic species have colonized both urban and rural forests in the Research Triangle area is concerning. I suspect that there may be some significant impacts of these species, particularly as the structure and trait composition of forests changes with ornamental species colonization. Removing these species would be an expensive, time-consuming, and likely futile exercise (Simmons et al. 2015). However, particularly in the case of ornamental species that are currently used in landscaping projects and appear to be just starting to move into forests, there is an opportunity to educate people about native plants and the impacts that introduced species can have on ecosystems. In some cities in the U.S., the movement of "pollinator-friendly landscaping", as well as xeriscaping in arid regions, have increased awareness and popularity of native plants in yards and gardens. Efforts like these could have an impact on urban forests in the Research Triangle area down the line.

Limitations and future directions

The effects I documented represent a snapshot in time, and urban development is ongoing in the Research Triangle. The effects of urbanization observed in my data are likely to become more pronounced over time, both in response to increasing development and because many effects likely take time to be seen in the abundance of often long-lived plant species. Species whose distributions are limited by dispersal may become less common in urban areas, along with herbaceous species with specialized habitat requirements that are often missing from urban habitat patches. The effects of altered urban environmental conditions, including a decline in phylogenetic diversity that may signal a paucity of ecological strategies that allow natural communities to be resilient to environmental change, may also become more pronounced over time. Planning to protect existing natural areas and efforts to mitigate environmental changes and restore habitat could help to reduce these effects in the future.

I also did not consider the amount of time since urban development has occurred around sites or the past land use of sites, which could determine the extent of responses to urbanization and explain patterns in vegetation that have been influenced by land use legacies. Plots sampled in this study were marked with metal conduit in accordance with the Carolina Vegetation Survey, and I hope that someone will resample them at a later date to look at how the vegetation changes over time. Along with land use history, there are also several environmental effects of urbanization that I did not measure in the field but could additionally explain some variation in plant community structure, including carbon dioxide, soil nitrogen, and flooding frequency. The strength of deer herbivory may also be expected to change along an urbanization gradient and can be an important determinant of plant species composition, so data on deer abundances or estimates of herbivory damage could also be illuminating.

This research has led me to wonder about several mechanisms linking urbanization effects and plant species composition, mainly considering dispersal. I found some apparent effects of urbanization on the composition of water-dispersed species, but as I did not measure flooding frequencies or observe seeds carried by water to sites (which is somewhat difficult to do) it is not entirely clear to me what effects the urban stream syndrome may have on seed dispersal by water. I also wonder to what degree do forest patches in urban areas act as a sink for seeds from the matrix (e.g., of ornamental species) and to what extent the matrix (e.g., backyards) act as sinks for seeds of native species that originate in forests.

Finally, when I was conducting my field work I noticed that there appeared to be very different attitudes regarding forest patches depending on where they were located (e.g., next to the road, in neighborhoods of different socioeconomic status) and what their intended or apparent purpose was (e.g., playground, Frisbee golf course, sewer right-of-way, conservation land). Depending on the intended use of the forest, it may or may not matter to anyone whether there are native or non-native species there, whether the patch acts as habitat for birds, or even whether it is aesthetically pleasing. Research on attributes of urban forests that matter to the people who use them and the extent to which these align with the goals of other stakeholders, such as conservation practitioners, could be useful for managing urban forests in ways that maximize benefits (Bryan et al. 2010, Smith et al. 2015).

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APPENDIX A: CATEGORICAL TRAIT DATA FOR SPECIES IN DATASET

Table A.1. Categorical trait data used in analyses. Data sources for Wetland Indicator Status (WIS) and Dispersal Mode are given; when not otherwise noted, WIS indices were determined using information on species' habitat preferences from Weakley (2010) and Matthews (2011). Information on growth form, nativity, horticultural usage, range, and evergreenness were also found in Weakley (2010).

Species	Growth Form	Nativity	Horticultural	Range	Evergreen	WIS	WIS Source	Dispersal Mode	Dispersal Source
Acalypha rhomboidea	Forb	Native	0	N	0	FACU	NWPL	Unassisted	Minor et al 2009; Hooper et al 2004
Acer floridanum	Tree	Native	0	N; S	0	FACW		Wind	Inferred from morphology and con-geners
Acer leucoderme	Tree	Native	0		0	FACW		Wind	Inferred from morphology and con-geners
Acer negundo	Tree	Native	0	N; S	0	FAC	NWPL	Wind; Water	Minor et al 2009; Cain et al 1998
Acer palmatum	Tree	Exotic	1	E and SE Asia	0			Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2015
Acer rubrum	Tree	Native	0		0	FAC	NWPL	Wind	Inferred from morphology and con-geners
Aesculus sylvatica	Shrub	Native	0	Endemic	0	FAC	NWPL	Vertebrate; Water	Howard 1992
Ageratina altissima	Forb	Native	0	N	0	FACU	NWPL	Wind	Inferred from morphology and congeners (Myers and Harms 2011)

Agrimonia parviflora	Forb	Native	0	N	0	FAC		Vertebrate	Minor et al. 2009
Agrostis perennans	Graminoid	Native	0	N; S	0	FACU	NWPL	Unknown	
Ailanthus altissima	Tree	Exotic	1	E and SE Asia	0	FACU	NWPL	Wind	Cain et al 1998
Albizia julibrissin	Tree	Exotic	1	Paleotropics	0	FACU		Wind; Vertebrate; Water	Meyer 2009
Allium	Forb		0		0	FACU	NWPL	Unassisted	
Allium canadense	Forb	Native	0	N; S	0	FACU	NWPL	Water; Unassisted	Mehrhoff et al 2003
Allium vineale	Forb	Exotic	0	Eurasia	0	FACU	NWPL	Unassisted	Minor et al. 2009
Alnus serrulata	Shrub	Native	0	N; S	0	OBL	NWPL	Wind; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Amaranthus hybridus	Forb	Exotic	0	N; S	0	FACU		Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2015
Ambrosia artemisiifolia	Forb	Native	0	N; S	0	FACU	NWPL	Unassisted	Minor et al 2009; Lavoie et al 2007
Amelanchier arborea	Shrub	Native	0	N; S	0	FAC	NWPL	Vertebrate	Flinn et al 2010
Ampelopsis brevipedunculata	Vine	Exotic			0			Vertebrate	
Amphicarpaea bracteata	Vine	Native	0	N; S	0	FAC	NWPL	Unassisted	Trapp 1988
Anemone americana	Forb	Native	0	N	0	FAC		Unassisted	Inferred from morphology and congeners
Aralia spinosa	Tree	Native	0	N; S	0	FAC	NWPL	Vertebrate	Sullivan 1992

Arisaema dracontium	Forb	Native	0	N; S	0	FACW	NWPL	Vertebrate	Minor et al 2009; Matlack 1994
Arisaema triphyllum	Forb	Native	0	N; S	0	FACW	NWPL	Vertebrate	Minor et al 2009; Matlack 1994
Arnoglossum atriplicifolium	Forb	Native	0	N	0	FAC		Wind	Inferred from morphology and congeners
Aronia arbutifolia	Shrub	Native	0	N; S	0	FACW	NWPL	Vertebrate	Rossell and Kesgen 2003
Arundinaria gigantea	Graminoid	Native	0	N; S	0	FACW	NWPL	Unassisted	Taylor 2006
Asarum canadense	Forb	Native	0	N; S	0	FACU	NWPL	Unassisted	Minor et al 2009; Matlack 1994
Asimina parviflora	Shrub	Native	0	S	0	UPL	NWPL	Vertebrate	Inferred from morphology and congeners
Asimina triloba	Shrub	Native	0	N	0	FAC	NWPL	Vertebrate; Water	Minor et al 2009; Thompson 1981
Asplenium platyneuron	Forb	Native	0	N	0	FACU	NWPL	Wind	Minor et al 2009
Athyrium asplenioides	Forb	Native	0	N; S	0	FAC	NWPL	Wind	Flinn et al 2010
Phyllostachys aurea	Graminoid	Exotic	1	E and SE Asia	0	FACU		Unknown	
Berberis bealei	Shrub	Exotic	1	E and SE Asia	B	FACU		Vertebrate	Allen et al 2006
Betula nigra	Tree	Native	0	N; S	0	FACW	NWPL	Wind; Water	Inferred from morphology and congeners
Bidens connata	Forb	Native	0	N; S	0	FACW		Vertebrate	Inferred from morphology and congeners
Bidens frondosa	Forb	Native	0	N; S	0	FACW	NWPL	Vertebrate; Water	Cain et al 1998; Neff and Baldwin 2005

