

## ABSTRACT

Thesis Title: CHANGES IN THE COMMUNITY  
STRUCTURE OF URBAN AND RURAL  
FOREST PATCHES IN BALTIMORE FROM  
1998 TO 2015

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Urban forests are often highly fragmented with many exotic species. Altered disturbance regimes and environmental pollutants influence urban forest vegetation. One of the best ways to understand the impacts of land-use on forest composition is through long-term research. In 1998, the Baltimore Ecosystem Study established eight forest plots to investigate the impacts of urbanization on natural ecosystems. Four plots were located in urban forest patches and four were located in rural forests. In 2015, I revisited these plots to measure abundances and quantify change in forest composition, diversity, and structure. Sapling, shrub, and seedling abundance were reduced in the rural plots. Alpha diversity and turnover was lower in the rural plots. Beta diversity was reduced in the rural plots. The structure of the urban plots was mostly unchanged, except for a highly reduced sapling layer. Beta diversity in the urban plots was consistent across surveys due to high species turnover.

CHANGES IN THE COMMUNITY STRUCTURE OF URBAN  
AND RURAL FOREST PATCHES IN BALTIMORE FROM  
1998 TO 2015

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## Chapter One: Ecology of Urban and Rural Forests in Maryland

Forest vegetation is determined by the physical geography and climate of a region, but is mediated by the successional stage and land-use context of the landscape (Franklin 1995). In this study, I investigated the structure, community composition, and species diversity of forest vegetation within urban and rural forest patches in Baltimore using long-term research plots. The biogeochemical and climactic attributes important to the distribution of plants within Maryland are reviewed to establish the ecological background of this study. I then highlight the environmental variables relevant to urban forest ecology in this area. These variables include urbanization, climate change, deer browsing, fire suppression, disease and insect infestations, and exotic plant invasions. When available, information on land-use context, management practices, and environmental policy related to the topic within Maryland and Baltimore is included. I then discuss urban land-use context and its influence on community composition and diversity as examined in other studies. Chapter one concludes with the hypothesis and expectations for this study.

### **Ecology and Vegetation of Baltimore**

#### *Physical Geography of Maryland*

Maryland is divided into five geographic provinces: Appalachian, Blue Ridge, Ridge and Valley, Piedmont, and Coastal Plain. Each region has distinct vegetation, topography, and substrate associations (Brush *et al.* 1980). The Baltimore metropolitan area resides on both the Piedmont and Coastal Plain provinces. The Fall Line, a geomorphological break between the Piedmont and the Coastal Plain provinces, intersects both Baltimore City and Baltimore County. The majority of land in Baltimore

county falls within the boundary of the Piedmont, save for a small area southeast of the Fall Line along the Chesapeake Bay (Plebuch 1960). Conversely, Baltimore City is primarily within the Coastal Plain province with the exception of land located within the northwest corner (Brush *et al.* 1980).

The Piedmont province ranges in elevation from 90m to 330m above sea level (Maryland Department of State Planning, 1973). Terrain in the Piedmont is hilly, a result of three different consolidated bedrock types (igneous, metamorphic, and sedimentary) eroding at different rates (Maryland Department of State Planning, 1973). This variation in topography results in soils that are usually well drained (Brush *et al.* 1980). The saprolite soils commonly found in the Piedmont, consists of thick and nutrient-rich silt-clay underlain by igneous and metamorphic rocks (Curtin *et al.* 2001). Conversely, the Coastal Plain is close to sea level, has less topographic variability, and includes extensive floodplains and tidal marshes (Curtin *et al.* 2001). Soils of the Coastal Plain are composed of fine silt, sand, clay, and gravel (Curtin *et al.* 2001). Beneath the unconsolidated sediments that characterize the surface layers of Coastal Plain soils is a thick layer of clay (U.S. Geological Survey 1982). This sub-surface clay layer has low-permeability which creates a continuously saturated surface environment, common to Coastal Plain soils (U.S. Geological Survey 1982).

The climate across Maryland is humid, with a mean annual temperature average of 7.2-12.8°C, warming as you near the Chesapeake Bay. In Baltimore, the mean annual winter temperature is 2.8°C and the average summer temperature is 25.6°C (NRCS 1998). Winter in Maryland is characterized by a prolonged period of cold temperatures during which most dominant species drop their leaves. Precipitation throughout Maryland

falls relatively evenly throughout the year and has annual averages of 76.2-127 cm year<sup>-1</sup> (Maryland Department of State Planning 1973) and in Baltimore 109.2 cm year<sup>-1</sup> (Doheny 1999). Maryland's ample and continuous rainfall enables leaching and proliferation of acidic soil profiles (Maryland Department of State Planning 1973). Periodic hurricanes and tornados are two of the major sources of climatic disturbances to forests in the Baltimore area (Peterson 2000).

### *Vegetation*

Forests in Maryland can be broadly categorized by two regions: Central Hardwood Region (CHR) and Southern Pine-Hardwood Region (SPHR) (Fralish 2003). Species distribution within each region is guided by climate, soil, and physical geography. In 1980, Brush and colleagues described all the forest-types found in Maryland, with four major vegetation association groups found in the Baltimore metropolitan area: Chestnut Oak-Post Oak-Blackjack Oak association, River Birch-Sycamore association, Tulip Poplar association, and Basket Oak association. Across all vegetation groups, including those found in Baltimore, oak (*Quercus* spp.) and hickory (*Carya* spp.) were the dominant trees. Unlike the other forest-types in Maryland, the four vegetation association groups found in Baltimore showed red maple (*Acer rubrum*), blackgum (*Nyssa sylvatica*) and flowering dogwood (*Cornus florida*) as important subdominant species within the groups (Brush *et al.* 1980). By 2006, dominance of some forested plots in Baltimore City and Baltimore County had shifted to tulip poplar (*Liriodendron tulipifera*) and several oak species (Groffman *et al.* 2006). The same associated species were present in the study plots, but the dominant species had shifted compared to Brush's 1980 forest-type categorization. More recently, Forest Inventory



Analysis (FIA) data from 2014 showed that red maple, followed by blackgum, tulip poplar, hickory (*Carya* spp.), and beech (*Fagus grandifolia*) were the most abundant species in Baltimore City and Baltimore County. Comparing FIA data from 2011 to 2014 shows a 24% decline in white oak (*Quercus alba*) abundance in Baltimore. These results are consistent with larger trends seen in the CHR. For example, a study in Virginia showed an increase in beech, red maple, tulip poplar, and a concomitant decline of oak species (Abrams 2003).

### *Land-Use History*

The Chesapeake Bay is the largest estuary in the United States. It is a vital habitat for marine life, but also a defining feature for terrestrial vegetation. During the Pleistocene, approximately 13,600 years ago, conifers dominated the forests surrounding the Chesapeake (Sprague *et al.* 2006). The coniferous tree species present at the end of the Pleistocene reflected a colder Mid-Atlantic climate. As the glaciers receded to the north, vegetation shifted from conifers to deciduous forests dominated by oak, hickory and in some areas, chestnut (*Castanea dentata*) (Brown *et al.* 1999; Curtin *et al.* 2001). From 5000 B.C. to the arrival of European settlers in 1600 A.D., closed-canopy oak and hickory forests dominated 95% of land in the Chesapeake Bay watershed (Braun, 1950; Foresman *et al.* 1997; Sprague *et al.* 2006). Pine (*Pinus* spp.), chestnut, and dogwood were also present, but white oak (*Qercus alba*) and black oak (*Quercus velutina*) were particularly abundant (Cowell 1995; Curtin *et al.* 2001). The dominance of oak-hickory forests were maintained prior to early seventeenth-century European settlement by the Native American practice of slash and burn agriculture (Abrams 1998). These frequent

understory burnings removed fire-intolerant species like maple and cherry (*Prunus* spp.) and stimulated oak regeneration (Nowacki & Abrams 2008).

Changing land-use practices and continued development have influenced community composition and have reduced the total forested area within Maryland (Sprague *et al.* 2006). After the arrival of early European settlers in 1600, land around the Chesapeake was gradually deforested and intentional burnings were abandoned (Nowacki & Abrams 2008). Timber harvesting, iron and chromium mining, agriculture, and the creation of transportation routes left an expansive and diverse forested area patchy and altered (Curtin *et al.* 2001; Sprague *et al.* 2006). The thick, nutrient-rich soils in the Piedmont were particularly prized for agriculture, and as a result, 80% of forests were cleared between 1800-1900 (Curtin *et al.* 2001; Brush 2009). Agriculture and mining practices transitioned into industrialization and urban development around 1850, and by 1950, many former farmlands had transitioned back to forests (Foresman *et al.* 1997).

The forests in the Baltimore area are the result of nearly 14,000 years of continuous anthropogenic forces on the landscape (Custer 1989). The total forested area in the Baltimore Metropolitan area is currently around 40,500 hectares, with annual losses averaging 100 hectares (Sprague *et al.* 2006; Outen 2011). Overall tree cover has been reduced in Maryland by 0.23% from 2001 to 2011 (Global Forest Watch 2014). Most forests throughout Maryland are positioned on abandoned farmland and few remnants of undisturbed forests exist. In Baltimore County, 34% of the land is currently forested, and of that percentage, only 315 forest patches are larger than 40 hectares (Outen 2011). The remaining forested area is composed of more than 9,000 disparate forest fragments (Outen 2011).

## Urban Forest Ecology

The field of urban ecology is focused on how the distribution and abundance of organisms are influenced by the integration of social, political, and biogeochemical drivers within the physical boundaries of cities (Pickett *et al.* 2001). Urban forest ecology, a sub-discipline of both forest ecology and urban ecology, has become particularly important in the context of an expanding urban population, an expansion that increases the interface between urban and rural landscapes (Radeloff *et al.* 2005). Despite providing many ecological, social, and recreational services, urban ecosystems have historically been given little attention for their environmental merit (McDonnell *et al.* 2008; Avins 2013). Studies of urban ecosystems processes generally highlight abiotic variables common in urban forests such as higher air and soil temperatures, increased nitrogen deposition, altered hydrology, and higher atmospheric carbon dioxide levels (Oke 1982; Brazel *et al.* 2000; Savva *et al.* 2010; Yesilonis & Pouyat 2012). These conditions represent anthropogenic factors that may alter carbon and nitrogen turnover and ecosystem functioning within forested ecosystems by altering net primary production (NPP) and biogeochemical cycles (Yesilonis & Pouyat 2012).

In spite of the trend towards studies that focus on ecosystem processes and services, it remains equally valuable to investigate how urbanization affects community composition, forest structure, and species diversity. Although the diversity of a forest is connected to ecosystem services (Vitousek 1990), floristic surveys conducted within urban forests provide another avenue to assess the impact of human-induced disturbance on fragmented forests (McPhearson *et al.* 2016). As an example, the diversity and abundance of species within a forest can determine the ability of that ecosystem to

provide food and habitat for fauna, or the ability to remove pollutants from the air, water, and soil ( Zipperer *et al.* 2012; Avins 2013; Johnson & Swan 2014). From an applied perspective, understanding the extent and impact of exotic plant species within an ecosystem is useful information that managers and policy makers can use to focus conservation efforts.

It has been widely observed that urbanization reduces species diversity and homogenizes plant functional diversity (Groffman *et al.* 2014). These changes result in fewer, more widespread, and “urban adaptable” species (McKinney 2006). At the same time, urban development creates a heterogeneous landscape pattern (Pickett & Cadenasso 1995). Therefore, an active area of research for urban ecologists is the relationship between cities and forest structure, community composition, and functional group representation (Pickett *et al.* 2008). Questions about species assemblage patterns in urban forest patches have led many to investigate the relevance of island biogeography theory (Davis & Glick 1978; Marzluff 2008; Niemelä 2014). Other important drivers currently being investigated in urban forest ecology are the urban heat island effect, increased deer browsing, canopy disturbance, forest management practices, and species invasions. To understand the dynamics of urban forests, sampling must first be taken of vegetation within both urban and neighboring rural forests. Such surveys provide a baseline against which future monitoring can be used to understand the impacts of urban disturbance on forest vegetation. With long-term data on species and environmental information, we may better understand the direction and magnitude of the impact of urbanization on the structure and functioning of regional ecosystems.

## Drivers of Change in Maryland Forests

In addition to clearing wide swathes of forests surrounding the Chesapeake Bay, European colonizers introduced pests and diseases. Most notably affected was American chestnut, which, prior to the 1920 introduction of chestnut blight, comprised as much as 30% of Maryland forests (Curtin *et al.* 2001; Sprague *et al.* 2006). More recently, urban land-use factors, insect infestations, white tailed deer (*Odocoileus virginianus*) browsing, and exotic plant species invasions have affected forests in Baltimore (Baltimore County EPS 2007; Outen 2011). Certain species, like oak and elm (*Ulmus* spp.), have been more vulnerable than other species to these environmental stresses. Declines in the density and dominance of such species in Maryland have altered the forest community (Abrams 2003; Sprague *et al.* 2006). It remains unclear if forests in urban and rural areas of Maryland may be disproportionately affected by these environmental factors.

### *Urbanization and Climate Change*

The development of cities has produced a patchy distribution of forest ecosystems juxtaposed with larger urban ecosystems (Pickett *et al.* 2008). Fragmentation and isolation alters seed source availability, dispersal, and seedling establishment in urban forests (Williams *et al.* 2009; Trentanovi *et al.* 2013). Vegetation regeneration in urban areas may be further restricted by an accompanying reduction in pollinator communities (Pauw 2007) and reduced seed viability as a consequence of reduced genetic variation in fragmented habitats (Young *et al.* 1996). Forest patches embedded in the urban matrix are exposed to higher air temperatures, increased nitrogen deposition, altered hydrology, and higher atmospheric carbon dioxide levels (Oke 1982; Brazel *et al.* 2000; Savva *et al.* 2010). Spatially derived restrictions on urban forest regeneration and anthropogenic

degradation of urban environments are likely to cause divergences in the community structure of urban and rural forests.

The modified biogeochemical environments associated with urban areas are attributed to factors such as vehicle emissions, impervious surfaces, industrial pollutants, and built up surfaces. Much research has focused on quantifying the rate and extent of atmospheric and hydrogeologic change in urban areas (Zogg *et al.* 1997; George *et al.* 2007; Savva *et al.* 2010). In a five-year study conducted along an urban to rural gradient in Baltimore, George *et al.* (2007) found that urban sites had atmospheric carbon dioxide levels averaging 66 ppm higher, with temperatures averaging 1.2-2.1°C higher, than suburban and rural sites. A more recent study reported soil temperatures in urban forests averaged annually 0.4°C higher than rural forests in the Baltimore Metropolitan area (Savva *et al.* 2010). This same study predicted that urbanization, concomitant with deforestation, could increase mean annual urban soils temperatures by as much as 2°C (Savva *et al.* 2010). Increased soil temperature influences microbial decomposition, nutrient cycling, fine-root respiration, and other factors that affect terrestrial vegetation (Zogg *et al.* 1997; Savva *et al.* 2010). The impact of urban-land use variables on forest ecosystems are critical determinates of the abundance and diversity of vegetation within an ecosystem. Still, the manner and degree to which urban forest vegetation responds to fragmentation and altered hydrologic, soil, and atmospheric conditions remains poorly understood.

Urban environments can serve as surrogates for the future effects of climate change across landscapes and regions (Carreiro & Tripler 2005). A recent National Climate Change Assessment reported a 70% increase in the amount of rainfall during

heavy precipitation events from 1958 to 2012 in the Mid-Atlantic, the highest increase reported in the U.S. (McKibben 2014). In a report that included Maryland, National Oceanic and Atmospheric Administration (NOAA) scientists noted that precipitation has increased nearly 1.27 cm decade<sup>-1</sup> and temperatures have risen over 1°C since 1985 in the Northeastern U.S. (Kunkel *et al.* 2013). The 2014 Intergovernmental Panel on Climate Change (IPCC) report noted greenhouse gas concentrations are at the highest recorded levels in 800,000 years, with concentrations 40% higher than pre-industrial times (Pachauri *et al.* 2014).

Changes in air temperature, precipitation, and carbon dioxide concentrations as a result of climate change are likely to have a strong impact on forest ecosystems (Kirilenko & Sedjo 2007). Plants may respond to climate change factors with adaptation or alteration of community composition and geographic distribution of species ranges (Rogers & McCarty 2000). Some of these predictions are already being observed. For example, some tree species have migrated northward in the U.S., with temperature increases related to anthropogenic climate change as the reported cause (Woodall *et al.* 2009; Cavanaugh *et al.* 2014). As urban areas often experience higher temperatures relative to surrounding areas (George *et al.* 2007), climate change may have a greater effect on species distributions in urban forests.

### *Fire Suppression*

Fire is an important source of disturbance for forested ecosystems. Fire directly affects nutrient cycling and soil hydrology, and indirectly influences forest succession, the evolution of plant traits, and plant assembly (Barnes *et al.* 1997). In the majority of Maryland, including Baltimore, the pre-settlement fire-return interval was between 7-12

years (Frost 1998). Changes in land-use and fire policies have altered the frequency, type, and severity of fire regimes throughout the Northeastern region of the U.S. (Nowacki & Abrams 2008). The displacement of Native Americans resulted in a decline of slash and burn agriculture, and large, property-destroying fires in the first half of the 20<sup>th</sup> century resulted in fire-reducing policies (Abrams 1998; Wade *et al.* 2000). This combination nearly eliminated periodic forest burnings, and as a result has changed the forest community in many areas (Nowacki & Abrams 2008).

Pre-settlement fire intervals slowed the transition from fire-adapted pioneer species to late-successional, shade-tolerant species (Barnes *et al.* 1997). The exclusion of fire from forested ecosystems has promoted fire-sensitive species, which typically grow more slowly and are more tolerant to densely shaded understories, at the expense of shade-intolerant species of oak and hickory (Nowacki & Abrams 2008; Hanberry *et al.* 2012). As forest canopies close, reduced evapotranspiration leads to increasing soil moisture. Nowacki and Abrams (2008) termed this component of forest succession *mesophication*. Mesophication produces feedback loops that facilitate the establishment of mesophytic species (Kreye *et al.* 2013). The increased moisture and reduced light levels create an environment that promotes shade-tolerant species to become more abundant (Abrams 2003). In addition to a changing microenvironment, the opportunity for fire is further reduced by the higher moisture content of the leaves mesophytic species (Kreye *et al.* 2013). These changes to the understory environment are drivers of succession from more shade-intolerant and xeric species to species more tolerant to mesophytic species (Nowacki & Abrams 2008; Burgess *et al.* 2015).

It has been repeatedly tested and argued that fire event reduction is a primary



driver of oak decline (Abrams 1990; Nowacki & Abrams 2008; Wade *et al.* 2000; Hanberry *et al.* al.; Hutchinson *et al.* 2012). One such study showed that oaks not only regenerate more abundantly in burned gaps, but repeated burnings reduce the frequency of red maple regeneration (Hutchinson *et al.* 2012). Furthermore, fire occurrence needs to coincide with a critical life-stage of oak development to successfully promote regeneration (Arthur *et al.* 2012). This finding suggests that repeated burnings, rather than isolated fire events, are necessary for oak forests to thrive. Reduced oak regeneration is problematic in Maryland, where oaks are considered keystone species due to their significant contribution to ecosystem processes, forest structure, and biodiversity (Baltimore County EPS 2007).

Over the last 60-70 years, the number of fire events in the Northeast has continued to decrease (Nowacki & Abrams 2008). In 2015, the Maryland Forest Service reported that only 105 hectares of forest experienced fires, and none were prescribed burns (Maryland Forest Service 2015). Although Sharper *et al.* (1986) suggested that fire frequency may increase in urban areas, fire is typically less frequent in these areas (U.S. Fire Administration 1999). Because fire frequency is low in Maryland, it seems likely that any impacts of fire suppression would be similar between urban and rural forests.

### *Deer Browsing*

Temperate forests provide habitat for white-tailed deer (*Odocoileus virginianus*). Prior to European settlement, wolves, mountain lions, and year-round hunting by Native Americans restricted white-tailed deer populations around the Chesapeake Bay (Maryland Department of Natural Resources 2014). After colonization, overhunting and deforestation reduced deer populations to the brink of extirpation such that, in 1900, deer

populations in Maryland had dwindled to isolated individuals in a few small sections of forests in western Maryland (Côté *et al.* 2004; Maryland DNR 2014). The density of deer has since increased as a result of wildlife management policies, loss of natural predators, and a decline in hunting (Côté *et al.* 2004). In fact, white tailed deer populations are currently at densities exceeding pre-settlement levels (Rooney & Waller 2003).

Overabundance of deer has led to over-browsing, which has directly modified forest structure and composition, and indirectly affected associated plants and animals (McShea *et al.* 1997; Rooney & Waller 2003; McGarvey *et al.* 2013).

Deer have been shown to reduce regeneration of oak, hickory, hemlock (*Tsuga canadensis*), northern white cedar (*Thuja occidentalis*), birch (*Betula* spp.), and many understory species (Frelich & Lorimer 1985; Abrams 1998; Rooney & Waller 2003; Abrams 2003). Browsing reduces biomass, which limits the capacity for growth and reproduction, ultimately lowering the relative abundance of palatable species (Rooney 2001). For example, deer preference for oak over other species may be increasing the abundances of red maple, black cherry (*Prunus serotina*), beech, mountain laurel (*Kalmia latifolia*), spicebush (*Lindera benzoin*), and multiflora rose (*Rosa multiflora*) in certain ecosystems (Abrams 1998; Tilghman 1989; Horsely *et al.* 2003; Rawinski 2008).

Unpalatable and well-protected species such as Japanese barberry (*Berberis thunbergii*), multiflora rose, and garlic mustard (*Alliaria petiolata*) are often avoided by deer, thus contributing to the proliferation of these non-native species in forest communities (Rawinski 2008). Heavy deer browsing also skews the overall forest structure towards medium and large stems, as smaller stems are consumed (Tilghman 1989; McGarvey *et al.* 2013).

Given that high deer populations are pervasive, the structure and composition of forest vegetation will be influenced by their selective feeding preferences (Horsley *et al.* 2003). These preferences could mean that oak and hickory species will continue to be over-browsed, giving an advantage to unpalatable non-native species. Côté and colleagues (2004) suggest that recovery of heavily browsed plant communities will require prolonged reduction of browsing and disturbance events such as those that occurred historically. Because Baltimore city and county both experience high deer populations, the impact of deer is expected to be severe. For example, one forest health assessment conducted in Maryland noted that without controls of the local deer population, oak regeneration will not be possible (Baltimore County EPS 2007).

The impacts of deer on forest vegetation are not likely to decrease in the near future. A moderate deer population in Maryland is estimated to be below 175,000 animals (Personal communication with DNR deer scientist Brian Eyeler). The reported deer population in Maryland in 2013 was 227,000, up 4,000 from 2012, despite a 10% increase in hunting (Maryland DNR 2014). This increase can be partially explained by regulations that historically limited taking female deer and the cultural preference for hunting male deer. Hunting males has little to no effect on population growth (Côté *et al.* 2004). Controlling the deer population in urban areas is particularly challenging since hunting is not typically permitted. To help reduce deer populations, many states, including Maryland, have introduced deer culling into forest management practices (Baltimore County EPS 2007). Weapons discharge ordinances in Baltimore City have restricted the ability of municipalities to enact deer management measures, in spite of an increasing deer population within city limits (Personal communication with DNR deer

scientist Brian Eyeler). Little is known about the distribution of deer populations across the urban to rural gradient (McDonnell & Hahs 2008), so it remains relatively unknown whether deer are impacting urban forests to the same extent as rural forests.

### *Insect Infestations and Disease*

As international hubs for trade and commerce, urban areas are more likely to experience introductions of non-native insects, often arriving in lumber or wooden shipping containers (Poland & McCullough 2006). The probability that these non-native pests become established is higher in urban areas, as there more commonly exists alternative host species closely related to the pests' native host species (Niemela & Mattson 1996). For example, mimosa webworm (*Homadaula anisocentra*), an introduced pest from China, was first reported in Washington D.C. (Knupp & Hoover 2001). The native host species of mimosa webworm is silk tree (*Albizia julibrissin*), found throughout Asia. In the United States, mimosa webworm feeds on native honeylocust (*Gleditsia triacanthos* L. var. *inermis*), a species related to silk tree (Knupp & Hoover 2001). Interestingly, mimosa webworm infestations on honeylocust trees have been positively correlated with urban land-use context indicating a role for urbanization-related stress in susceptibility (Sperry *et al.* 2001).

Introduced phytophagous insects are often able to thrive because their new environments lack the ecological controls present in their native habitats. Additionally, the new host species are often not lack defenses or tolerance which may provide the invading insect a competitive advantage (Niemela & Mattson 1996). Intensive feeding occurring as the result of un-regulated insect feeding on a native host may severely damage the host and can lead to spread of disease if the invading insect is a vector for a

plant pathogen. For example, Liebhold et al. (2013) found that the Northeastern region has the highest abundance of damaging invasive insects and host genera in the United States (Liebhold *et al.* 2013). These findings support the hypothesis that urban centers may be at a higher risk for insect and disease infestations because of the potential for higher plant biodiversity (deriving from non-native species) in these areas (McKinney 2006).

One particularly devastating forest pest is the gypsy moth (*Lymanthia dispar*). Gypsy moth is an introduced generalist feeder, but oak-hickory forests located in Northeastern U.S. are one of the most susceptible forest types to gypsy moth predation (Johnson *et al.* 2006; Haynes *et al.* 2013). In an outbreak event, the invasive moths defoliate oak trees and other species. Defoliation, resulting from an outbreak, puts physiological stress on oaks that may result in dieback, decreased acorn production in subsequent seasons, and even death (Gottshalk 1990). Oak decline due to a gypsy moth infestation may also create the opportunity for other species to gain dominance. For example, increased basal area of red maple trees and saplings was positively correlated to oak decline after a widespread defoliation in northern Pennsylvania (Fajvan & Wood 1996). In 2013, gypsy moths defoliated 47.2 acres of forest in Maryland (United States Department of Agriculture 2015). Although stand defoliation was minimal in 2013, there is the potential for greater amounts of gypsy moth infestations in the future due to climate change. Outbreaks within the gypsy moth's range span a large geographic area, yet Haynes et al. (2013) found a synchrony in outbreak events that was correlated with similar weather conditions in each region, specifically precipitation. As climate change has increased precipitation in the Mid-Atlantic (Kirilenko & Sedjo 2007; McKibben

2014), gypsy moth infestations may cause increased damage to oak-hickory forests in this region.

Another invasive insect that impacts forests in Maryland is the Emerald Ash Borer (*Agilus planipennis*). Emerald ash borer (EAB) is a beetle that feeds specifically on the phloem of ash species (*Fraxinus* spp.) (Haack 2002). The beetle's large range reflects the geographic distribution of ash species (MacFarlane & Meyer 2005). When attacked, most stands die within three years (Haack *et al.* 2002). Mortality of ash stands reduces forest productivity and, as a result, limits the ability of that forest to sequester carbon (Flower *et al.* 2013). A study by McFarlane and Meyer (2005) found that urban forests containing significant ash populations are at an increased risk for EAB infestation. The authors attribute this risk to the low genetic diversity of ash in urban forests, resulting in a lower level of resistance (McFarlane & Meyer 2005). Baltimore city has an approximate density of 16 ash trees per hectare of developed land (Kovacs *et al.* 2010). Although EAB is currently restricted to isolated areas in the mid-Atlantic, including parts of Maryland and Virginia (Poland & McCullough 2006; Flower *et al.* 2013), a model developed by Kovacs *et al.* (2010) predicts that EAB infestations will be reported in every county of Maryland by 2017. If ash trees in urban areas have lower levels of EAB resistance as suggested by McFarlane and Meyer (2005), EAB infestations will have a disproportionately large impact on ash trees in Baltimore city.

Introduced pathogens have also damaged native tree populations. For example, Dutch elm disease (DED) is an exotic wilting disease affecting many elm species (*Ulmus* spp.) caused by the fungi *Ophiostoma ulmi* and *Ophiostoma novo-ulmi*. DED is vectored by three species of elm bark beetle (*Hylurgopinus rufipes*, *Scolytus multistriatus*, and

*Scolytus schevyrewi*). Introduction of these beetles to the United States has been traced to infested logs arriving from Europe in the 1920's, reaching Baltimore around 1934 (Gibbs 1978). The spread of DED was initially slow and restricted to localized areas due to a limited breeding population of the beetle, but has since widely expanded (Gibbs 1978). American elm (*Ulmus americana*) is highly susceptible to DED, whereas slippery elm (*Ulmus rubra*) has a greater resistance (Schlarbaum et al. 1997). American elm was once considered a major riparian species and was a common street tree (Lovett *et al.* 2006). Decimation of this species by DED has changed the urban street tree landscape and the riparian forest landscape throughout the United States. In many Midwestern and Northeastern cities, infected elm trees were replaced by maple or ash trees (Poland & McCullough 2006). The replacement of American elm trees with other species changes the local seed source pool in urban areas. As street trees are common seed source for neighboring urban forests (McKinney 2007), a change in the street tree species population has likely affected urban forest composition.

In terms of introduced pathogens in North America, perhaps none is as well documented as that of the dramatic alterations of eastern deciduous forests by chestnut blight (*Cryphonectria parasitica*) (Schlarbaum *et al.* 1997; Curtin *et al.* 2001; Sprague *et al.* 2006). This wind-borne pathogenic fungus, has all but eliminated the American chestnut from eastern North American forests (Schlarbaum *et al.* 1997). Prior to the introduction of chestnut blight in 1920, the American chestnut comprised as much as 30% of Maryland forests (Curtin *et al.* 2001; Sprague *et al.* 2006). At that time, the demise of the American chestnut generated an opportunity for oak and elm expansion (Nowacki & Abrams 2008). American chestnut currently survives as an extremely rare

understory stump sprout in mesic habitats within the Eastern U.S. (Griffin 1992).

Exotic insect feeders and diseases are capable of extirpating plant species and causing disruptions to ecosystem processes at nearly every trophic level. Gypsy moth, emerald ash borer, Dutch elm disease, and chestnut blight are major pests and diseases of trees important to the Mid-Atlantic area. Other important pests and pathogens that threaten forest health in the Mid-Atlantic include dogwood anthracnose, beech bark disease, hemlock woolly adelgid, white pine blister rust, oak wilt, and butternut canker (United States Department of Agriculture 2015). Some of the affected tree species are so reduced by disease or defoliation that they are now considered rare in their native ranges. In urban areas, pests and pathogens may inflict greater damage on forests due to decreased host fitness (McFarlane & Meyer 2005), warmer temperatures that enhance climate suitability for exotic pests (Tubby & Webber 2010), or higher incidences of related host taxa that are palatable for exotic insects (Niemela & Mattson 1996). The health and diversity of forests within urban environments may therefore be at a higher risk than forests outside the urban matrix.