Bignonia capreolata	Vine	Native	0	N; S	0	FAC	NWPL	Wind	
Boehmeria cylindrica	Forb	Native	0	N; S	0	FACW	NWPL	Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Botrypus virginianus	Forb	Native	0	N; S	0	FACU	NWPL	Wind	Minor et al 2009; Matlack 1994
Brachyelytrum erectum	Graminoid	Native	0	N	0	FACU	NWPL	Wind	Montgomery 1977
Bromus pubescens	Graminoid	Native	0	N	0	FACU	NWPL	Unassisted	Minor et al 2009; Cain et al 1998
Callitriche heterophylla	Forb	Native	0	N; S	0	OBL	NWPL	Vertebrate; Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Campsis radicans	Vine	Native	0	N; S	0	FAC	NWPL	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2015
Cardamine angustata	Forb	Native	0	N	0	FACU	NWPL	Unassisted	Inferred from congeners (Carlsen et al 2009)
Cardamine dissecta	Forb	Native	0	N	0			Unassisted	Inferred from congeners (Carlsen et al 2009)
Cardamine hirsuta	Forb	Exotic	0	Europe	0	FACU	NWPL	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Carex abscondita	Graminoid	Native	0	N	0	FAC	NWPL	Unassisted	Inferred from congeners
Carex amphibola	Graminoid	Native	0	N	0	FAC	NWPL	Unassisted	Minor et al 2009; Cain et al 1998
Carex appalachica	Graminoid	Native	0	N	0	FACU		Unassisted	Inferred from congeners (Flinn et al. 2010)
Carex aureolensis	Graminoid	Native	0	N; S	0	FACW		Unassisted	Inferred from congeners

Carex blanda	Graminoid	Native	0	N; S	0	FAC	NWPL	Unassisted	Minor et al 2009; Cain et al 1998
Carex bromoides	Graminoid	Native	0	N; S	0	FACW	NWPL	Unassisted	Flinn et al 2010
Carex careyana	Graminoid	Native	0	N	0	FAC		Unassisted	Inferred from con-geners
Carex caroliniana	Graminoid	Native	0	N	0	FACU	NWPL	Unassisted	Inferred from con-geners
Carex cephalophora	Graminoid	Native	0	N	0	FACU	NWPL	Unassisted	Minor et al 2009; Cain et al 1998
Carex corrugata	Graminoid	Native	0		0	FACW	NWPL	Unassisted	Inferred from con-geners
Carex crebriflora	Graminoid	Native	0	S	0	FACW	NWPL	Unassisted	Inferred from con-geners
Carex crinita	Graminoid	Native	0	N	0	OBL	NWPL	Water	Flinn et al 2010
Carex debilis	Graminoid	Native	0	N; S	0	FAC	NWPL	Unassisted	Inferred from con-geners
Carex digitalis	Graminoid	Native	0	N; S	0	UPL	NWPL	Unassisted	Minor et al 2009; Cain et al 1998
Carex festucacea	Graminoid	Native	0	N	0	FAC	NWPL	Unassisted	Inferred from con-geners
Carex flaccosperma	Graminoid	Native	0	N	0	FAC	NWPL	Unassisted	Inferred from con-geners
Carex gracillima	Graminoid	Native	0	N	0	FACU	NWPL	Unassisted	Flinn et al 2010
Carex grisea	Graminoid	Native	0	N	0	FACU	NWPL	Unassisted	Minor et al 2009; Cain et al 1998
Carex hirtifolia	Graminoid	Native	0	N	0	FAC		Unassisted	Inferred from con-geners
Carex intumescens	Graminoid	Native	0	N; S	0	FACW	NWPL	Water	Flinn et al 2010
Carex kraliana	Graminoid	Native	0	N	0	FAC		Unassisted	Inferred from con-geners

Carex laevivaginata	Graminoid	Native	0	N	0	OBL	NWPL	Unassisted	Inferred from congeners
Carex laxiculmis	Graminoid	Native	0	N	0	FACW		Unassisted	Inferred from congeners
Carex lupulina	Graminoid	Native	0	N	0	OBL	NWPL	Unassisted	Inferred from congeners
Carex lurida	Graminoid	Native	0	N; S	0	OBL	NWPL	Unassisted	Inferred from congeners
Carex oxylepis	Graminoid	Native	0	N; S	0	FACW	NWPL	Unassisted	Inferred from congeners
Carex pigra	Graminoid	Native	0	Endemic	0	FACW	NWPL	Unassisted	Inferred from congeners
Carex planispicata	Graminoid	Native	0	N	0	FAC		Unassisted	Inferred from congeners
Carex prasina	Graminoid	Native	0	N	0	OBL	NWPL	Unassisted	Flinn et al 2010
Carex radiata	Graminoid	Native	0	N	0	FAC	NWPL	Unassisted	Flinn et al 2010
Carex rosea	Graminoid	Native	0	N	0	FACU	NWPL	Unassisted	Minor et al 2009; Cain et al 1998
Carex squarrosa	Graminoid	Native	0	N; S	0	FACW	NWPL	Unassisted	Inferred from congeners
Carex tribuloides	Graminoid	Native	0	N	0	FACW	NWPL	Unassisted	Inferred from congeners
Carex typhina	Graminoid	Native	0	N	0	FACW	NWPL	Unassisted	Inferred from congeners
Carex willdenowii	Graminoid	Native	0	N	0	UPL	NWPL	Unassisted	Inferred from congeners
Carpinus caroliniana	Tree	Native	0	N; S	0	FAC	NWPL	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Carya cordiformis	Tree	Native	0	N	0	FACU	NWPL	Vertebrate	Minor et al 2009
Carya glabra	Tree	Native	0	N; S	0	FACU	NWPL	Vertebrate	Minor et al 2009

Carya ovalis	Tree	Native	0	N	0	FACU	NWPL	Vertebrate	Minor et al 2009
Carya ovata	Tree	Native	0	N; S	0	FACU	NWPL	Vertebrate	Minor et al 2009
Carya pallida	Tree	Native	0	N	0	FACU		Vertebrate	Minor et al 2009
Carya tomentosa	Tree	Native	0	N; S	0	FACU		Vertebrate	Minor et al 2009
Celastrus orbiculatus	Vine	Exotic	0	E and SE Asia	0	FACU	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Celtis laevigata	Tree	Native	0	N; S	0	FACW	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Celtis occidentalis	Tree	Native	0	N	0	FACU	NWPL	Vertebrate	Minor et al 2009; Stiles 1980
Cerastium brachypetalum	Forb	Exotic	0	Europe	0	FACU		Unassisted	Inferred from congeners (Cain et al. 1998)
Cercis canadensis	Tree	Native	0	N; S	0	FACU	NWPL	Wind	Minor et al 2009; Willson et al 1990
Chaerophyllum procumbens	Forb	Native	0	N; S	0	FACW	NWPL	Unassisted	Minor et al 2009; Römermann et al 2005
Chamaecrista nictitans	Forb	Native	0	N; S	0	FACU	NWPL	Unassisted	Inferred from morphology
Chasmanthium latifolium	Graminoid	Native	0	N; S	0	FACU	NWPL	Unknown	
Chasmanthium laxum	Graminoid	Native	0	N; S	0	FAC	NWPL	Unknown	
Chimaphila maculata	Subshrub	Native	0	N; S	B	FACU		Wind	Gilliam 2014
Chionanthus virginicus	Shrub	Native	0	N; S	0	FAC	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Cinna arundinacea	Graminoid	Native	0	N	0	FACW	NWPL	Wind	Montgomery 1977