### *Invasive Plant Species*

Forest health is reduced by the rapid and aggressive establishment, growth, and seed dispersal of invasive plant species (Shifley *et al.* 2012). By overtaking forests and displacing native species, invasive species alter the community structure, diversity and ecosystem function (Vitousek 1990). For example, invasive species can affect ecosystem processes by accelerating decomposition, which can result in a loss of nitrogen (Ashton *et al.* 2005). Conversely, if the invader is a nitrogen fixer, nitrogen availability may increase (Vitousek & Walker 1989). Invaders may also reduce primary productivity by blocking



sunlight to native vegetation (Vitousek 1990). The mechanism underlying these invasions is the *enemy release hypothesis* which argues that when plant species experience a competitive release from their natural enemies in a new environment, they may become invasive (Keane & Crawley 2002) by outcompeting native plant species (Vila & Weiner 2004). A competitive advantage could also be derived from a phenologic mismatch between a plant invader and its new environment. For example, plant invaders that leaf-out in early spring will reduce the amount of usable light available to native species by shading them out. These reductions in light may alter growth, regeneration, budburst timing, and quantities of native species (Smith 2013).

The U.S. Fish and Wildlife and the National Park Service reported over sixty invasive species in the Mid-Atlantic, with another nineteen species on a “plants to watch” list (Swearingen et al. 2010). Many of these invasive species can rapidly change an ecosystem, and their presence represents a threat to Maryland forests. These threats may be particularly strong in urban areas, as some temperate climate cities have experienced extended spring growing seasons (Imhoff *et al.* 2010). In Washington, D.C., and Baltimore, urbanization, associated with the creation of forest fragments, influenced the timing of autumn more strongly than spring (Elmore *et al.* 2012). These results suggest that the urban heat island effect has a diverse effect on the growing season between cities. A long-term study is needed to assess the rate and extent of any invasions in Baltimore.

### **Biotic Homogenization of Urban Forests**

In addition to the natural factors described above, the assembly of plant communities in urban areas is facilitated by human manipulation of the landscape and choice in species planted in the landscape (Swan *et al.* 2011). For example, when exotic

species escape from planted areas and become established in urban forests, species richness may increase (Kowarik 2003; McDonnell & Hahs 2008). However, phylogenetic and functional diversity is typically lower than the increase in biodiversity (Knapp *et al.* 2012). In other words, urban forest communities may have higher species richness, but a narrower range of lineages as compared to rural forests (McKinney 2006; Groffman *et al.* 2014). The narrowing of trait diversity may be attributed the harsh ecological filtering effect of highly urban areas. The plant species that thrive in urban environments typically have similar traits and life-histories that are a result of increased tolerance to disturbed habitats (Johnson & Swan, 2014). Native species may become extirpated from urban areas by competitive suppression from non-native species or because they are poorly adapted to urban environmental conditions (Kühn & Klotz 2006; Knapp *et al.* 2012). Formerly distinct plant communities become similar through the loss of niche-specific and rare flora, resulting in lower beta diversity (Williams *et al.* 2009; Knapp *et al.* 2012). On a larger scale, beta diversity may actually be increasing. For example, vegetation in urban habitats may diverge from vegetation in neighboring rural habitats (McKinney 2006). Alpha diversity may increase as a result of the uneven loss of rare species (Schwartz *et al.* 2006), or decrease due to exotic species gains (McDonnell & Hahs 2008).

The degree of urbanization contributes to both the biodiversity of the community as well as the exploitation level of invasive colonizers (Marzluff 2008; Trentanovi *et al.* 2013). Although low to moderate urbanization may actually increase richness, moderate to high urbanization decreases richness (Schwartz *et al.* 2006; McKinney 2008). Ecosystem homogenization can therefore be predicted to increase as urban development

continues to encroach on undisturbed areas. In Baltimore, the dynamics of species turnover are relatively unknown.

### **Summary and Conclusion**

Vegetation in urban areas is determined by a combination of natural and human mediated processes (Johnson & Swan 2014). Future research in this area should elucidate the complex relationship between urban forest vegetation and the urban environment (Grimm *et al.* 2000; Johnson & Swan 2014). Investigating this topic is important because of the ecosystem services urban forests provide such as habitat for wildlife (Marzluff 2008), cultural significance for city residents (Grove *et al.* 2006), and purification of air and water (Kirilenko & Sedjo 2007). The need for these services is expected to increase as the urban expansion encroaches on rural landscapes (Radeloff *et al.* 2005). Long-term research has the potential to address some the questions surrounding the vulnerability and resilience of urban plant communities. Such research also provides unique opportunities to study the impact of human-induced disturbance on the diversity of species within a forest, habitat structure, and the spread of exotic species.

In spite of the clear need to understand the effects of urbanization on forested ecosystems, there is a limited amount of long-term data addressing this topic (Grimm *et al.* 2000). Within the small number of studies that do investigate long-term urban ecosystem processes, few have attempted to quantify how all layers of vegetation respond to urbanization. This gap in knowledge prevents us from fully understanding the dynamics, and perhaps the resilience, of urban forests.

### *Re-visiting a Long-Term Study in Baltimore*

In 1998, the Baltimore Ecosystem Study (BES), a component of the U.S. National Science Foundation funded Long-Term Ecological Research (LTER) network, established eight permanent forest plots within the Baltimore metropolitan area. Four plots were in rural Baltimore County and four plots were in Baltimore City. The plots were established to investigate the long-term impacts of urbanization on natural ecosystems. Groffman and et al. (2006) conducted a thorough soil and vegetation assessment of these plots and described the forest structure as “well developed with canopy and subcanopy tree layers, shrub and vine layers, and herbaceous cover” in both urban and rural plots. They also found that the urban plots had greater species richness than the rural plots and both plot types had a relatively small number of invasive species. There was also greater shrub density and higher basal area in the rural plots, but greater sapling, seedling, and herb density in the urban plots. The authors attributed these differences to a greater amount of canopy cover in the rural plots. Lastly, the authors predicted that the structure and composition of the vegetation in the urban plots would diverge from the rural plots.

These LTER plots were resampled in this study to determine the extent of change since 1998. The foremost goal of this project was to determine whether in plant community composition, diversity, and structure differed between the urban and rural plot-types. I chose to focus on these particular factors because community composition within forests is an outcome of both site history and disturbance regime (Pickett 1989). Therefore, the analyses used in this study were aimed at understanding how the plant community composition within these plots relates to urbanization within Baltimore. The

goals of this study were achieved using floristic data, land-use history, and indicator species information to draw meaningful conclusions about the structure and diversity of Baltimore area forests.

### *Hypothesis and Objectives*

The central hypothesis was that changes in vegetation composition would be greater in the urban plots as compared to the rural plots with the presumption that abiotic and biotic stresses would differ in the urban plots. I expected this outcome to include an increase in the amount of exotic species and a decline in native species in the urban plots. Additionally, I anticipated community assemblages to change most markedly in the herbaceous and shrub layers since the generation times of these layers are generally shorter than that of the tree layer. Taking into consideration the mesophication of the forest as succession progresses, I expected to observe a decline in deciduous hardwood species and an increase in deciduous soft wood species in both plot-types.

## Chapter Two: Methodology

### Site Description

The eight BES LTER plots are located in the Baltimore metropolitan region of Maryland. Four of the study plots, designated as “urban” plots, are located within Baltimore City, and four of the study plots, designated as “rural” plots, are located in Baltimore County (Figure 1). All plots were located in the Gwynns Falls watershed in the Piedmont Plateau region of Baltimore (Groffman *et al.* 2006).

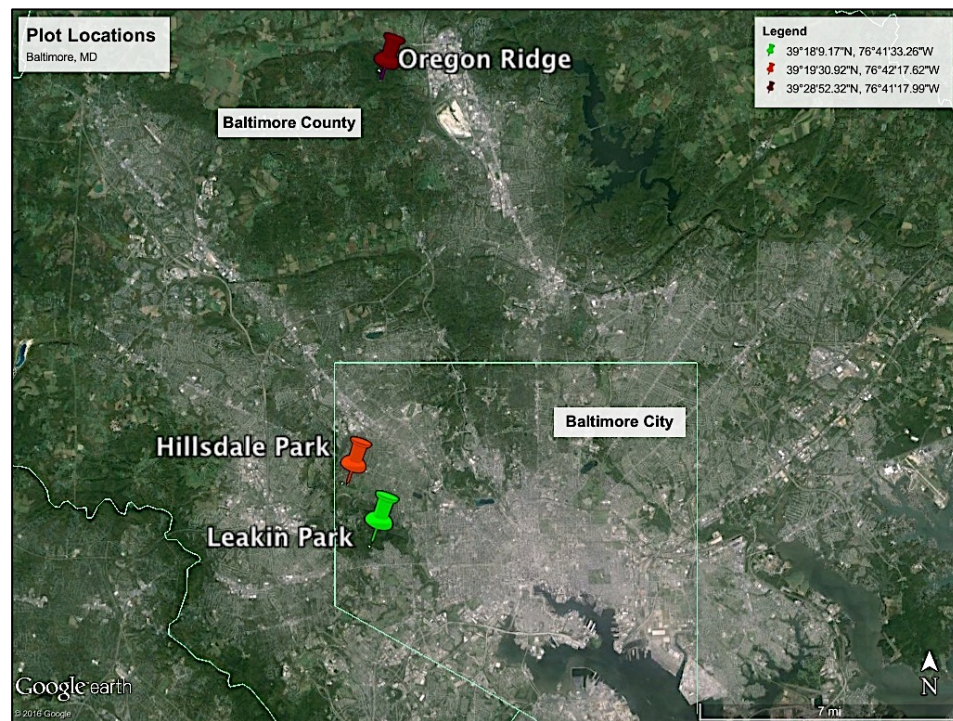


Figure 1. Locations of three forest fragment sites established in Baltimore, Maryland, as part of the BES LTER network. The rural plots were located in Oregon Ridge Park in Baltimore, County. The urban plots are located in Hillsdale and Leakin Park in Baltimore City.

All plots were in forest stands determined by the BES to be roughly 80-100 years of age and to have at least 80% continuous forest canopy at the time of their establishment in 1998 (Groffman *et al.* 2006). All four rural plots were located within

Oregon Ridge Park, approximately 16 km outside the Baltimore City limit in Cockeysville, Maryland (Figure 1 & 2). Elevation within the park ranges from 104-192 meters above sea level (Baltimore County EPS 2007). Land use in this area is primarily dedicated to agriculture, recreational forests, and residential housing (Doheny 1999). Oregon Ridge Park is positioned within 364 hectares of continuous forest (Baltimore County EPS 2007). This area was extensively logged in the 1800's to provide fuel for iron production, but has since been allowed to regenerate starting in the early 1850's (Brooks *et al.* 1979).

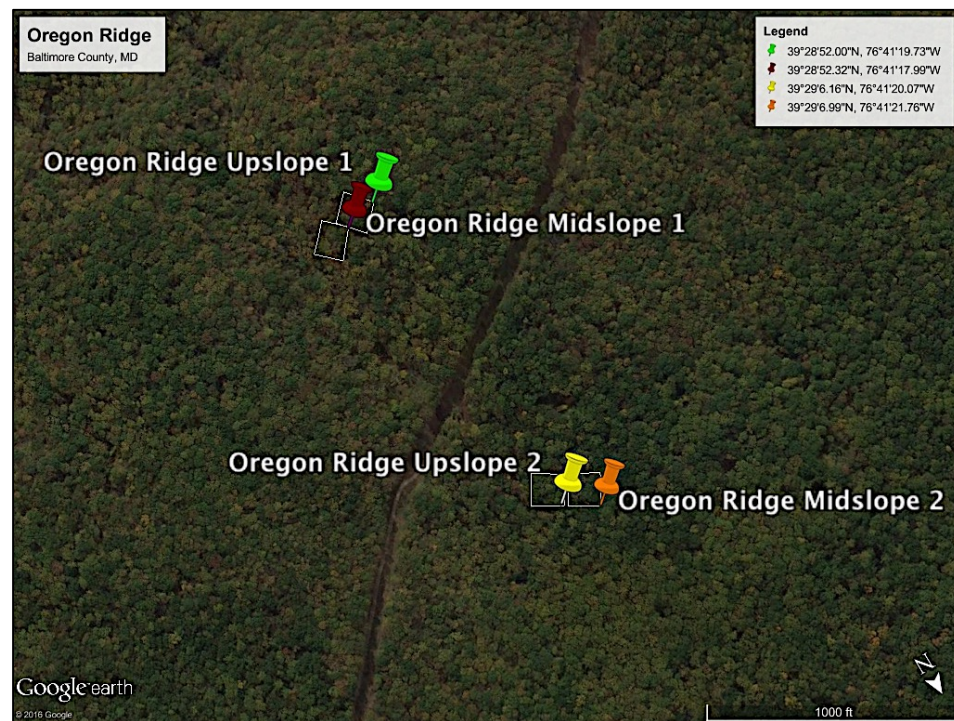


Figure 2. The locations of four designated “rural” forest plots located in Oregon Ridge Park as part of the BES-LTER.

Two urban plots were located in Leakin Park and two urban plots were located in Hillsdale Park (Figure 3). The National Land Cover Database classifies the area surrounding the urban parks as medium-density developed land (U.S. Geologic Survey



2011 edition, amended 2014). The forests in these city parks are relatively undisturbed (NRSC 1998).

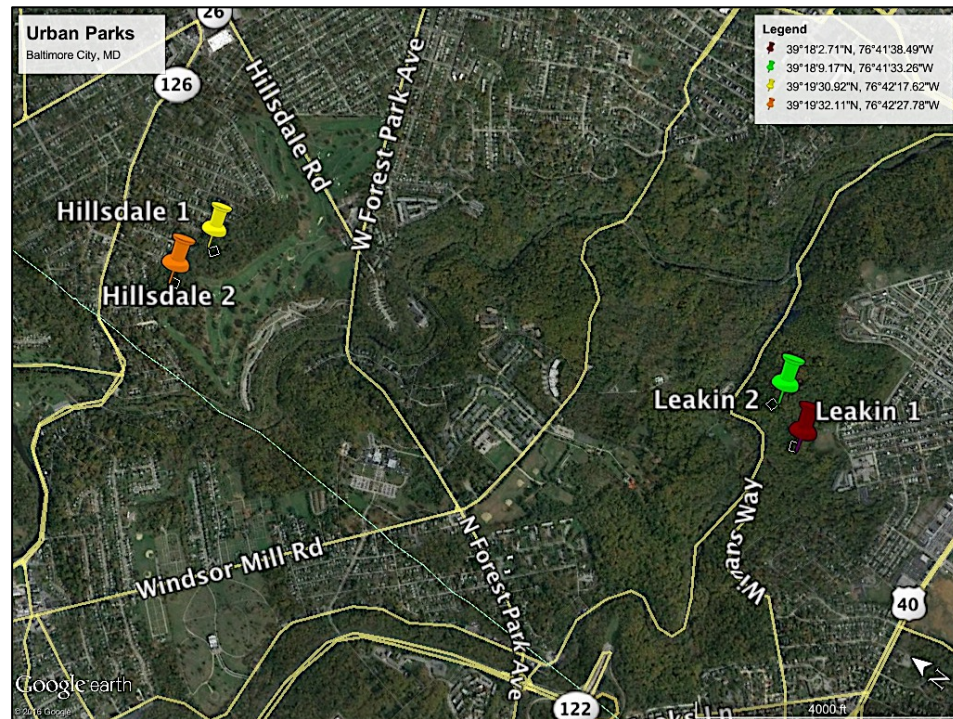


Figure 3. The locations of four designated “urban” forest plots located in Hillsdale and Leakin Park as part of the BES-LTER.