Circaea canadensis	Forb	Native	0	N	0	FACU	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Citrus trifoliata	Tree	Exotic	1	E and SE Asia	0	FAC		Vertebrate	Inferred from morphology and con-geners
Clematis terniflora	Vine	Exotic	1	E and SE Asia	0	FACU	NWPL	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Clematis viorna	Vine	Native	0	N	0	FAC		Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Clematis virginiana	Vine	Native	0	N; S	0	FAC	NWPL	Wind; Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Cain et al. 1998
Commelina communis	Forb	Exotic	0	Eurasia	0	FAC	NWPL	Unassisted	Minor et al 2009; Ohtsuka and Ohsawa 1994
Commelina virginica	Forb	Native	0	N; S	0	FACW	NWPL	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Conoclinium coelestinum	Forb	Native	0	N; S	0	FAC	NWPL	Wind	Myers and Harms 2011
Conyza canadensis	Forb	Native	0	N; S	0	FAC		Wind	Dauer et al. 2006
Coreopsis verticillata	Forb	Native	1	Endemic	0	FAC		Unknown	
Cornus amomum	Shrub	Native	0	N	0	FACW	NWPL	Vertebrate	Stiles 1980

Cornus florida	Tree	Native	0	N; S	0	FACU	NWPL	Vertebrate	Minor et al 2009; Czarnecka 2005
Corylus americana	Shrub	Native	0	N	0	FACU	NWPL	Unassisted	Minor et al 2009; Beattie and Culver 1981
Crataegus	Shrub	Native	0		0			Vertebrate	Inferred from congeners
Cryptotaenia canadensis	Forb	Native	0	N	0	FAC	NWPL	Unassisted	Minor et al 2009; Williams 1994
Cynoglossum virginianum	Forb	Native	0	N	0	FAC		Vertebrate	Cipollini et al 1993
Dactylis glomerata	Graminoid	Exotic	0	Europe	0	FACU	NWPL	Unassisted	Minor et al. 2009
Danthonia spicata	Graminoid	Native	0	N	0	FACU		Vertebrate	Minor et al 2009; McIntyre et al. 1995
Daucus carota	Forb	Exotic	0	Europe	0	UPL	NWPL	Vertebrate	Minor et al. 2009
Desmodium perplexum	Forb	Native	0	N; S	0	FAC		Vertebrate	Inferred from morphology and congeners (Matlack et al 1994)
Dichanthelium acuminatum	Graminoid	Native	0	N; S	0	FAC	NWPL	Unassisted	Inferred from congeners
Dichanthelium boscii	Graminoid	Native	0	N; S	0	FAC		Unassisted	Inferred from congeners
Dichanthelium clandestinum	Graminoid	Native	0	N	0	FAC	NWPL	Unassisted	Inferred from congeners
Dichanthelium commutatum	Graminoid	Native	0	N; S	0	FACU	NWPL	Unassisted	Kirkman et al 2004
Dichanthelium dichotomum	Graminoid	Native	0	N; S	0	FAC	NWPL	Unassisted	Inferred from congeners
Dichanthelium laxiflorum	Graminoid	Native	0	N; S	0	FACU	NWPL	Unassisted	Inferred from congeners
Dichanthelium polyanthes	Graminoid	Native	0	N	0	FAC		Unassisted	Inferred from congeners

Dichondra carolinensis	Forb	Native	0	S	0	FACW	NWPL	Unknown	
Dioscorea polystachya	Vine	Exotic	0	E Asia	0	FAC		Unassisted	Minor et al 2009; Harrison et al. 2001
Dioscorea villosa	Vine	Native	0	N	0	FAC	NWPL	Unassisted	Minor et al. 2009
Diospyros virginiana	Tree	Native	0	N; S	0	FAC	NWPL	Vertebrate; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Elaeagnus pungens	Shrub	Exotic	1	E and SE Asia	B	FACU		Vertebrate	Weakley 2012
Elaeagnus umbellata	Shrub	Exotic	1	E and SE Asia	0	FACU		Vertebrate	Minor et al 2009; Swearington et al. 2002
Elephantopus carolinianus	Forb	Native	0	N; S	0	FACU	NWPL	Wind	Kirkman et al 2004
Elymus hystrix	Graminoid	Native	0	N; S	0	UPL	NWPL	Unassisted	Inferred from congeners
Elymus macgregorii	Graminoid	Native	0	N	0	FACW		Unassisted	Inferred from congeners
Elymus villosus	Graminoid	Native	0	N; S	0	FACU	NWPL	Unassisted	Minor et al 2009; Bockelmann et al 2003
Elymus virginicus	Graminoid	Native	0	N; S	0	FACW	NWPL	Unassisted	Minor et al 2009; Bockelmann et al 2003
Endodeca serpentaria	Forb	Native	0	N; S	0	UPL	NWPL	Unassisted	Kirkman et al 2004
Epifagus virginiana	Forb	Native	0	N; S	0	FACU		Unknown	
Erechtites hieracifolia	Forb	Native	0	N; S	0	FAC		Wind	based on morphology
Erigeron philadelphicus	Forb	Native	0	N	0	FACU	NWPL	Wind	Flinn et al 2010; Montgomery 1977
Euonymus alatus	Shrub	Exotic	0	E and SE Asia	B	FACU		Vertebrate	Inferred from morphology and congeners

Euonymus americanus	Subshrub	Native	0	N; S	B	FAC	NWPL	Vertebrate	Stiles 1980
Euonymus fortunei	Shrub	Exotic	1	E and SE Asia	B	FACW		Vertebrate	Stiles 1980
Eupatorium serotinum	Forb	Native	0	N; S	0	FAC	NWPL	Wind	Flinn et al 2010; Montgomery 1977
Eurybia divaricata	Forb	Native	0	N	0	FAC		Wind	Flinn et al 2010; Britton and Brown 1913
Fagus grandifolia	Tree	Native	0	N; S	0	FACU	NWPL	Vertebrate	Minor et al 2009
Festuca subverticillata	Graminoid	Native	0	N	0	FACU	NWPL	Wind	Minor et al 2009; Cain et al 1998
Fraxinus americana	Tree	Native	0	N; S	0	FACU	NWPL	Wind	Inferred from morphology and congeners
Fraxinus pennsylvanica	Tree	Native	0	N; S	0	FACW	NWPL	Wind	Minor et al 2009; Cain et al 1998
Galium aparine	Forb	Native	0	N; S	0	FACU	NWPL	Vertebrate	Minor et al 2009; Fischer et al 1996
Galium circaezans	Forb	Native	0	N; S	0	UPL	NWPL	Unassisted	Matlack et al 1994
Galium obtusum	Forb	Native	0	N	0	FACW	NWPL	Unassisted	Flinn et al 2010
Galium pilosum	Forb	Native	0	N; S	0	FAC		Unassisted	Inferred from morphology and congeners
Galium triflorum	Forb	Native	0	N; S	0	FACU	NWPL	Vertebrate	Minor et al 2009; Fischer et al 1996
Galium uniflorum	Forb	Native	0	N; S	0	FACU	NWPL	Unassisted	Inferred from morphology and congeners
Gelsemium sempervirens	Vine	Native	0	S	B	FAC	NWPL	Unknown	

Geranium maculatum	Forb	Native	0	N	0	FACU	NWPL	Unassisted	Minor et al 2009; Matlack 1994
Geum canadense	Forb	Native	0	N	0	FACU	NWPL	Vertebrate	Minor et al 2009; Thompson 1981
Geum vernum	Forb	Native	0	N	0	FACU	NWPL	Vertebrate	Inferred from morphology and congeners
Glechoma hederacea	Forb	Exotic	0	Eurasia	0	FACU	NWPL	Unassisted	Minor et al 2009; Hutchings and Price 1999
Gleditsia triacanthos	Tree	Native	1	N; S	0	FAC	NWPL	Vertebrate	Minor et al 2009; Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Glyceria striata	Graminoid	Native	0	N	0	OBL	NWPL	Wind; Vertebrate; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Gonolobus suberosus	Vine	Native	0	N; S	0	FACW	NWPL	Wind	Inferred from morphology
Goodyera pubescens	Forb	Native	0	N	0	FACU	NWPL	Wind	Sorrells and Warren 2011
Hamamelis virginiana	Shrub	Native	0	N; S	0	FACU	NWPL	Vertebrate; Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Hedera helix	Vine	Exotic	1	Europe	B	FACU	NWPL	Vertebrate	Minor et al 2009; Swearington et al. 2002
Helianthus decapetalus	Forb	Native	0	N	0	FACU	NWPL	Unknown	
Hexastylis arifolia	Forb	Native	0	Endemic	B	FAC	NWPL	Unassisted	Sorrells and Warren 2011
Hexastylis minor	Forb	Native	0	Endemic	B	FACU		Unassisted	Inferred from congeners
Hibiscus syriacus	Shrub	Exotic	1	E and SE Asia	0	FACU		Wind	Inferred from morphology

Hieracium venosum	Forb	Native	0	N	0	FACU		Wind	Inferred from congeners
Houstonia caerulea	Forb	Native	0	N	0	FACU	NWPL	Unknown	
Humulus japonicus	Vine	Exotic	1	E and SE Asia	0	FACU	NWPL	Wind; Water	PA Department of Conservation and Natural Resources 2009
Hydrophyllum canadense	Forb	Native	0	N	0	FACU	NWPL	Unknown	
Hydrophyllum virginianum	Forb	Native	0	N	0	FAC	NWPL	Unknown	
Hylodesmum nudiflorum	Forb	Native	0	N	0	FAC		Vertebrate	Inferred from morphology and congeners
Hypericum hypericoides	Subshrub	Native	0	N; S	0	FACU	NWPL	Wind; Vertebrate; Water	Tisdale et al 1959; Comes et al 1978
Hypericum nudiflorum	Subshrub	Native	0		0	FACW	NWPL	Wind; Vertebrate; Water	Tisdale et al 1959; Comes et al 1978
Hypericum perforatum	Subshrub	Exotic	0	Europe	0	FAC	NWPL	Wind; Vertebrate; Water	Inferred from morphology and congeners
Hypericum punctatum	Forb	Native	0	N; S	0	FAC	NWPL	Wind; Vertebrate; Water	Tisdale et al 1959; Comes et al 1978
Ilex aquifolium	Tree	Exotic	1	Europe	B	FACU		Vertebrate	Inferred from morphology and congeners
Ilex cornuta	Shrub	Exotic	1	E and SE Asia	B	FACU		Vertebrate	Inferred from morphology and congeners

Ilex vomitoria	Shrub	Exotic	1	E and SE Asia	B	FAC	NWPL	Vertebrate	Inferred from morphology and congeners
Ilex decidua	Tree	Native	0	N; S	0	FACW	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Ilex opaca	Tree	Native	0	N; S	B	FACU	NWPL	Vertebrate	Stiles 1980
Ilex verticillata	Tree	Native	0	N	0	FACW	NWPL	Vertebrate	Stiles 1980
Impatiens capensis	Forb	Native	0	N; S	0	FACW	NWPL	Unassisted	Minor et al 2009; Cain et al 1998
Ionactis linariifolia	Forb	Native	0	N	0	FACU		Wind	Inferred from morphology
Isotrema macrophylla	Vine	Native						Unknown	
Juglans nigra	Tree	Native	0	N	0	FACU	NWPL	Vertebrate	Minor et al 2009; Cain et al 1998
Juncus coriaceus	Graminoid	Native	0	S	0	FACW	NWPL	Wind	Inferred from morphology and congeners
Juncus effusus	Graminoid	Native	0	N; S	0	FACW	NWPL	Wind; Vertebrate; Water	Flinn et al 2010; Pakeman et al 2002; Neff and Baldwin 2005
Juncus tenuis	Graminoid	Native	0	N; S	0	FAC	NWPL	Wind	Minor et al 2009; Cain et al. 1998
Juniperus virginiana	Tree	Native	0	N; S	1	FACU	NWPL	Vertebrate	Minor et al 2009; Stiles 1980
Krigia dandelion	Forb	Native	0	N	0	FAC	NWPL	Wind	Inferred from morphology
Lactuca	Forb	Native	0	N; S	0	FACU	NWPL	Wind	Inferred from morphology
Lactuca canadensis	Forb	Native	0		0	FACU	NWPL	Wind	Inferred from morphology
Lactuca floridana	Forb	Native	0		0	FACU	NWPL	Wind	Inferred from morphology

Laportea canadensis	Forb	Native	0	N	0	FAC	NWPL	Unassisted	Montgomery 1977
Leersia virginica	Graminoid	Native	0	N; S	0	FACW	NWPL	Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Lespedeza cuneata	Subshrub	Exotic	0	E and SE Asia	0	FACU	NWPL	Vertebrate	Eddy et al 2003
Ligustrum japonicum	Shrub	Exotic	1	E and SE Asia	B	UPL	NWPL	Vertebrate	Inferred from morphology and congeners
Ligustrum lucidum	Shrub	Exotic	1	E and SE Asia	B	FACU		Vertebrate	Inferred from morphology and congeners
Ligustrum obtusifolium	Shrub	Exotic	1	E and SE Asia	B	FACU		Vertebrate	Inferred from morphology and congeners
Ligustrum sinense	Shrub	Exotic	1	E and SE Asia	B	FACU	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Lindera benzoin	Shrub	Native	0	N	0	FAC	NWPL	Vertebrate	Minor et al 2009; Matlack 1994
Liquidambar styraciflua	Tree	Native	0	N	0	FAC	NWPL	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Liriodendron tulipifera	Tree	Native	0	N; S	0	FACU	NWPL	Wind; Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Liriope muscari	Forb	Exotic	1	E and SE Asia	B	FAC		Vertebrate	Inferred from morphology and congeners
Lobelia cardinalis	Forb	Native	0	N; S	0	FACW	NWPL	Unassisted	Inferred from congeners

Lonicera japonica	Vine	Exotic	1	E and SE Asia	0	FAC	NWPL	Vertebrate	Minor et al 2009; Swearington et al 2002
Lonicera sempervirens	Vine	Native	0	N	0	FACU	NWPL	Vertebrate	Stiles 1980
Luzula acuminata	Graminoid	Native	0	N	0	FAC	NWPL	Unknown	
Luzula echinata	Graminoid	Native	0	N	0	FACU	NWPL	Unknown	
Lycopus	Forb	Native	0	N; S	0	OBL	NWPL	Water	Moon and Hong 2006
Lycopus americanus								Water	Flinn et al 2010
Lycopus virginicus								Water	Moon and Hong 2006
Lysimachia ciliata	Forb	Native	0	N	0	FACW	NWPL	Water	Andersson et al 2000
Magnolia grandiflora	Tree	Native	1	S	B	FACU	NWPL	Vertebrate	Inferred from morphology and congeners
Magnolia tripetala	Tree	Native	0	N	0	FACU	NWPL	Vertebrate	Inferred from morphology and congeners
Magnolia virginiana	Tree	Native	1	N; S	B	FACW	NWPL	Vertebrate	Stiles 1980
Mahonia bealei	Shrub	Exotic	1		B				
Maianthemum racemosum	Forb	Native	0	N	0	FACU	NWPL	Vertebrate	Thompson 1979
Medicago lupulina	Forb	Exotic	0	Europe	0	FACU	NWPL	Vertebrate; Water	Yan et al 2009
Melica mutica	Graminoid	Native	0	N; S	0	FAC		Unknown	
Menispermum canadense	Vine	Native	0	N	0	FACU	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008