Engineer Thomas Dekay Winans purchased the historic Crimea Estate (modern day Gwynns Falls Leakin Park area) in 1855 (O’Donnell *et al.* 2006). The Olmstead brothers consulted with the city of Baltimore to purchase the estate in 1904 and then again in 1933. The city eventually acquired the 28 hectare estate in 1948, and the estate has remained a public park since (O’Donnell *et al.* 2006). Much of the specific site history remains unknown, as relatively few records exist regarding property use (O’Donnell *et al.* 2006).

The Howard Park Civic Association (HPCA) describes Hillsdale Park as a narrow 14 hectare tract of forest that is situated between a golf course and residential housing



(HPCA n.d.). According to the HPCA website, this park has been relatively unused for recreation, but it is a common location for illegal dumping (HPCA n.d.). Prior land-use of Hillsdale Park is unknown. The area around Hillsdale and Leakin Park is approximately 146 meters above sea level (NRSC 1998).

Three of the urban forest plots have high-fertility soil underlain with igneous rock-types (Hillsdale 1, Hillsdale 2, and Leakin 1), whereas the remaining urban plot (Leakin 2) resides on low-fertility soil underlain with metamorphic rock-types (Groffman *et al.* 2006). Hillsdale 1 has soils classified as Jackland (fine, smectitic, mesic Aquic Hapludalfs). Hillsdale 2 and Leakin 1 have soils classified as Legore (Fine-loamy, mixed, active, mesic Ultic Hapludalfs). Leakin 2 has soils classified as Occaquon (fine-loamy, mixed, semiactive, mesic Inceptic Hapludults) (Table 1) (Groffman *et al.* 2006; Soil Survey Staff n.d.).

The bedrock in Oregon Ridge is predominantly Loch Raven Schist, a hard crystalline igneous rock (Baltimore County EPS 2007). Three of the plots in Oregon Ridge (Upslope 1, Upslope 2, and Midslope 1) have soils classified as Glenelg (fine-loamy, mixed, semiactive, mesic Typic Hapludults). Midslope 2 has soils classified as Manor (coarse-loamy, micaceous, mesic Typic Dystrudepts) (Table 1) (Groffman *et al.* 2006; Soil Survey Staff n.d.). Both Glenelg and Manor soils are considered well-drained and acidic with low fertility (NRCS 1976; Groffman *et al.* 2006).

Table 1. The site, identification, land-use classification, size, and soils associated with eight forest plots in Baltimore, Maryland established in previous BES-LTER studies and resampled in this study.

Location	Plot ID	Abbreviation	Plot-Type	Size (m)	Soil Series
Oregon Ridge	Upslope 1	ORUP1	Rural	40 x 40	Glenelg
Oregon Ridge	Midslope 1	ORMID1	Rural	40 x 40	Glenelg
Oregon Ridge	Upslope 2	ORUP2	Rural	40 x 40	Glenelg
Oregon Ridge	Midslope 2	ORMID2	Rural	40 x 40	Manor
Leakin Park	Leakin 1	Leakin1	Urban	40 x 40	Legore
Leakin Park	Leakin 2	Leakin2	Urban	40 x 40	Occaquon
Hillsdale Park	Hillsdale 1	Hill1	Urban	30 x 30	Jackland
Hillsdale Park	Hillsdale 2	Hill2	Urban	30 x 30	Legore

### General Sampling Overview

All plots were initially established and sampled in June-August of 1998. The plots were then resampled in June-August of 2015. Vegetation layers were categorized as trees, saplings, shrubs and vines, herbs, and seedlings. All layers were sampled to characterize the structure and composition of the forest community represented by the plots. The 1998 survey developed a sampling protocol that used different sampling methods for the different layers. The sampling protocol for floristic and structural data collected in 2015 followed these methods. Great effort was expended to ensure that the data collection between the 1998 and 2015 surveys corresponded with a similar level of detail. This consistent sampling was critical to reduce variation due to sampling error and to allow legitimate comparison. Figures 4a and 4b show an example of the urban and rural forest plots.



Figure 4. Images of a rural plot in Oregon Ridge Park (a) and an urban plot in Hillsdale Park (b).

### Plot Establishment

In 1998, all eight plots were permanently outlined with metal markers buried at or below the soil line. Six of the plots were 40×40m (1600m<sup>2</sup>). The Hillsdale 1 and 2 plots were 30×30m (900m<sup>2</sup>). Between each of the plot corners, metal markers were placed at 10m intervals. Metal markers inside the plot borders designated the quadrat locations. Metal plot markers were relocated in 2016 using a metal detector. Once located, each plot was flagged and divided, as in 1998, into sixteen 10×10m subplots (nine in the Hillsdale plots) and marked with flags (Figure 5). Each subplot was then further divided into four 5×5m subplots (Figure 5). One of the four 5×5m subplots in each 10×10m subplot was used for all vegetation sampling below the tree layer. Within each of these particular 5×5m subplots, two 2×0.5m (1<sup>2</sup>m) quadrats were outlined. The quadrats were arranged perpendicular to each other (Figure 5). Thus, there were sixteen 5×5m subplots in each

40×40m plot, with a total of 32 quadrats. In the two 30×30m plots, there were nine 5×5m subplots, with a total of 18 quadrats.

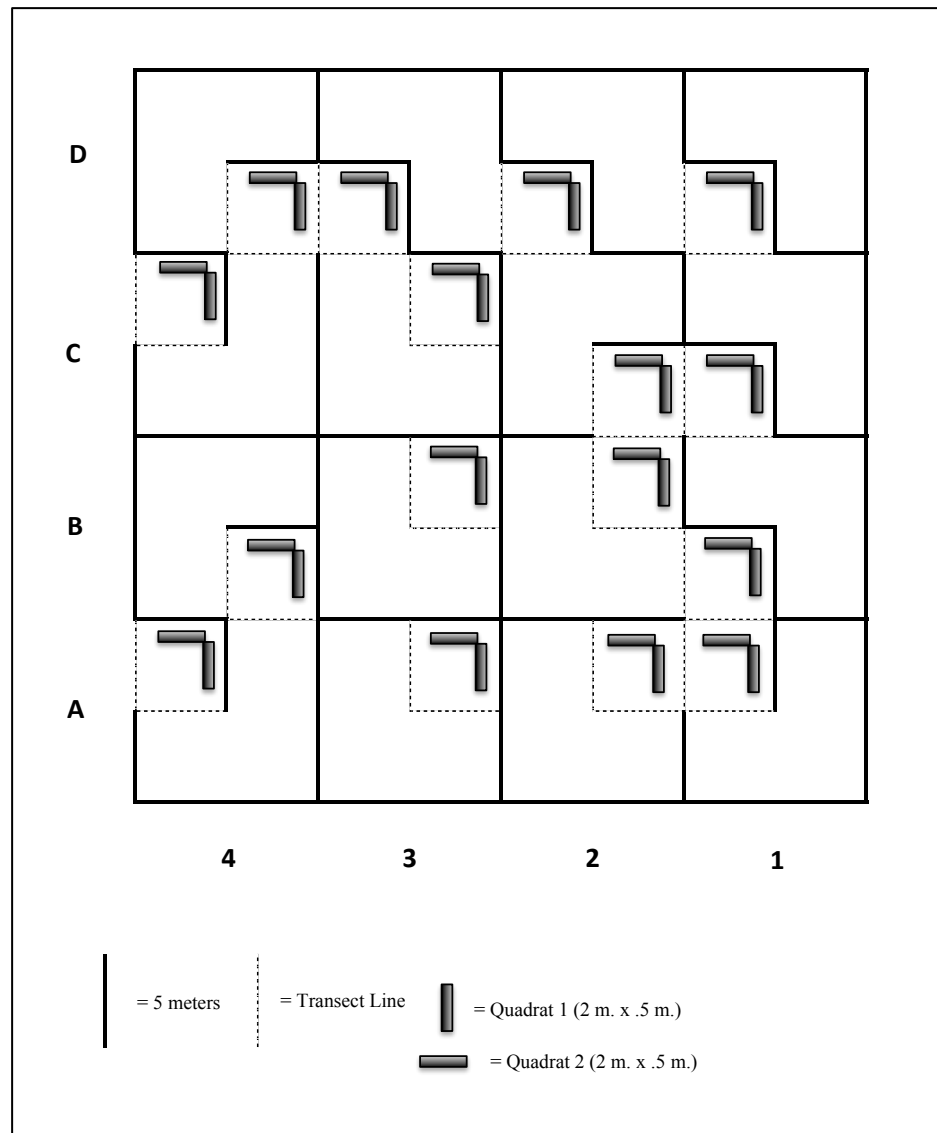


Figure 5. Layout of plots established in four urban and four rural plots in Baltimore. Each alphanumeric box represents the 10×10m subplot area used to sample trees and measure canopy cover. Within each 10×10m subplot, the dotted line designates the 5×5 m area used for all other vegetation sampling. The entire 5×5m subplot was used to sample saplings. The dotted line represents the line used for transect measurement of shrubs, vines, and woody debris. The two perpendicular rectangles within the 5×5m subplots represent two 2×0.5m quadrats used to sample herbs, seedlings, and ground cover.

## Survey Methods

Vegetation was sampled according to the protocol used in the 1998 survey. The original methods and raw data files from the 1998 study are held by Dr. Steward Pickett and can be obtained upon request. The sampling methods are summarized below.

**Tree Layer:** All individuals with a diameter at breast height (DBH)  $\geq 8\text{cm}$  were identified as trees. DBH was measured using diameter tape. Canopy level (canopy, subcanopy, or understory) for each tree was visually determined based on crown height. The tag number from previous sampling was recorded or a tag was added in the event an individual was untagged. The height of the tallest tree in each 10×10m subplot was measured using an Opti-Logic Corporation Insight 100LH Rangefinder.

**Sapling Layer:** All individuals classified as tree species that measured  $< 8\text{cm}$  DBH were identified as saplings. DBH was measured to the nearest hundredth decimal place using General Ultratech digital calipers. As with the tree layer, canopy level (canopy, subcanopy, or understory) for each sapling was visually determined. The existing tag number from previous sampling was recorded or a tag was added in the event of a new, untagged individual. The height of the tallest sapling in each 5×5m subplot was measured using an Opti-Logic Corporation Insight 100LH Rangefinder.

**Vine and Shrub Layer:** Species determined to be shrubs or vines were measured along transects. The lower and left perimeters of each 5×5m subplot were used as the two transect lines (Figure 5). Measurement of vines and shrubs began at the transect line that ran parallel to the numeric axis on the plot layout going in the direction towards the alphabetic axis (Figure 5). Sampling then progressed to the second transect line that ran parallel to the alphabetic axis on the plot layout (Figure 7). Measurements were recorded

in 1m segments starting with 0-1m as the first segment and ending with the tenth at 9-10m. For each segment, all shrub and vine species that touched the transect line were measured in centimeters using a metric ruler. To be recorded, plants had to have a diameter  $\geq 5$ cm. The height of the tallest shrub along each pair of transects for each 5×5m subplot was measured using an Opti-Logic Corporation Insight 100LH Rangefinder. If shrub and vines species had less than a 10cm gap while touching the line, the recording for that species was considered one continuous measurement. Vines were also measured when present on a tree or sapling. In these cases the vine was identified and the percentage of the vine that reached the canopy was visually estimated and recorded in 5% increments.

**Woody Debris:** Woody debris was measured along the transect lines using the same protocol for shrubs and vines as described above. Dead trunks and large branches were described as coarse woody debris and small branches and chunks of bark were considered fine woody debris. If woody debris had less than a 10cm break while touching the line, it was considered one continuous measurement.

**Herb and Seedling Layer:** All seedlings and herbaceous species were identified, tallied, and percent cover visually estimated within each 2×0.5m quadrat.

**Ground Cover:** For each 2×0.5m quadrat, percent cover was visually estimated for leaf litter, woody debris, bare soil, vegetation cover, as well as any other item found (trash, fungi, tree trunk, etc.).

**Canopy Cover:** Canopy gap percentage was visually estimated in increments of 5% within each 10×10m. At each subplot, all field technicians estimated canopy gap

independently and a final estimate of missing canopy was determined as a consensus value. A template from the Forest Service's field manual used in the forest inventory analysis (FIA) program was used to orient the field crew to different organizations and aggregations of canopy cover (U.S. Forest Service 2005).

**Voucher Specimens:** Voucher specimens and photos were obtained for each species. Specimens were collected from outside the plots so as not to disturb the long-term study. The vouchers were archived at the Norton-Brown Herbarium at the University of Maryland, College Park. The photographic record of the plant specimens can be found online at <https://www.flickr.com/photos/133989661@N04/albums>.

### **Data Analysis**

Vegetation in the Oregon Ridge Park and Leakin Park plots was sampled for the complete 40×40m plot size in 1998 as well as in 2015. However, only data from 30×30m of each plot were used in this analysis to allow comparison with the 30×30m Hillsdale plots. This reduction was achieved by eliminating row 4 and column D (Figure 4) from data analysis in both years.

#### *Plot Descriptive Statistics and Analysis*

For each plot and at each layer, the number of species was used to calculate species richness. The relative abundance of species within each layer was determined by calculating the proportion of individuals of a particular species to the total number of individuals in that plot. These values were then averaged for each plot-type. Tree and sapling density were determined by calculating the number of stems per unit area (stems/hectare). Total basal area was calculated from DBH measurements for each species per unit area (m<sup>2</sup>/hectare) using the following equation:

$$BA = \left(\frac{DBH}{2}\right)^2 \times \pi$$

Basal area (BA) values were used to represent the size class of tree and saplings. BA was summarized as the average value for each species in each plot type. Percent or amount of cover per unit area was used for structural analysis because shrub, vine, herb, and seedling individuals were not calculated. Percent ground cover was measured as the relative herb and seedling cover per quadrat (2×0.5m), averaged per plot and plot-type. Canopy structure was determined as the relative number of understory, sub-canopy, and canopy trees per plot. The USDA-NRCS PLANTS database was used to determine exotic and native status of all plant species (USDA-NRCS 2016). Exotic species abundance was determined as the ratio of non-native and invasive species per forest layer and per plot. Tree and sapling size-class were determined by calculating the distributions of DBH measurements across each plot and plot-type. Tree growth was determined by calculating the difference in total basal area of each species between 1998 and 2015 then averaging the difference across plot-types. Tree and sapling turnover was determined by summing individual mortality, retention, and recruitment per species per plot.

### *Ordination*

To measure compositional similarity among the plots, I created an ordination based on pair-wise similarity or dissimilarity of the plots in low-dimensional space (Legendre & Legendre 2012). To create the ordination, abundance data from both 1998 and 2015 were entered into separate site-by-species matrices for each forest layer. For each layer, a distance matrix was calculated using Bray-Curtis dissimilarity, a semi-metric index of distance between site vectors (McCune & Grace 2002). Bray-Curtis



dissimilarity was chosen for this study because it does not interpret shared absence of species in different sites as a similarity between those sites (Legendre & Gallagher 2001). Each distance-matrix was then used in a non-metric multidimensional scaling (NDMS) ordination. NDMS is considered the most robust unconstrained ordination method, as it makes none of the distributional assumptions that are common in other ordination methods (Minchin 1987; Ludwig & Reynold 1988). Points that are close to one another on the NDMS graph represent plots that are more similar to each other, and points that are further apart represent plots that are less similar (Legendre & Legendre 2012). The points representing a given plot-type and year have lines connecting them into a convex hull, a geometrical polygon defined by the species used in the calculation of the site vector (Eddy 1977). The relative size and position of the polygons within the ordination space were used to assess compositional similarities or differences between plot-types and years. The NDMS ordination was created in R version 2.3-0 using the “vegan” (Oksanen et al. 2015) (Team 2013).