Microstegium vimineum	Graminoid	Exotic	0	E and SE Asia	0	FAC	NWPL	Wind; Vertebrate; Water	Swearington 2004
Mikania scandens	Vine	Native	0	N; S	0	FACW	NWPL	Wind	Inferred from morphology and con-geners
Mitchella repens	Forb	Native	0	N; S	B	FACU	NWPL	Vertebrate	Stiles 1980
Morella cerifera	Shrub	Native	1	S	0	FAC	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2016
Morus alba	Tree	Exotic	1	E and SE Asia	0	UPL	NWPL	Vertebrate	Inferred from morphology and con-geners
Morus rubra	Tree	Native	0	N; S	0	FACU	NWPL	Vertebrate	Minor et al 2009; Stiles 1980
Muhlenbergia frondosa	Graminoid	Native	0	N	0	FAC	NWPL	Unassisted	Minor et al 2009
Muhlenbergia schreberi	Graminoid	Native	0	N; S	0	FAC	NWPL	Unassisted	Minor et al 2009
Murdannia keisak	Forb	Exotic	0	E Asia	0	OBL	NWPL	Vertebrate	Dunn and Sharitz 1990
Myosotis macrosperma	Forb	Native	0	N	0	FAC	NWPL	Unknown	
Nandina domestica	Shrub	Exotic	1	E and SE Asia	B	FACU		Vertebrate; Water	Meisenburg and Fox 2002
Nemophila aphylla	Forb	Native	0	N	0	FACW	NWPL	Unknown	
Nyssa sylvatica	Tree	Native	0	N; S	0	FAC	NWPL	Vertebrate	Minor et al 2009
Onoclea sensibilis	Forb	Native	0	N	0	FACW	NWPL	Wind	Flinn et al 2010
Ophioglossum pycnostichum	Forb	Native	0	N; S	0	FACW	NWPL	Wind	Inferred from morphology and con-geners
Ornithogalum nutans	Forb	Exotic	1	W Asia	0	FAC		Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2016

Osmorhiza longistylis	Forb	Native	0	N	0	FACU	NWPL	Vertebrate	Minor et al 2009; Matlack 1994
Osmunda spectabilis	Forb	Native	0	N; S	0	OBL	NWPL	Wind	Inferred from morphology and congeners
Ostrya virginiana	Tree	Native	0		0	FACU	NWPL	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Oxalis	Forb	Native	0	N; S	0	FACU	NWPL	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Oxalis dillenii	Forb	Native	0	N; S	0	FACU	NWPL	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Oxydendrum arboreum	Tree	Native	0	N	0	UPL	NWPL	Wind	Schwartz et al 2001
Parthenocissus quinquefolia	Vine	Native	0	N; S	0	FACU	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Passiflora incarnata	Vine	Native	1	N; S	0	FACU		Vertebrate	Inferred from morphology and congeners
Passiflora lutea	Vine	Native	0	N; S	0	FAC		Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Pedicularis canadensis	Forb	Native	0	N	0	FACU	NWPL	Unknown	
Peltandra virginica	Forb	Native	0	N; S	0	OBL	NWPL	Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Perilla frutescens	Forb	Exotic	1	E and SE Asia	0	FACU	NWPL	Unassisted	Minor et al 2009
Persicaria [*hydropiperoides* + *punctata*]	Forb	Native	0		0	OBL	NWPL	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008

Persicaria arifolia	Vine	Native	0	N; S	0	OBL	NWPL	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Persicaria hydropiperoides	Forb	Native	0	N; S	0	OBL	NWPL	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Persicaria longiseta	Forb	Exotic	0	Asia	0	FAC	NWPL	Unassisted	Inferred from congeners
Persicaria punctata	Forb	Native	0	N; S	0	OBL	NWPL	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Persicaria virginiana	Forb	Native	0	N; S	0	FAC	NWPL	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Phegopteris hexagonoptera	Forb	Native	0	N	0	FAC	NWPL	Wind	Inferred from morphology and congeners
Phryma leptostachya	Forb	Native	0	N	0	FACU	NWPL	Vertebrate	Minor et al 2009; Holm 1913
Phytolacca americana	Forb	Native	0	N; S	0	FACU	NWPL	Vertebrate	Minor et al 2009; Matlack 1994
Pilea pumila	Forb	Native	0	N; S	0	FACW	NWPL	Water	Neff and Baldwin 2005
Pinus taeda	Tree	Native	0	S	1	FAC	NWPL	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Platanus occidentalis	Tree	Native	0	N	0	FACW	NWPL	Wind	Inferred from morphology
Poa autumnalis	Graminoid	Native	0	N; S	0	FAC	NWPL	Unassisted	Inferred from morphology and congeners (Cain et al. 1998)
Poa compressa	Graminoid	Exotic	0	Europe	0	FACU	NWPL	Unassisted	Inferred from morphology and congeners (Cain et al. 1998)

Podophyllum peltatum	Forb	Native	0	N; S	0	FACU	NWPL	Vertebrate	Minor et al 2009; Matlack 1994
Polygonatum biflorum	Forb	Native	0	N; S	0	FACU	NWPL	Wind	Flinn et al 2010
Polystichum acrostichoides	Forb	Native	0	N; S	B	FACU	NWPL	Vertebrate	Minor et al 2009; Matlack 1994
Pontederia cordata	Forb	Native	0	N; S	0	OBL	NWPL	Unknown	
Potentilla canadensis	Forb	Native	0	N; S	0	FAC		Unassisted	Matlack 1994
Potentilla indica	Forb	Exotic	0	Asia	0	FACU	NWPL	Unknown	
Potentilla simplex	Forb	Native	0	N; S	0	FACU	NWPL	Unknown	
Nabalus altissimus	Forb	Native	0	N	0	FACU	NWPL	Unknown	
Nabalus serpentarius	Forb	Native	0	N	0	FACU		Unknown	
Prunella vulgaris	Forb	Exotic	0	Eurasia	0	FACU	NWPL	Water	Andersson et al. 2000
Prunus caroliniana	Tree	Native	1	S	B	FACU	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Prunus serotina	Tree	Native	0	N; S	0	FACU	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Prunus serrulata	Tree	Exotic	1	E and SE Asia	0	FACU		Vertebrate	Inferred from morphology and congeners
Pueraria montana	Vine	Exotic	0	E and SE Asia	0	UPL	NWPL	Unassisted	Inferred from morphology
Pyrus calleryana	Tree	Exotic	1	E and SE Asia	0	FACU		Vertebrate	Inferred from morphology and congeners
Quercus alba	Tree	Native	0	N	0	FACU	NWPL	Vertebrate	Minor et al 2009