#### *Diversity and Evenness*

To measure the diversity and evenness of tree and sapling species at each site, I used Hill numbers, also known as effective species numbers or *true diversities* (Jost 2010). Hill numbers use a single family of equations to calculate effective species numbers based on the relative abundances of observed species. The effective species number is the number of species required to achieve a certain diversity value if all species were equally abundant (Hill 1973). Hill numbers are standardized versions of Gini-Simpson and Shannon-Weiner indices that allow comparison across samples. Within the equation defined by Hill (1973), the variable  $q$  is the order of diversity:

$${}^qD = \left( \sum_s p_s^q \right)^{\frac{1}{1-q}}$$

When  $q=0$ , the effective species number is the observed richness. As  $q$  approaches 1, diversity is given in terms of the effective species number of the Shannon-Weiner index. When  $q=2$ , diversity is given in terms of the effective species number of the Gini-Simpson index. The larger the  $q$  value, the less sensitive the equation is to rare species. In fact, Hill described a  $q$  of 1 as the number of common species and a  $q$  of 2 as the number of abundant species (Hill 1973). Therefore, a  $q$  of 2 does not take into account rare species, making it essentially the proportion of dominant species in a community (Jost 2010). Hill numbers can also be used to measure evenness, as it is inversely related to dominance (Magurran & McGill 2011). The closer the effective species number of a  $q$  of 1 or 2 is to the effective species number of a  $q$  of 0, the more even the community (Jost 2010). Hill numbers, therefore, are preferred to traditional expressions of diversity because of how intuitively communities can be compared (Chao et al. 2014). Hill numbers were calculated in R version 2.3-0 using the “vegan” (Oksanen et al. 2015) (Team 2013).

### *Alpha and Beta Diversity*

Of the many ways to measure beta diversity between communities, I chose to use the definition put forth by R.H. Whittaker in 1960. In that paper he defines beta diversity as “the extent of change in community composition, or degree of community differentiation, in relation to a complex gradient of environment, or a pattern of environments.” Regional (gamma) diversity is dissected into two statistically independent

components: alpha diversity ( $\alpha$ ), the average diversity in a single site; and beta diversity ( $\beta$ ), the relative change in species composition between sites (Jost 2007). I therefore averaged the richness values within the urban and rural plots to determine their alpha diversities. To quantify beta diversity, I first used a monotonic transformation (Jaccard index) to standardize the data so that all site distances are on a scale of 0-1. This standardization allowed me to easily compare sites despite having used different methods of data collection at each forest layer. Beta diversity was then calculated separately for the urban and rural plots in 1998 and 2015 using the average pair-wise comparisons of distance for each group (Legendre & Cáceres 2013). I then compared the beta diversity values of the four groups to determine the relative compositional dissimilarity between plot-type and survey year.

The amount of species turnover in the plots was determined by calculating beta turnover. Beta turnover ( $\beta_T$ ) was determined using the following equation:

$$\beta_T = \frac{|g + l|}{2\bar{\alpha}}$$

Where  $g$  is the number of species gained,  $l$  is the number of species lost, and  $\bar{\alpha}$  is the average species richness (McCune & Grace 2002). By examining alpha and beta diversities and turnover, I was able to assess differences in vegetation between the urban and rural plots and how beta diversity has changed through time.

### *Statistical Analysis*

Given that the plots in 1998 are spatially correlated to the 2015 plots, I would have ideally used a two-way repeated-measures analysis of variance (ANOVA) to compare multiple means with two dependent variables. However, ANOVAs hold the

assumption that data are normally distributed and have homogeneity of variance.

Abundance and cover data in this study were not normally distributed and had highly heterogeneous variance, as determined by a Levene's test. These violations required me to log transform all abundance cover data. Data were not transformed for any other analyses.

Although an ANOVA can be robust to heteroscedasticity, samples with highly unequal variances may produce incorrect or misleading results (Wilcox 1995). Even with the log transformation, much of the abundance data had high levels of heteroscedasticity, requiring a test that does not have the assumptions of equal variance. To overcome the lack of heteroscedasticity, I used a Welch's variance-weighted analysis of variance (Welch-ANOVA), as it is more appropriate for use when groups have unequal variances (Wilcox 1995).

*P*-values were determined by the *F*-values computed from either a one-way analysis of variance (ANOVA) or a Welch-ANOVA. Regular ANOVAs were used in growth, canopy, and diversity analyses. Welch-ANOVAs were used in all abundance, and cover analyses. Tukey's *post hoc* test was performed after a regular ANOVA and Games-Howell *post hoc* test was performed after a Welch-ANOVA when a significance value ( $p < 0.05$ ) was determined by the analysis of variance. All multivariate statistics were performed in R version 2.3-0 using the "stats" package (Team 2013). The Games-Howell *post hoc* test was done using the R package "userfriendlyscience" (Peters 2016).

## Chapter Three: Results

Analyses of community composition and structure of plot vegetation were conducted on each forest layer. Diversity analyses were done for trees, saplings, and for the total forest community only. The results chapter begins with the findings for each forest layer and follows with results of the analyses performed on data from the vegetation community.

### Tree Layer

#### *Composition*

The three most abundant tree species within the rural plots were *Liriodendron tulipifera*, *Acer rubrum*, and *Nyssa sylvatica* with each constituting approximately 17-23% of the total tree community (Figure 6a). *Quercus alba*, *Quercus montana*, and *Carya glabra* were the next most abundant species in the rural plots, each accounting for approximately 10% of total tree community (Figure 6a). Species composition was similar in the urban plots but relative abundance was more evenly distributed across several species in the urban compared to the rural plots (Figure 6b). Although 60% of all trees consisted of the three most common species in the rural plots, these same species accounted for less than 40% of the individuals found in the urban plots (Figure 6a and b). In 1998, the two most abundant trees in the rural and urban plots were *Liriodendron tulipifera* and *Quercus* spp. (Groffman et al. 2006). In 2015, these species remained abundant, but *Acer rubrum* had increased and was included in the most abundant tree category in both the urban and rural plots (Figure 6a and b).

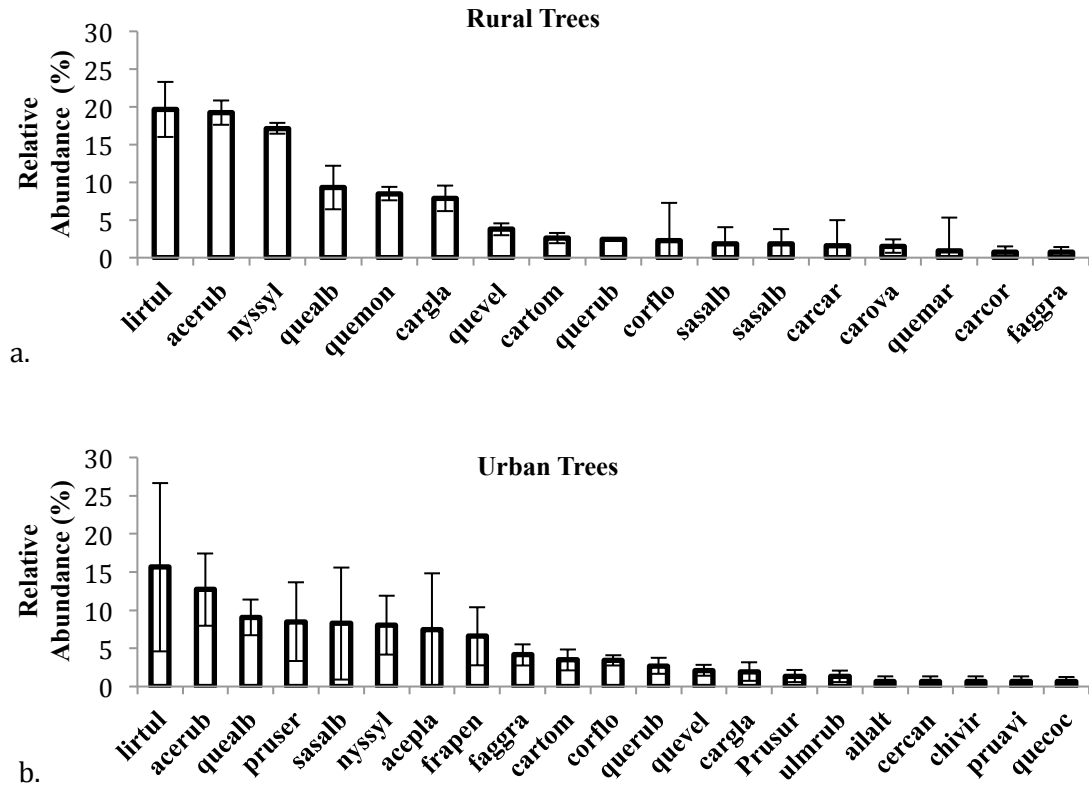


Figure 6. Mean ( $\pm$  SE) relative abundance of tree species in rural (a) and urban (b) forest plots established in Baltimore presented in order of rank abundance within each plot-type. Relative abundances were determined by taking the ratio of the number of individuals of a species to the total number of individuals in a plot. Each bar is the mean of the urban and rural plots ( $n = 4$ ). Species labels are the first three letters of the genus followed by the first three letters of the specific epithet. A species code key can be found in Appendix 1.

The change in species individual abundance (turnover) in the tree layer was evaluated by summing the number of individuals that had died, been recruited from the sapling layer, or retained as trees in the plots since 1998. The overall turnover trend in both the urban and rural plots was that more trees were recruited to the tree layer from the sapling layer than were lost to mortality (Figure 7a and b). The species that experienced the highest overall gains in recruitment into the tree layer from the sapling layer in the rural plots were *Acer rubrum*, *Liriodendron tulipifera*, *Nyssa sylvatica*, and *Carya glabra* (Figure 7a). The species with the highest mortality in the rural plots were *Quercus rubra*,

*Liriodendron tulipifera*, and *Cornus florida* (Figure 7a). In the urban plots, the greatest gains were *Acer rubrum*, *Nyssa sylvatica*, and *Liriodendron tulipifera* individuals (Figure 7b). The species with the highest mortality in the urban plots were *Cornus florida*, *Fraxinus americana*, and *Liriodendron tulipifera* (Figure 7b). Gains and losses were not mutually exclusive, so at the individual plot level, the appearance of *Liriodendron tulipifera* in both categories is not contradictory.

Four plots lost all individuals of three tree species due to mortality without recruitment. In the rural plots, Oregon Ridge Upslope 1 lost all individuals of *Carya ovalis* and Oregon Ridge Midslope 1 lost all individuals of *Quercus rubra* (Figure 7a). In the urban plots, Hillsdale 1 and Hillsdale 2 lost all individuals of *Fraxinus americana* (Figure 7b). Although recruitment of existing species occurred in all plots, there were no new species recruited to the tree layer in either the rural or urban plots (Figure 7).

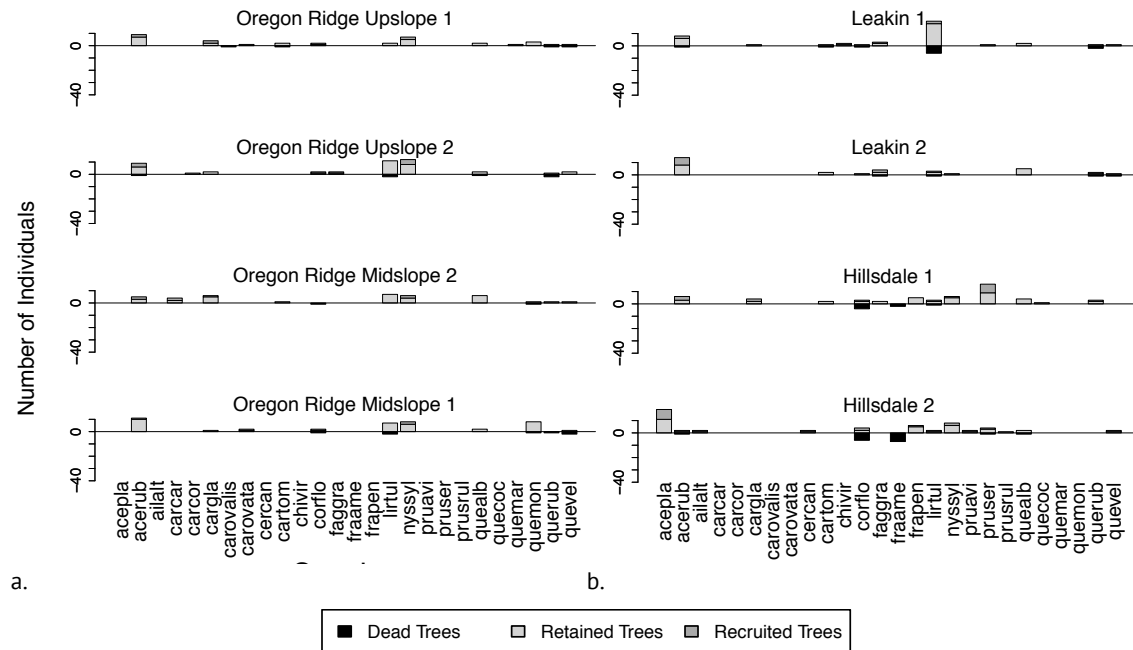


Figure 7. Death, retention, and recruitment of trees within rural (a) and urban (b) plots established in 1998 in Baltimore and resampled in 2015. Individuals that died between the 1998 and 2015 surveys were considered losses to the tree layer. Individuals that were recruited since 1998 were considered gains to the tree layer. Species that were counted as trees in both surveys were considered retained. Each bar represents the gain or loss of individuals of a species. The bars are organized vertically with loss below the horizontal axis and presence above. Panel a shows the rural plots and panel b shows the urban plots. The bars are color-coded to indicate status, as illustrated in the diagram legend. Species labels are the first three letters of the genus followed by the first three letters of the specific epithet. A species code key can be found in Appendix 1.

### Structure

Tree abundance was not significantly different between the urban and rural plots or between the 1998 and 2015 surveys (Table 2). There was also no significant difference in the basal area (BA) of trees between the urban and rural plots or between corresponding plots between survey years (Table 2).

Table 2. Tree basal area and abundance measurements for urban and rural plots in Baltimore in 1998 and 2015. Values are mean ( $\pm$  SE) for each group ( $n=4$ ). There were no significant differences between groups according to Welch-ANOVA. For basal area,  $p$ -value= 0.87 (F-value=0.24) and for abundance  $p$ -value= 0.06 (F-value=3.24).

<b>Trees</b>		
<i>Group</i>	<i>Basal Area (m<sup>2</sup>/ha)</i>	<i>Abundance (stems/ha)</i>
<b>Urban 1998</b>	0.28 $\pm$ 0.06	333.33 $\pm$ 37.95
<b>Rural 1998</b>	0.32 $\pm$ 0.05	291.67 $\pm$ 15.3
<b>Urban 2015</b>	0.35 $\pm$ 0.06	402.77 $\pm$ 13.89
<b>Rural 2015</b>	0.31 $\pm$ 0.06	372.22 $\pm$ 28.87

*Quercus* spp. and *Liriodendron tulipifera* had the highest BA in all the plots in 1998 and 2015 (Figure 8a-d). The average BA of *Liriodendron tulipifera* in the rural plots was nearly double the average of the urban plots in 2015 due to the loss of some



large urban trees between 1998 and 2015 (Figure 8a and b). As with species abundance, BA was more evenly distributed across species in the urban plots than in the rural plots.

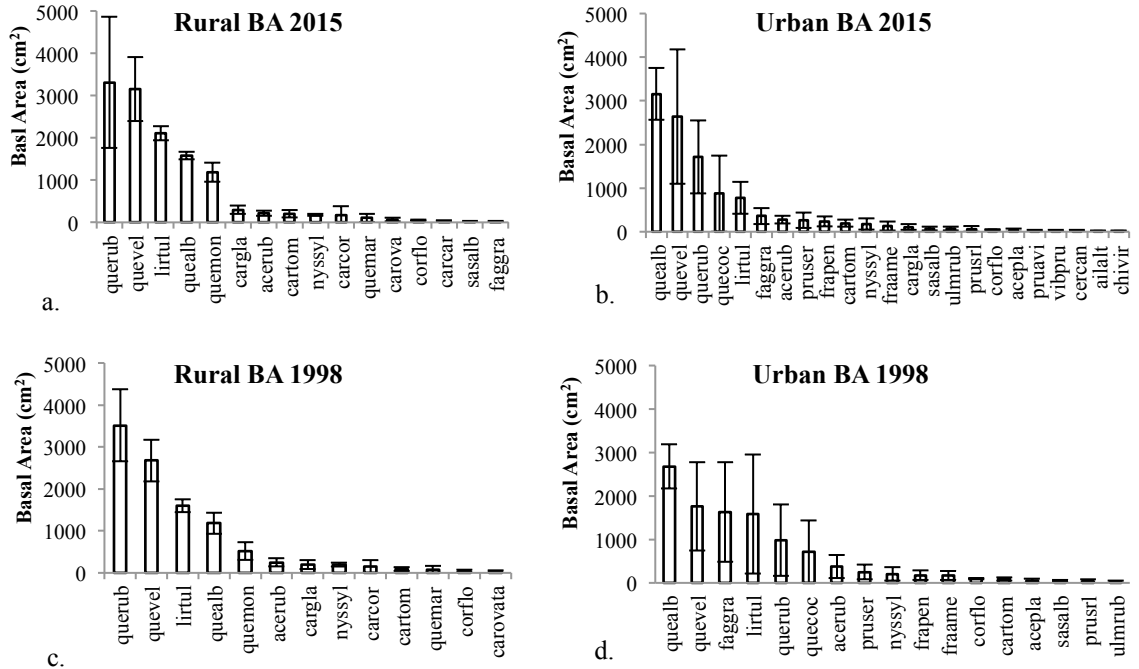


Figure 8. Average basal area (BA) of trees in rural and urban plots in Baltimore in 2015 and 1998 presented in order of rank abundance within each plot-type. BA was calculated for individuals within each plot using the equation  $BA = \left(\frac{DBH}{2}\right)^2 \times \pi$ . Bars are the average BA ( $\pm$  SE) per species within rural (a) and urban (b) plots in 2015 and rural (c) and urban (d) plots in 1998 ( $n = 4$ ). Species labels are the first three letters of the genus followed by the first three letters of the specific epithet. A species code key can be found in Appendix 1.

Relative growth of the six most abundant tree species (*Liriodendron tulipifera*, *Carya tomentosa*, *Quercus rubra*, *Quercus alba*, *Nyssa sylvatica*, *Acer rubrum*) was compared between the urban and rural plots. Only two species had significantly different growth rates between the urban and rural plots. *Liriodendron tulipifera* ( $p$ -value=0.002,  $F$ -value=10.77) and *Carya tomentosa* ( $p$ -value=0.002,  $F$ -value=12.64) had higher growth rates in the urban plots, as compared to those species in the rural plots (data not shown).

Canopy cover was approximately 85% in all plots and did not differ between the urban and rural plots or between years ( $p$ -value = 0.29, F-value=1.09).

### *Diversity*

In 2015, the average species richness of trees was 10.5 in the rural plots and 12.3 in the urban plots, but richness was not significantly different between the urban and rural plots or between years (Table 3). Likewise, diversity and evenness of the tree layer did not differ between the urban and rural plots in 1998 or 2015 (Table 3). Although it appears that the 1998 plot groups were tending toward being more even than the corresponding 2015 plots, differences were not significant ( $p$ -value=0.086; Table 3).

Table 3. Species diversity and evenness of the tree layer in urban and rural plots for Baltimore in 1998 and 2015. Values are the mean ( $\pm$  SE) of each group ( $n=4$ ). No significant differences were found ( $p < 0.05$ ) for richness  $p$ -value=0.089, (F-value=2.737), effective Shannon,  $p$ -value=0.937, (F-value=0.135), effective Gini-Simpson,  $p$ -value=0.993 (F-value=0.028), or evenness,  $p$ -value=0.857 (F-value=2.795).

<b>Trees</b>				
<i>Group</i>	<i>Richness</i>	<i>Effective Shannon</i>	<i>Effective Gini-Simpson</i>	<i>Evenness</i>
<b>Urban 1998</b>	10 $\pm$ 1.08	7.37 $\pm$ 1.3	6.06 $\pm$ 1.46	3.94 $\pm$ 1.19
<b>Rural 1998</b>	9.25 $\pm$ 0.48	7.38 $\pm$ 0.59	6.14 $\pm$ 0.67	3.11 $\pm$ 0.3
<b>Urban 2015</b>	12.25 $\pm$ 0.85	8.08 $\pm$ 1.05	5.97 $\pm$ 1.06	6.28 $\pm$ 1
<b>Rural 2015</b>	10.5 $\pm$ 0.05	7.78 $\pm$ 0.59	6.36 $\pm$ 0.5	4.14 $\pm$ 0.33

### **Sapling Layer**

#### *Composition*

In 2015, *Nyssa sylvatica* was the most abundant sapling species in the rural plots, followed by *Carya* spp. (Figure 9a). As with tree species, the distribution of sapling species was fairly even in the urban plots resulting in no single most abundant species (Figure 9b). Additionally, many species were found in only one out of the four urban

plots. Abundance of any given species was highly variable across the urban plots (note large standard errors) (Figure 9b). This trend was similar to the urban plots in 1998 (Groffman *et al.* 2006). Also similar to the findings in 1998, *Liriodendron tulipifera* and *Quercus* spp. were rarely found in the urban and rural sapling layer.

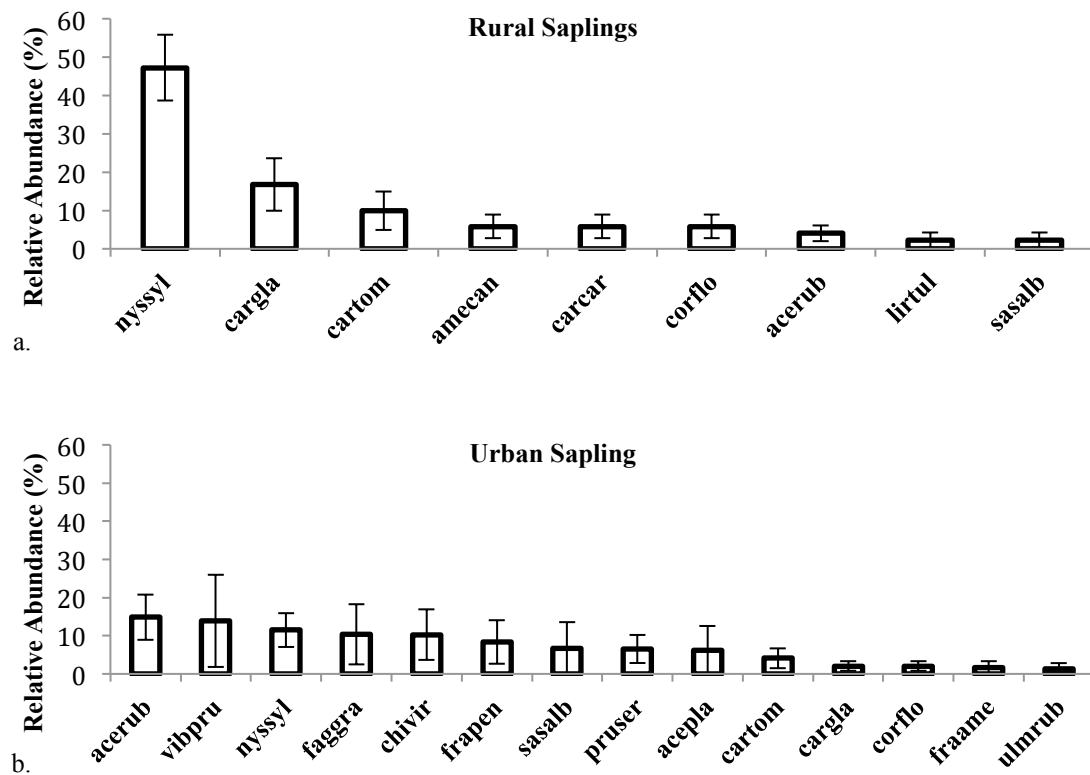


Figure 9. Relative abundance of sapling species in rural (a) and urban (b) forest plots established in Baltimore presented in order of rank abundance within each plot-type. Relative abundances were determined by taking the ratio of the number of individuals of a species to the total number of individuals in a plot. Each bar is the mean ( $\pm$  SE) of the urban and rural plots ( $n = 4$ ). Species labels are the first three letters of the genus followed by the first three letters of the specific epithet. A species code key can be found in Appendix 1.

In contrast to the tree layer, the overall turnover trend in the sapling layer were that losses exceeded gains (Figure 10a and b). More than 50% of all species present in each urban plot and 33% of all species present in each rural plot experienced a greater

than 50% loss of individuals from the sapling layer (Figure 10). Overall, the losses appeared to be much greater in the urban plots than the rural plots (Figure 10a and b).

Losses were more due to sapling mortality than to sapling recruitment into the tree layer (Figure 10a and b). In the rural plots, Oregon Ridge Upslope 1 lost all individuals of *Amelanchier canadensis*, *Cornus florida*, and *Fraxinus americana*. Oregon Ridge Upslope 2 lost all individuals of *Acer rubrum*, *Amelanchier canadensis*, *Carpinus caroliniana*, *Carya tomentosa*, *Castanea dentata*, *Prunus serotina*, *Quercus montana*, and *Viburnum prunifolium*. Oregon Ridge Midslope 1 lost all individuals of *Acer rubrum*, *Amelanchier canadensis*, *Carya cordiformis*, and *Prunus serotina*. Oregon Ridge Midslope 2 lost all individuals of *Amelanchier canadensis*, *Fraxinus americana*, and *Sassafras albidum*.

In the urban plots, Leakin 1 lost all individuals of *Carya cordiformis*, *Cornus florida*, *Liriodendron tulipifera*, *Tilia americana*, and *Magnolia macrophylla*. Leakin 2 lost all individuals of *Carya cordata* and *Liriodendron tulipifera*. Hillsdale 1 lost all individuals of *Fraxinus americana*, *Liriodendron tulipifera*, *Quercus rubra*, *Carya glabra*, *Amelanchier canadensis*, and *Morus alba*. Hillsdale 2 lost all individuals of *Fraxinus americana*, *Cornus florida*, *Carpinus caroliniana*, *Ulmus rubra*, and *Morus alba*.

The magnitudes of these losses are in contrast with the minimal gains in the sapling layer observed. Leakin 1 recruited a single *Acer rubrum* and a single *Fagus grandifolia* individual. Leakin 2 gained a single *Carya tomentosa* individual. Hillsdale 1 likewise recruited a single *Carya tomentosa* individual, whereas Hillsdale 2 gained no individuals. The rural plots also had minimal gains. Oregon Ridge Upslope 1 recruited a

single *Carya tomentosa* individual, whereas the rest of the rural plots had no recruited sapling individuals.

All plots retained a portion of the sapling community from the 1998 survey. The species with the highest retention in the urban plots were *Acer rubrum*, *Nyssa sylvatica*, and *Fagus grandifolia* (figure 10). In the rural plots, *Nyssa sylvatica*, *Carya glabra*, and *Carya tomentosa* were the most retained species (Figure 10).

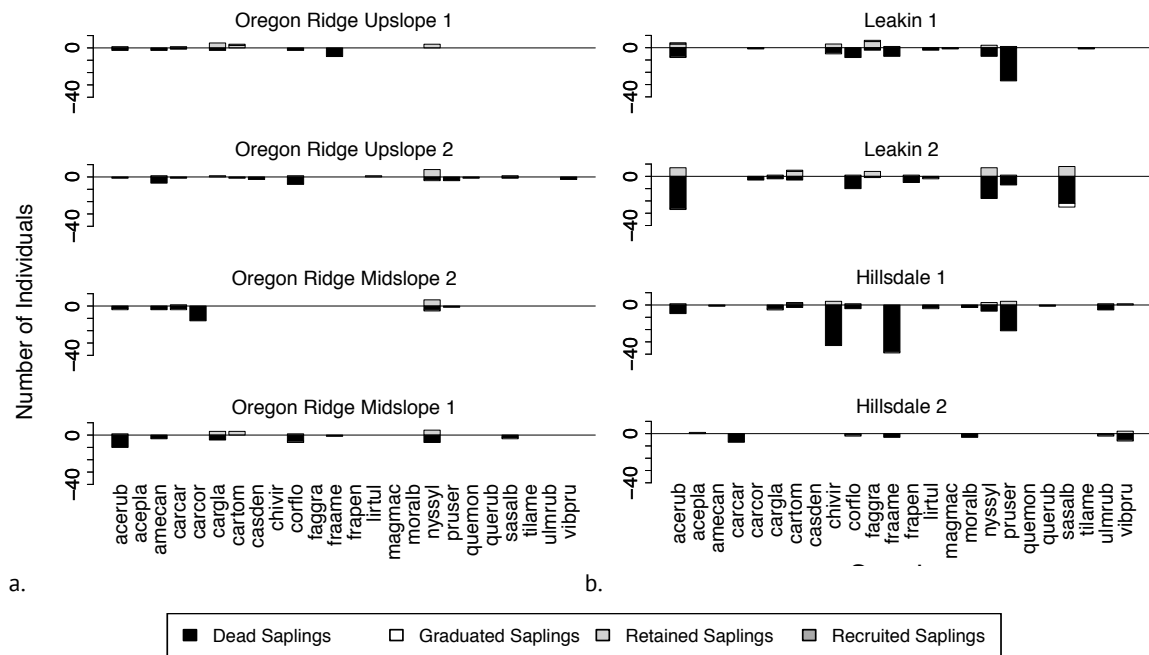


Figure 10. Diagram illustrating the distribution of death, graduation, retention and recruitment of saplings within rural (a) and urban (b) plots established in 1998 in Baltimore and resampled in 2015. Individuals that died between the 1998 and 2015 survey were considered losses to the sapling layer. Individuals that were recruited since 1998 were considered gains to the sapling layer. Species that were counted as saplings in both surveys were considered retained. Each bar represents the gain or loss of individuals of a species. The bars are organized vertically with loss below the horizontal axis and presence above. Panel a shows the rural plots and panel b shows the urban plots. The bars are color-coded to indicate status, as illustrated in the diagram legend. Species labels are the first three letters of the genus followed by the first three letters of the specific epithet. A species code key can be found in Appendix 1.

## Structure

Between 1998 and 2015, mean abundance of saplings was significantly reduced from 1005.6 stems per hectare to 205.6 stems per hectare in the rural plots and from 380.6 stems per hectare to 119.4 stems per hectare in the urban plots (Table 4). However, there was no significant difference in the mean sapling basal area between the urban and rural plots or between survey years (Table 4).