Quercus falcata	Tree	Native	0	N; S	0	FACU	NWPL	Vertebrate	Minor et al 2009
Quercus lyrata	Tree	Native	0	N	0	OBL	NWPL	Vertebrate	Minor et al 2009
Quercus michauxii	Tree	Native	0	N; S	0	FACW	NWPL	Vertebrate	Minor et al 2009
Quercus nigra	Tree	Native	0	S	0	FAC	NWPL	Vertebrate	Minor et al 2009
Quercus pagoda	Tree	Native	0	N	0	FACW	NWPL	Vertebrate	Minor et al 2009
Quercus phellos	Tree	Native	0	N	0	FAC	NWPL	Vertebrate	Minor et al 2009
Quercus rubra	Tree	Native	0	N	0	FACU	NWPL	Vertebrate	Minor et al 2009
Quercus shumardii	Tree	Native	0	N; S	0	FAC	NWPL	Vertebrate	Minor et al 2009
Quercus velutina	Tree	Native	0	N	0	FACU		Vertebrate	Minor et al 2009
Ranunculus abortivus	Forb	Native	0	N	0	FACW	NWPL	Unassisted	Minor et al 2009; Matlack 1994
Ranunculus recurvatus	Forb	Native	0	N	0	FAC	NWPL	Vertebrate	Montgomery 1977
Rhododendron periclymenoides	Shrub	Native	0	N	0	FAC	NWPL	Unknown	
Rosa multiflora	Shrub	Exotic	1	Asia	0	FACU	NWPL	Vertebrate	Minor et al 2009
Rubus	Subshrub	Native	0	N; S	0	FAC		Vertebrate	Minor et al 2009
Rubus flagellaris	Subshrub	Native	0	N; S	0	FACU	NWPL	Vertebrate	Minor et al 2009
Rubus pensilvanicus	Subshrub	Native	0	N; S	0	FAC	NWPL	Vertebrate	Minor et al 2009
Rudbeckia laciniata	Forb	Native	0	N	0	FACW	NWPL	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2016
Ruellia caroliniensis	Forb	Native	0	N; S	0	FACU	NWPL	Unassisted	Kirkman et al 2004
Sagittaria latifolia	Forb	Native	0	N; S	0	OBL	NWPL	Water	Inferred from congeners (Flinn et al 2010)

Salix nigra	Tree	Native	0	N	0	OBL	NWPL	Wind; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Salvia lyrata	Forb	Native	0	N; S	0	FACU	NWPL	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Sambucus canadensis	Shrub	Native	0	N; S	0	FAC	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Sanguinaria canadensis	Forb	Native	0	N; S	0	UPL	NWPL	Vertebrate	Minor et al 2009; Matlack 1994
Sanicula canadensis	Forb	Native	0	N; S	0	FACU	NWPL	Vertebrate	Montgomery 1977
Sanicula smallii	Forb	Native	0	N	0	FACU		Vertebrate	Montgomery 1977
Sassafras albidum	Tree	Native	0	N; S	0	FACU	NWPL	Vertebrate	Minor et al 2009; Stiles 1980
Saururus cernuus	Forb	Native	0	N; S	0	OBL	NWPL	Unknown	
Sceptridium biternatum	Forb	Native	0	N	0	FAC	NWPL	Wind	inferred from morphology
Scleria oligantha	Graminoid	Native	0	N; S	0	FACU	NWPL	Unknown	
Scutellaria elliptica	Forb	Native	0	N; S	0	FACU		Unassisted	Inferred from morphology and congeners
Scutellaria integrifolia	Forb	Native	0	N; S	0	FACW	NWPL	Unassisted	Kirkman et al 2004
Scutellaria lateriflora	Forb	Native	0	N; S	0	FACW	NWPL	Unassisted; Water	Minor et al 2009; Kirkman et al 2004
Silene virginica	Forb	Native	0	N	0	FAC		Unknown	
Sisyrinchium angustifolium	Forb	Native	0	N; S	0	FACW	NWPL	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2016

Smallanthus uvedalius	Forb	Native	0	N; S	0	FACW		Unknown	
Smilax bona-nox	Vine	Native	0	N; S	B	FACU	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Shcneider and Sharitz 1988
Smilax glauca	Vine	Native	0	N; S	0	FACU	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Schneider and Sharitz 1988
Smilax pulverulenta	Vine	Native	0	N	0	FACU	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Schneider and Sharitz 1988
Smilax rotundifolia	Vine	Native	0	N; S	B	FAC	NWPL	Vertebrate	Minor et al 2009; Schneider and Sharitz 1988
Solanum carolinense	Forb	Native	0	N; S	0	FACU	NWPL	Vertebrate	Minor et al 2009; Inferred from morphology and congeners
Solanum ptychanthum	Forb	Native	0	N; S	0	FACU	NWPL	Vertebrate	Inferred from morphology and congeners
Solidago	Forb	Native	0		0			Wind	
Solidago arguta	Forb	Native	0	N; S	0	UPL	NWPL	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Solidago caesia	Forb	Native	0	N	0	FAC		Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008

Solidago canadensis	Forb	Native	0	N	0	FACU	NWPL	Wind	Inferred from morphology and congeners
Solidago gigantea	Forb	Native	0	N	0	FACW	NWPL	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Solidago juncea	Forb	Native	0	N	0	FAC		Wind	Inferred from morphology and congeners
Solidago nemoralis	Forb	Native	0	N	0	FAC		Wind	Inferred from morphology and congeners
Solidago puberula	Forb	Native	0	N	0	FACU	NWPL	Wind	Inferred from morphology and congeners
Solidago rugosa	Forb	Native	0	N; S	0	FAC	NWPL	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Spiranthes ovalis	Forb	Native	0	S	0	FAC	NWPL	Wind	Inferred from morphology and congeners
Staphylea trifolia	Shrub	Native	0	N	0	FAC	NWPL	Wind; Vertebrate	Minor et al 2009; Garwood and Horvitz 1985; Willson et al 1990
Stellaria graminea	Forb	Exotic	0	Europe	0	FACU	NWPL	Unassisted	Inferred from congeners
Stellaria media	Forb	Exotic	0	Europe	0	UPL	NWPL	Unassisted	Minor et al 2009; Harvey 2000
Stellaria pubera	Forb	Native	0	N; S	0	FACW		Unassisted	Minor et al 2009; Harvey 2000
Styrax grandifolius	Tree	Native	0	N	0	FACU	NWPL	Vertebrate	Inferred from morphology and congeners

Symphoricarpos orbiculatus	Shrub	Native	0	N	0	FACU	NWPL	Wind	Minor et al 2009
Symphyotrichum	Forb	Native	0	N;S	-1	FACW	NWPL	Wind	
Symphyotrichum lanceolatum	Forb	Native	0	N	0	FACW	NWPL	Wind	Inferred from morphology and congeners
Symphyotrichum lateriflorum	Forb	Native	0	N; S	0	FACW	NWPL	Wind	Inferred from morphology and congeners
Symphyotrichum racemosum	Forb	Native	0	N; S	0	FACW	NWPL	Wind	Minor et al 2009
Thalictrum thalictroides	Forb	Native	0	N	0	FACU	NWPL	Unassisted	Inferred from morphology
Tiarella cordifolia	Forb	Native	0	N	0	FAC	NWPL	Unassisted	Flinn et al 2010; Montgomery 1977
Tilia americana	Tree	Native	0	N; S	0	FACU	NWPL	Wind	Flinn et al 2010
Toxicodendron radicans	Vine	Native	0	N; S	0	FAC	NWPL	Vertebrate	Minor et al 2009; Cain et al 1998
Thyrsanthella difformis	Vine	Native	0	N; S	0	FACW	NWPL	Unknown	
Tradescantia virginiana	Forb	Native	0	N	0	FACU	NWPL	Unknown	
Trillium cuneatum	Forb	Native	0	Endemic	0	FACW		Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Ulmus alata	Tree	Native	0	N; S	0	FACU	NWPL	Wind; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Young and Young 1992
Ulmus americana	Tree	Native	0	N; S	0	FACW	NWPL	Wind; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Young and Young 1992

Ulmus rubra	Tree	Native	0	N	0	FAC	NWPL	Wind; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Young and Young 1992
Uvularia perfoliata	Forb	Native	0	N	0	FACU	NWPL	Unassisted	Thompson 1979
Uvularia sessilifolia	Forb	Native	0	N	0	FAC	NWPL	Unassisted	Thompson 1979
Vaccinium elliottii	Shrub	Native	0		0	FACW	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Vaccinium formosum	Shrub	Native	0	Endemic	0	OBL	NWPL	Vertebrate	Inferred from morphology and congeners
Vaccinium fuscatum	Shrub	Native	0	N; S	0	FAC	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Vaccinium pallidum	Shrub	Native	0	N	0	FACU		Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Vaccinium stamineum	Shrub	Native	0	N; S	0	FACU	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Verbesina alternifolia	Forb	Native	0	N	0	FAC	NWPL	Wind; Vertebrate	Minor et al 2009; Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Verbesina occidentalis	Forb	Native	0	N	0	FACU	NWPL	Wind; Vertebrate	Minor et al 2009; Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Veronica hederifolia	Forb	Exotic	0	Europe	0	FACU		Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2016

Veronica officinalis	Forb	Exotic	0	Eurasia	0	FACU	NWPL	Wind	Minor et al 2009
Viburnum acerifolium	Shrub	Native	0	N	0	UPL	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Viburnum dilatatum	Shrub	Exotic	1	E and SE Asia	0	FACU		Vertebrate	Inferred from morphology and congeners
Viburnum prunifolium	Shrub	Native	0	N	0	FACU	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Viburnum rafinesquianum	Shrub	Native	0	N	0	FAC		Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Viburnum rufidulum	Shrub	Native	0	N; S	0	UPL	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Vinca minor	Vine	Exotic	1	Europe	B	FACU		Unassisted	Sonday 2010
Viola [affinis + sororia]	Forb	Native	0		0	FAC		Unassisted	
Viola affinis	Forb	Native	0	N	0	FACW	NWPL	Unassisted	Inferred from morphology and congeners
Viola palmata	Forb	Native	0	N; S	0	FACU	NWPL	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Viola sororia	Forb	Native	0	N; S	0	FAC	NWPL	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Viola striata	Forb	Native	0	N	0	FACW	NWPL	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Vitis [cinerea + vulpina]	Vine	Native	0	N; S	0	FAC		Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008

Vitis aestivalis	Vine	Native	0	N; S	0	FACU	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Vitis cinerea	Vine	Native	0	N; S	0	FACW	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Vitis labrusca	Vine	Native	0	N	0	FACU	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Vitis rotundifolia	Vine	Native	0	S	0	FAC	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Vitis vulpina	Vine	Native	0	N; S	0	FAC	NWPL	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Wisteria sinensis	Vine	Exotic	1	E and SE Asia	B	FACU		Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
Xanthorhiza simplicissima	Forb	Native	0		0	FACW	NWPL	Unknown	

WIS = Wetland Indicator Status; NWPL = National Wetland Plant List; FAC = Facultative; FACU = Facultative Upland; FACW = Facultative Wetland; UPL = Upland; OBL = Obligate Wetland; B = Broadleaved evergreen

APPENDIX B: TRAIT DATA ACQUISITION AND PROCESSING FROM TRY DATABASE

I downloaded data from the TRY database (Kattge et al. 2011) for three traits: seed mass, specific leaf area, and leaf nitrogen content. Some species had data in TRY listed under a synonymous species name; for a few others, there was no data for that species in TRY but there was data for closely related species. For these species, I matched them to the synonym or closest relative to find data (Table B.1).

Table B.1. Matches between species in community dataset and species in TRY database.

Species	**Name used in TRY**	**Explanation for match**	**Reference**
Carex aureolensis	*Carex frankii*	Synonym	Weakley et al. 2012
Dichondra carolinensis	*Dichondra repens*	Congener	
Hylodesmum nudiflorum	*Desmodium glutinosum*	Close relative	Qian and Jin 2016
Ionactis linariifolia	*Ionactis alpina*	Congener	
Krigia dandelion	*Krigia virginica*	Close relative	Qian and Jin 2016
Myosotis macrosperma	*Myosotis virginiana*, *Myosotis verna*	Synonyms	USDA plants
Rubus pensilvanicus	*Rubus argutus*	Close relative	Weakley et al. 2012
Ruellia caroliniensis	*Ruellia strepens*	Close relative	Qian and Jin 2016
Scutellaria integrifolia	*Scutellaria incana*	Synonym	USDA plants
Smilax pulverulenta	*Smilax herbacea*	Synonym	Weakley et al. 2012
Spiranthes ovalis	*Spiranthes vernalis*	Congener	
Symphyotrichum racemosum	*Aster vimineus*	Synonym	Weakley et al. 2012
Eurybia divaricata	*Aster divaricatus*	Synonym	USDA plants

The TRY database contains data from numerous databses from around the world. For seed mass, all species in my dataset with data in TRY were covered by only three databases (Table B.2), since most species were included in the Royal Botanical Gardens Kew Seed Information Database or the USDA Plants database. I also limited the number of databases used to calculate mean specific leaf area (Table B.2), because there was very high variation in specific leaf area across datasets for a number of species. One likely reason for this is that some databases contain data from experiments and observational studies that attempt to capture much of the possible variation in traits for some species, and the geographic coverage of databases included in TRY is large. Another concern was that some of the variability for species could come from the different ways that specific leaf area is measured in different studies. Selected the smallest set of data sources needed to represent all of the study species that were found in the TRY database reduced the variability in species' mean specific leaf area for many species. For one species (*Hypericum perforatum*) whose standard deviation in specific leaf area was greater than the mean, I restricted data to observations from only one database (the LEDA trait database). I used all datasets for leaf nitrogen content, as this trait is less commonly measured than specific leaf area (Table B.2). Unlike specific leaf area, there was not exceedingly high variation in leaf nitrogen within species across datasets.

Table B.2. Database sources of data on each continuous trait, accessed from the TRY database.

Seed mass	**Specific leaf area**	**Leaf nitrogen**
KEW Seed Information Database (SID)	Chinese Traits	Altitudinal Vicariants Spain
Midwestern and Southern US Herbaceous Species Trait Database	Flora Italia Functional Traits Hoard (FIFTH)	Catalonian Mediterranean Forest Trait Database
PLANTSdata USDA	Floridian Leaf Traits Database	Cedar Creek Savanna SLA, C, N Database
	Global A, N, P, SLA Database	Chinese Leaf Traits Database
	Global Leaf Robustness and Physiology Database	Chinese Traits
	GLOPNET - Global Plant Trait Network Database	ECOCRAFT
	Herbaceous Leaf Traits Database Old Field New York	Ecological Flora of the British Isles
	Leaf Allometry Dataset	Flora Italia Functional Traits Hoard (FIFTH)
	Leaf Area, Dry Mass and SLA Dataset	French Massif Central Grassland Trait Database
	Leaf Economic Traits Across Varying Environmental Conditions	Global 15N Database

	Leaf Structure and Economic Spectrum	Global A, N, P, SLA Database
	Midwestern and Southern US Herbaceous Species Trait Database	Global Leaf Robustness and Physiology Database
	Nutrient Resorption Efficiency Database	Global Respiration Database
	Overton/Wright New Zealand Database	GLOPNET - Global Plant Trait Network Database
	Photosynthesis and Leaf Characteristics Database	Leaf and Whole Plant Traits Database
	Plant Traits for Grassland Species (Konza Prairie, Kansas, USA)	Leaf Ash Content in China's Terrestrial Plants
	Plant Traits for Pinus and Juniperus Forests in Arizona	Leaf Economic Traits Across Varying Environmental Conditions
	The LEDA Traitbase	Leaf N-Retention Database
		Leaf Nitrogen and Phosphorus for China's Terrestrial Plants
		Leaf Photosynthesis and Nitrogen at Oak Rich Dataset
		Leaf Physiology Database
		Leaf Structure and Chemistry
		Leaf Structure and Economic Spectrum
		Leaf Structure, Venation and Economic Spectrum
		Leaf Traits in Central Apennines Beech Forests
		Nutrient Resorption Efficiency Database
		Plant Physiology Database
		Plant Traits for Grassland Species (Konza Prairie, Kansas, USA)
		Plant Traits for Pinus and Juniperus Forests in Arizona
		Reich-Oleksyn Global Leaf N, P Database
		Roots Of the World (ROW) Database
		Sheffield & Spain Woody Database
		The Americas N&P database
		The Netherlands Plant Traits Database
		The VISTA Plant Trait Database