Table 4. Sapling density and dominance measurements for urban and rural plots in Baltimore in 1998 and 2015. Values are the mean ( $\pm$  SE) for each group ( $n=4$ ). Values in a column not followed by the same letter were significantly different ( $p < 0.05$ ) according to Welch-ANOVA with the Games-Howell *post hoc* test (density,  $p$ -value= 0.004, (F-value=13.368), dominance,  $p$  value= 0.211 (F-value=2.037)).

<b>Saplings</b>		
<i>Group</i>	<i>Basal Area (m<sup>2</sup>/ha)</i>	<i>Density (stems/ha)</i>
<b>Urban 1998</b>	0.0049 $\pm$ 0.0009 <sup>A</sup>	1005.55 $\pm$ 280.12 <sup>A</sup>
<b>Rural 1998</b>	0.0039 $\pm$ 0.0006 <sup>A</sup>	380.56 $\pm$ 50.18 <sup>A</sup>
<b>Urban 2015</b>	0.0032 $\pm$ 0.0013 <sup>A</sup>	205.56 $\pm$ 76.24 <sup>B</sup>
<b>Rural 2015</b>	0.0026 $\pm$ 0.0003 <sup>A</sup>	119.44 $\pm$ 15.96 <sup>B</sup>

Although total BA was unaffected, the distribution of BA across species was highly variable between plots in the sapling layer, and no single species or group of species dominated BA across the plots (Figure 11).

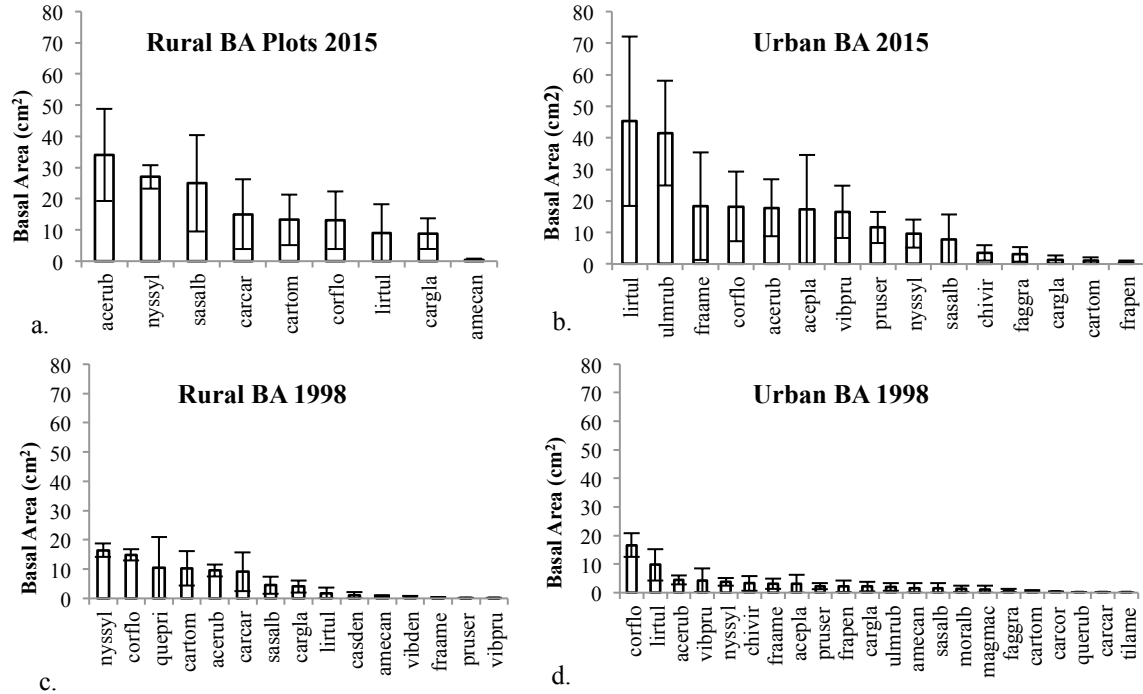


Figure 11. Average basal area (BA) of saplings in rural and urban plots in Baltimore in 2015 and 1998 presented in order of rank abundance within each plot-type. BA was calculated for individuals within each plot using the equation  $BA = \left(\frac{DBH}{2}\right)^2 \times \pi$ . Bars are the average BA ( $\pm$  SE) per species within the rural (a) and urban (b) plots in 2015 and the rural (c) and urban (d) plots in 1998 ( $n = 4$ ). Species labels are the first three letters of the genus followed by the first three letters of the specific epithet. A species code key can be found in Appendix 1.

### Diversity

In 2015, species richness was 5.25 in the rural plots and 6.5 in the urban plots, but there was no significant difference richness, diversity, or evenness of sapling species between the urban and rural plots or between years (Table 5).

Table 5. Species diversity and evenness of the sapling layer in urban and rural plots for Baltimore in 1998 and 2015. Values are the mean ( $\pm$  SE) of each group ( $n=4$ ). According to ANOVA, no significant difference were found ( $p < 0.05$ ) for richness,  $p$ -value=0.089 (F-value=2.737), effective Shannon,  $p$ -value=0.993 (F-value=0.028), effective Gini-Simpson  $p$ -value=0.993 (F-value=0.028), or evenness  $p$ -value=0.09 (F-value=2.73).

<b>Saplings</b>				
<i>Group</i>	<i>Richness</i>	<i>Effective Shannon</i>	<i>Effective Gini-Simpson</i>	<i>Evenness</i>
<b>Urban 1998</b>	11 $\pm$ 1.08	7.44 $\pm$ 0.63	5.77 $\pm$ 0.5	5.23 $\pm$ 0.93
<b>Rural 1998</b>	9 $\pm$ 0.56	6.26 $\pm$ 0.64	5.06 $\pm$ 0.56	4.06 $\pm$ 1.62
<b>Urban 2015</b>	6.5 $\pm$ 0.87	4.97 $\pm$ 0.5	4.15 $\pm$ 0.5	2.35 $\pm$ 0.06
<b>Rural 2015</b>	5.25 $\pm$ 1.65	3.83 $\pm$ 1.35	3.83 $\pm$ 1.08	1.42 $\pm$ 0.63

## Shrub Layer

### Composition

*Viburnum acerifolium* and *Vaccinium* spp. were the most common shrubs in the rural plots in both 1998 and 2015. Rural shrub composition was similar in 1998, with the exception of an increase in *Vaccinium* spp. relative abundance from 6.5% in 1998 to 45% in 2015 (Figure 12a and b). This increase was accompanied by a concomitant decrease in *Viburnum acerifolium* relative abundance from 93% in 1998 to 45% in 2015 (Figure 12a and c). The rural plots lost *Rhododendron periclymenoides*, *Ilex verticillata*, and *Viburnum dentatum*, and gained only *Rosa multiflora*.

*Lindera benzoin* remained the most common shrub in the urban plots between the 1998 and 2015 surveys (Figure 12b). In fact, *Lindera benzoin* increased in relative proportion from 63% in 1998 to 91% in 2015 (Figure 12b and d). The relative proportion of *Viburnum acerifolium* was reduced from 25% in 1998 to less than 1% in 2015 (Figure 12b and d). The urban plots lost *Viburnum dentatum* and *Vaccinium* spp., but gained *Euonymus americanus* (Figure 12b and d).



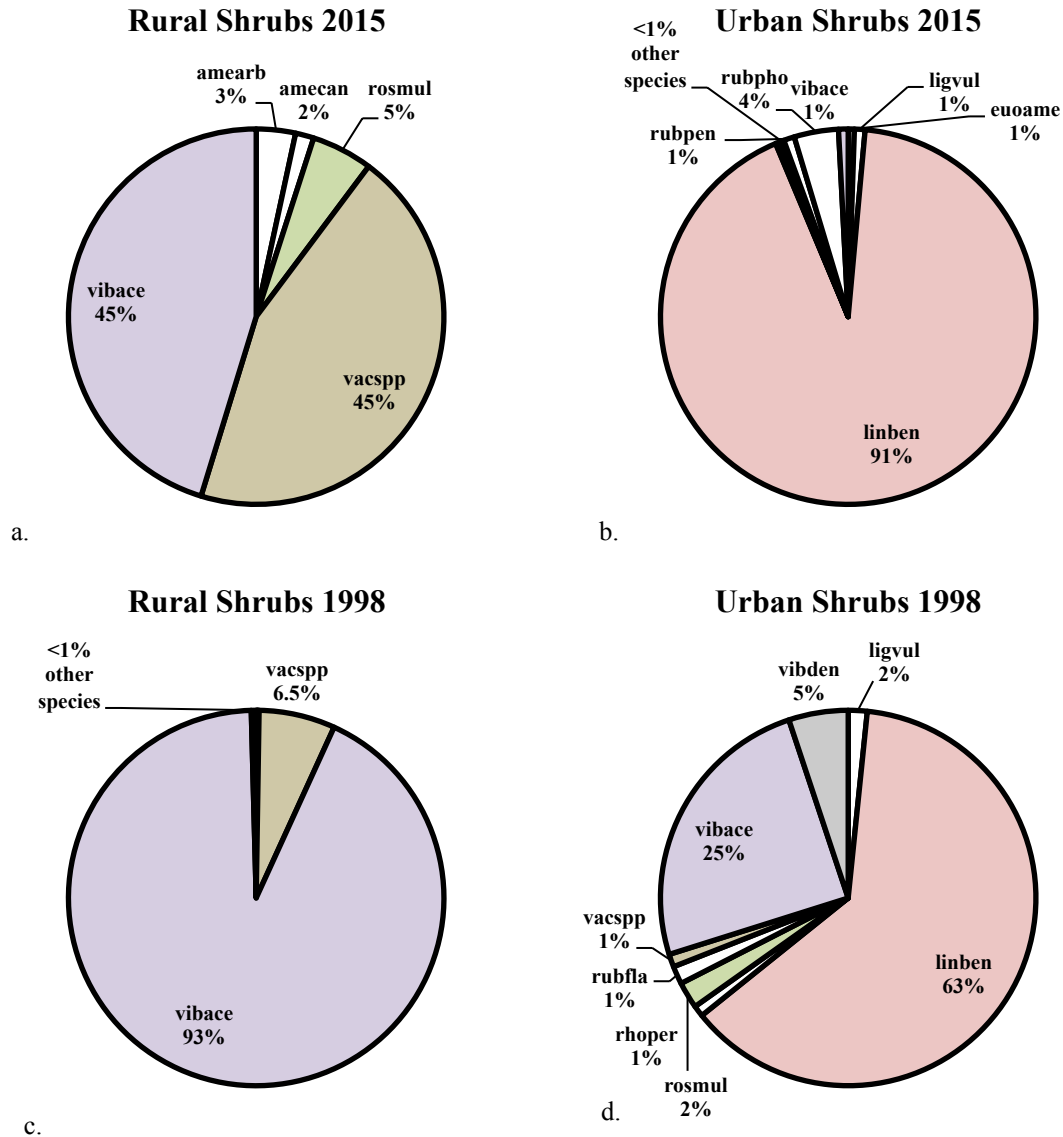


Figure 12. Relative proportion of shrub species in urban and rural plots in Baltimore in 1998 and 2015. The top panels show the relative shrub composition in 2015 (a and b) and the bottom show 1998 (c and d). The rural plots are on the left panels (a and c) and the urban plots are on the right (b and d). Percentages were calculated as the proportion of a species (measured in cm of cover) within the urban and rural plots in 1998 and 2015. Species with color designations indicate the most common species or highlight a loss or gain of a species to the group. Species labels are the first three letters of the genus followed by the first three letters of the specific epithet. A species code key can be found in Appendix 1.

## Structure

The rural and urban plots did not differ in shrub cover in 2015 ( $p$ -value= 0.062) (Figure 13). Shrubs cover significantly decreased in the rural plots between 1998 and 2015 ( $p$ -value=0.004), but did not change between 1998 and 2015 in the urban plots ( $p$ -value=0.867) (Figure 13). In 1998, the mean amount of shrub cover was 6406 cm per plot in the rural plots and 2928 cm per plot in the urban plots. In 2015, the mean amount of shrub cover was 116 cm per plot in the rural plots and 2078 cm per plot in the urban plots.

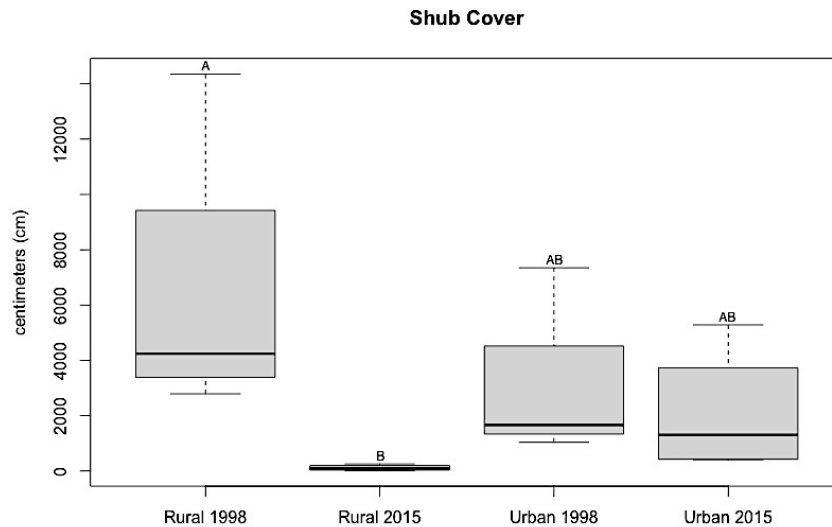


Figure 13. Box and whisker diagram of shrub cover in urban and rural plots in Baltimore in 1998 and 2015. The upper and lower limits of each box indicate the 75<sup>th</sup> and 25<sup>th</sup> percentiles, respectively. The bar dissecting each box is the median value of that group ( $n = 4$ ). The upper and lower limits of the whiskers indicate the maximum and minimum values for that group. The same letters above each box and whisker plot represent no difference whereas distinct letters represent a statistically significant difference as determined by Welch-ANOVA with the Games-Howell *post hoc* test ( $p < 0.05$ ). F-value= 11.855,  $p$ -value = 0.005.

## Vine Layer

### *Composition*

*Vitis* spp. were the most common taxa in the rural plots in 2015. *Vitis* spp., *Parthenocissus quinquefolia*, and *Smilax rotundifolia* were fairly equally prevalent in the rural plots in 1998 (Figure 14c). *Vitis* spp. have since increased in relative abundance from 37% in 1998 to 86% in 2015 (Figure 14a and c). *Parthenocissus quinquefolia* and *Smilax rotundifolia* decreased in relative abundance by 75% and 92%, respectively (Figure 14a and c). *Toxicodendron radicans*, *Celastrus orbiculatus* and *Lonicera japonica* were new vine species to the rural plots in the 2015 survey (Figure 14a and c).

*Celastrus orbiculatus* was the most common species in the urban plots in 2015 (Figure 14a and b). The urban plots were previously dominated by *Hedera helix* in 1998 (Figure 14d). *Celastrus orbiculatus* has increased in relative abundance from 5% in 1998, to 51% in 2015 (Figure 14b and d). *Hedera helix* has decreased in relative abundance from 64% in 1998 to 27% in 2015. There were no new vine species in the urban plots, but *Toxicodendron radicans* was lost in 2015 (Figure 14b and d).

Vine cover in urban plots consisted of 89% exotic species while vine cover in the rural plots consisted of only 4% exotic species. The relative proportion of exotic vines in 1998 was 80% in the urban plots. There were no exotic vines found in the rural plots in 1998. The most common exotic vine species in the 2015 survey was *Celastrus orbiculatus* in the urban plots (Figure 14a and b). *Celastrus orbiculatus* increased in relative abundance in the urban plots by 920% from 1998 to 2015.