I supplemented data on seed mass and leaf nitrogen for some species missing from TRY with a dataset compiled by Coyle et al. (2014) for Eastern North American tree species. These were: *Aesculus sylvatica*, *Amelanchier arborea*, *Aralia spinosa*, *Carya pallida*, *Celtis laevigata*, *Crataegus* sp., *Ilex decidua*, *Ilex vomitoria*, *Magnolia tripetala*, *Magnolia virginiana*, *Prunus caroliniana*, *Pyrus calleryana*, *Quercus lyrata*, *Quercus phellos*, *Sassafras albidum*, *Staphylea trifolia*, *Styrax grandifolius*, and *Ulmus alata*. I also found data from other sources for three of several species missing from the TRY database that had high cover within plots (maximum relative cover >10%). These were: specific leaf area for *Lindera benzoin* (Cipollini et al. 1993; data used were for control plants), seed mass for *Microstegium vimineum* (Huebner 2011; data used were for forest interior plants), and specific leaf area for *Elaeagnus umbellata* (Brantley et al. 2011).

APPENDIX C: MISSING AND ADDED SPECIES FROM URBAN SITES COMPARED TO REFERENCE COMMUNITY TYPES

Table C.1. Species frequently missing from and species frequently added to the 14 most urban plots in the dataset, when compared to reference community type descriptions. Missing species are those absent from at least 70% of plots where expected to occur based on reference community descriptions, and added species are those found in at least 40% of plots where they were not expected to occur based on reference community descriptions. Asterisks mark exotic species.

Missing species	Added species
Forbs and graminoids	**Forbs and graminoids**
Carex grayi	*Arisaema* [*pusillum* + *quinatum* + *stewardsonii* + *triphyllum*]
Chasmanthium latifolium	*Athyrium asplenioides*
Commelina virginica	*Botrypus virginianus*
Dichanthelium commutatum	*Carex amphibola*
Dichanthelium yadkinense	*Carex oxylepis*
Endodeca serpentaria	*Cinna arundinacea*
Eurybia divaricata	*Elephantopus carolinianus*
Festuca subverticillata	*Galium circaezans*
Galium triflorum	*Glyceria striata*
Juncus coriaceus	*Impatiens capensis*
Laportea canadensis	*Juncus* [*effusus* + *pylaei*]
Oxalis sp.	*Leersia virginica*
Persicaria virginiana	*Liriope muscari* *
Phryma leptostachya	*Phryma leptostachya*
Pilea pumila	*Poa* [*autumnalis* + *cuspidata*]
Podophyllum peltatum	*Potentilla indica* *
Polygonatum biflorum	*Ranunculus abortivus*
Stellaria pubera	*Sceptridium* sp.
Symphyotrichum	*Solidago* sp.
Thalictrum thalictroides	*Thalictrum thalictroides*
Verbesina alternifolia	**Vines**
Verbesina occidentalis	*Dioscorea* [*quaternata* + *polystachya* + *villosa*]
Vines	*Hedera helix* *
[*Matelea* + *Gonolobus*]	*Vitis* [*cinerea* + *vulpina*]
Smilax hispida	**Shrubs**
Thyrsanthella difformis	*Elaeagnus pungens* *

Shrubs and subshrubs	*Elaeagnus umbellata* *
Aesculus sylvatica	*Ilex cornuta* *
Corylus americana	*Nandina domestica* *
Lespedeza cuneata *	*Rosa multiflora* *
Trees	*Rubus* sp.
Betula nigra	*Viburnum* [*dentatum* + *rafinesquianum*]
Carya cordiformis	*Viburnum prunifolium*
Carya ovata	**Trees**
Diospyros virginiana	*Acer rubrum*
Ostrya virginiana	*Albizia julibrissin* *
Oxydendrum arboreum	*Carya tomentosa*
Platanus occidentalis	*Cercis canadensis*
Quercus michauxii	*Diospyros virginiana*
Quercus shumardii	*Fagus grandifolia*
Ulmus rubra	*Ilex decidua*
	Juniperus virginiana
	Morus rubra
	Nyssa sylvatica
	Pinus taeda
	Pyrus calleryana *
	Quercus nigra
	Quercus phellos
	Quercus rubra
	Quercus velutina

APPENDIX D: CATEGORIZATION OF LAND USE/LAND COVER DATA FOR CREATION OF RESISTANCE RASTERS TO MAKE LEAST-COST PATHS

Land cover data from the National Land Cover Dataset differed between 1992 and subsequent years in the way that categories were named and the methods used to distinguish categories (Fry et al. 2009). Thus to compare least-cost path models based on land cover from two different time periods, I translated each land cover code from 1992 and 2011 into a broader land cover category from which I assigned a resistance to movement. Resistance values used to create least-cost paths were based on the structure and degree of human domination of the broad categories, with forest given the lowest resistance to movement (Table D.1).

Table D.1. Comparison of land use/land cover categories from the National Land Cover Dataset in 1992 and 2011, with designated resistance values.

2011 code	**2011 Description**	**2011 Resistance category**	**2011 Resistance value**	**1992 code**	**1992 Description**	**1992 Resistance category**	**1992 Resistance value**
11	Open Water	High Resistance	100	11	Open Water	High Resistance	100
22	Developed, Low Intensity	Human-Dominated Low Resistance	50	21	Low Intensity Residential	Human-Dominated Low Resistance	50
23	Developed, Medium Intensity	Medium Resistance	75	21	Low Intensity Residential	Human-Dominated Low Resistance	50
24	Developed, High Intensity	High Resistance	100	22	High Intensity Residential	High Resistance	100
24	Developed, High Intensity	High Resistance	100	23	Commercial/Industrial/ Transportation	High Resistance	100

31	Barren Land (Rock/Sand/Clay)	Medium Resistance	75	31	Bare Rock/Sand/Clay	Medium Resistance	75
31	Barren Land (Rock/Sand/Clay)	Medium Resistance	75	32	Quarries/Strip Mines/Gravel Pits	Medium Resistance	75
23	Developed, Medium Intensity	Medium Resistance	75	33	Transitional	Medium Resistance	75
41	Deciduous Forest	Forest	1	41	Deciduous Forest	Forest	1
42	Evergreen Forest	Forest	1	42	Evergreen Forest	Forest	1
43	Mixed Forest	Forest	1	43	Mixed Forest	Forest	1
52	Shrub/Scrub	Open Natural	10	51	Shrubland (*absent from data)	NA	NA
71	Grassland/Herbaceous	Open Natural	10	71	Grassland/Herbaceous (*absent from data)	NA	NA
81	Pasture/Hay	Open Natural	10	81	Pasture/Hay	Open Natural	10
82	Cultivated Crops	Human-dominated Open	25	82	Row Crops(*absent from data)	NA	NA
21	Developed, Open Space	Human-dominated Open	25	85	Urban/Recreational Grasses	Human-dominated Open	25
71	Grassland/Herbaceous	Open Natural	10	85	Urban/Recreational Grasses	Human-dominated Open	25
90	Woody Wetlands	Forest	1	91	Woody Wetlands	Forest	1
95	Emergent Herbaceous Wetlands	Open Natural	10	92	Emergent Herbaceous Wetlands	Open Natural	10

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