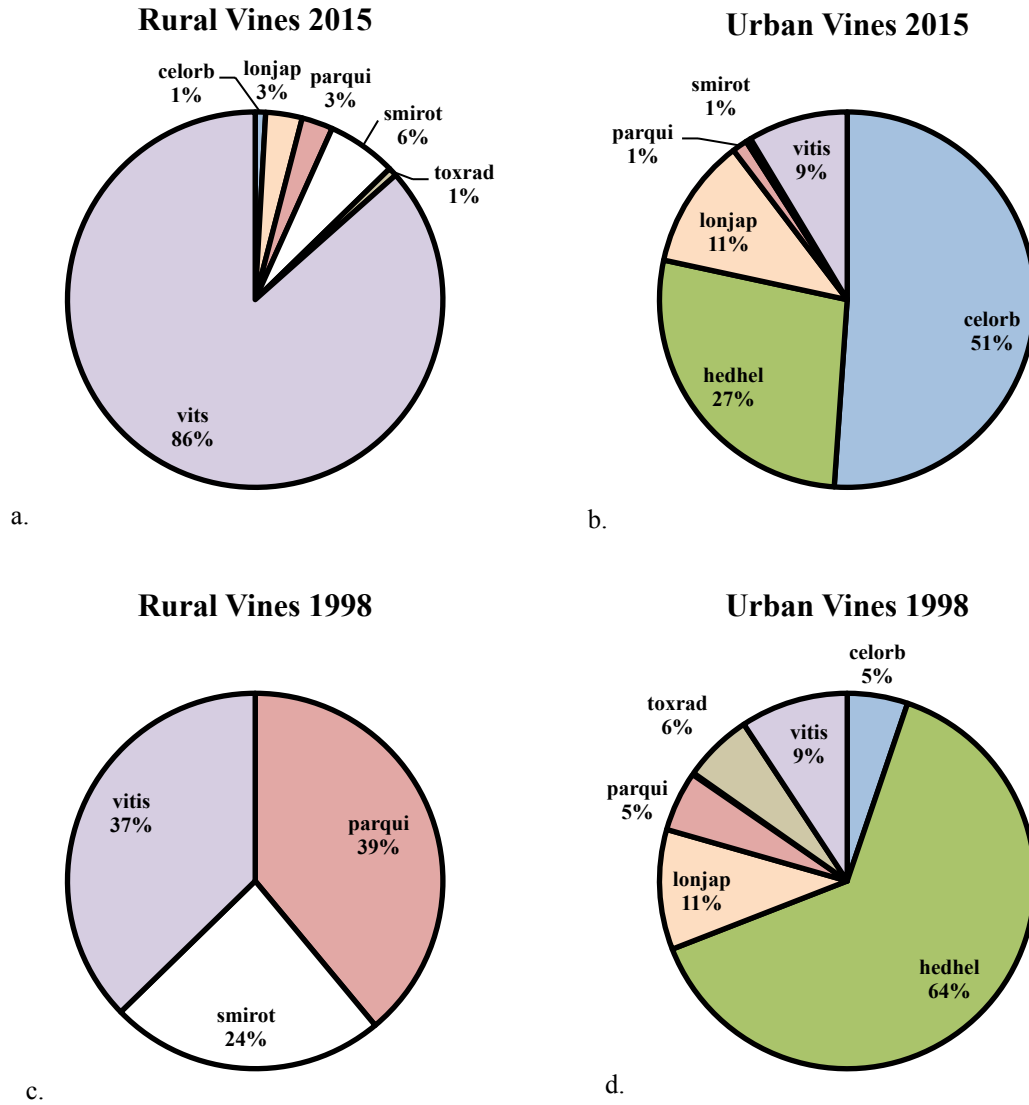


Figure 14. Relative proportion of vines species in urban and rural plots in Baltimore in 1998 and 2015. The top panels show the relative vine composition in 2015 (a and b) and the bottom show 1998 (c and d). The rural plots are on the left panels (a and c) and the urban plots are on the right (b and d). Percentages were calculated as the proportion of a species (measured in cm of cover) within the urban and rural plots in 1998 and 2015. Species with color designations indicate the most common species or highlight a loss or gain of a species to the group. Species labels are the first three letters of the genus followed by the first three letters of the specific epithet. A species code key can be found in Appendix 1.

## Structure

Vine abundance was significantly greater in the urban plots as compared to the rural plots in 2015 ( $p$ -value=0.005) (Figure 15). There was no significant difference in the amount of vine cover between the urban and rural plots in 1998 ( $p$ -value=0.348). Vine abundance did not differ between survey years within the rural plots ( $p$ -value=0.275) or urban plots ( $p$ -value=0.924) (Figure 15). In 1998, the mean amount of vine cover was 206.8 cm per plot in the rural plots and 1578 cm per plot in the urban plots. In 2015, the mean amount of vine cover was 48.8 cm per plot in the rural plots and 1377 cm per plot in the urban plots.

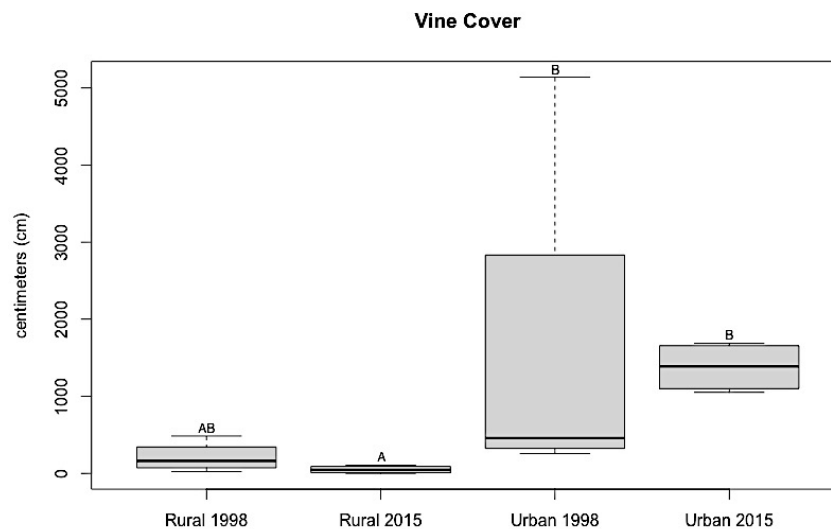


Figure 15. Box and whisker diagram of vine abundance in urban and rural plots in Baltimore in 1998 and 2015. The upper and lower limits of each box indicate the 75<sup>th</sup> and 25<sup>th</sup> percentiles, respectively. The bar dissecting each box is the median value of that group ( $n = 4$ ). The upper and lower limits of the whiskers indicate the maximum and minimum values for that group. The same letters above each box and whisker plot represent no difference whereas distinct letters represent a statistically significant difference as determined by Welch-ANOVA with the Games-Howell *post hoc* test ( $p < 0.05$ ). F-value = 7.596,  $p$ -value = 0.024.

## Seedling Layer

### *Composition*

*Prunus serotina*, *Amelanchier arborea*, and *Acer rubrum* were the most common rural seedling species in 2015. *Amelanchier canadensis*, *Carya glabra*, and *Acer rubrum* were the most common rural seedlings in 1998 (Figure 16d). Between 1998 and 2015, *Prunus serotina* and *Acer rubrum* increased in relative proportion by 320% and 122%, respectively (Figure 16a and c). *Carya glabra* had a similar relative abundance in 1998 and 2015 (Figure 16 and c). The increased relative abundance of *Amelanchier arborea* and the decrease relative abundance of *Amelanchier canadensis* may be a result of an identification discrepancy between these taxa. As a genus, *Amelanchier* spp. increased by 33% from 1998 to 2015 in the rural plots (Figure 16a and c).

*Fraxinus* spp. (*F. americana* and *F. pennsylvanica*) were the most common species in the urban plots in 2015 (Figure 16b). In 1998, the relative abundance of seedling species was fairly evenly distributed in the urban plots with no single dominant seedling species (Figure 16d). Since 1998, the relative proportion of *Fraxinus* spp. has increased by 63% (Figure 16b and d). *Prunus serotina* and *Acer rubrum* decreased in relative abundance by 88% and 55%, respectively (Figure 16b and d).

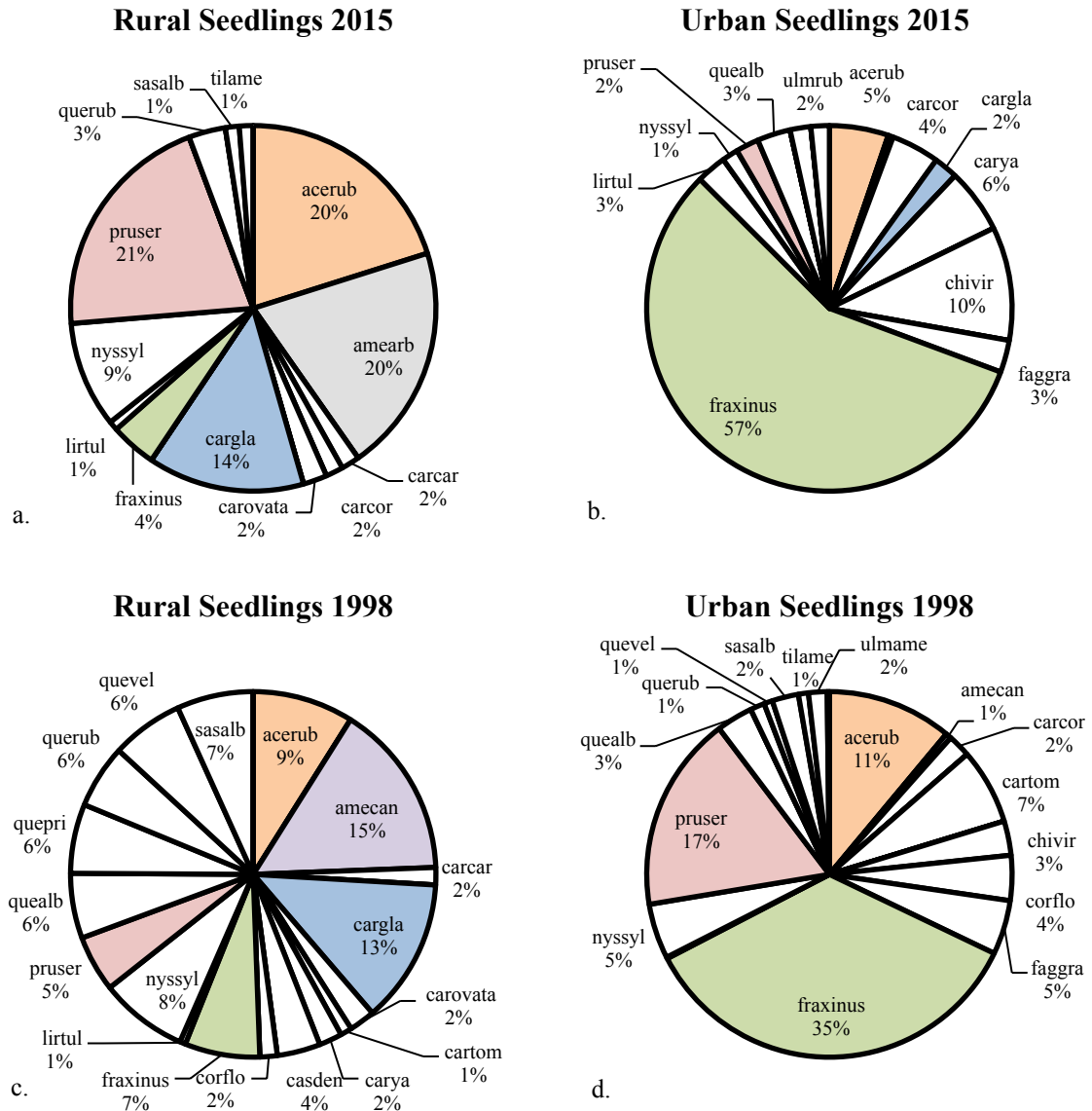


Figure 16. Relative proportion of seedling species in urban and rural plots in Baltimore in 1998 and 2015. The top panels show the relative seedling composition in 2015 (a and b) and the bottom show 1998 (c and d). The rural plots are on the left panels (a and c) and the urban plots are on the right (b and d). Percentages were calculated as the proportion of a species (measured in cm of cover) within the urban and rural plots in 1998 and 2015. Species with color designations indicate the most common species or highlight a loss or gain of a species to the group. Species labels are the first three letters of the genus followed by the first three letters of the specific epithet. A species code key can be found in Appendix 1.

## Structure

The percentage of seedling cover significantly declined in the rural plots from 1998 to 2015 ( $p$ -value=0.003) (Figure 17). No difference occurred in the percentage of seedling cover within the urban plots between 1998 and 2015 ( $p$ -value=0.217), nor between the urban and rural plots in 2015 ( $p$ -value=0.509) (Figure 17). In 1998, the mean percentage of seedling cover per plot was 5.4% for the rural plots and 11% for the urban plots. In 2015, the mean percentage of seedling cover per plot was 0.7% for the rural plots and 3.6% for the urban plots.

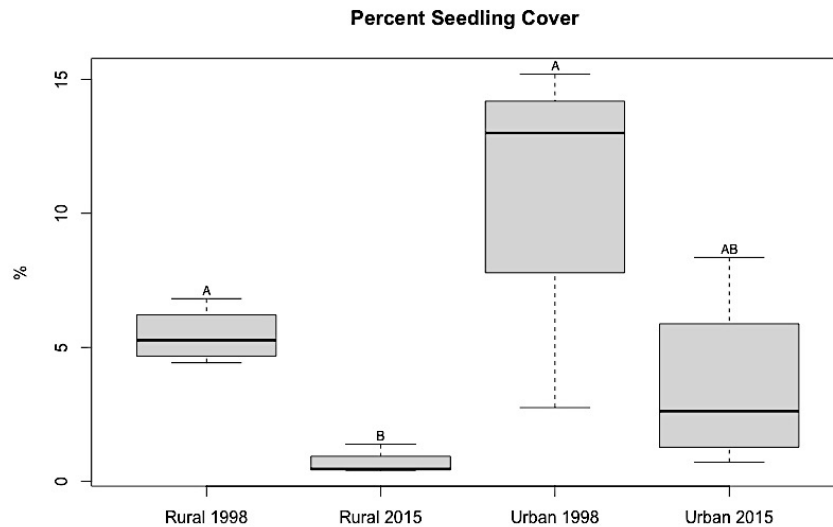


Figure 17. Box and whisker diagram of percent seedling cover in urban and rural plots in Baltimore in 1998 and 2015. The upper and lower limits of each box indicate the 75<sup>th</sup> and 25<sup>th</sup> percentiles, respectively. The bar dissecting each box is the median value of that group ( $n = 4$ ). The upper and lower limits of the whiskers indicate the maximum and minimum values for that group. The same letters above each box and whisker plot represent no difference whereas distinct letters represent a statistically significant difference as determined by Welch-ANOVA with the Games-Howell *post hoc* test ( $p < 0.05$ ). F-value =22.287,  $p$ -value = 0.002.



## Herb Layer

### Structure

There was no significant difference in the percentage of herbaceous plant cover between the urban and rural plots or between survey years ( $p$ -value = 0.140) (Figure 18). In 1998, the mean percentage of herb cover per plot was 4.8% for the rural plots and 11% for the urban plots. In 2015, the mean percentage of herb cover per plot was 4.5% for the rural plots and 2.2% for the urban plots. The lack of significant differences between groups was likely due to low power associated with the small number of plots (Figure 17).

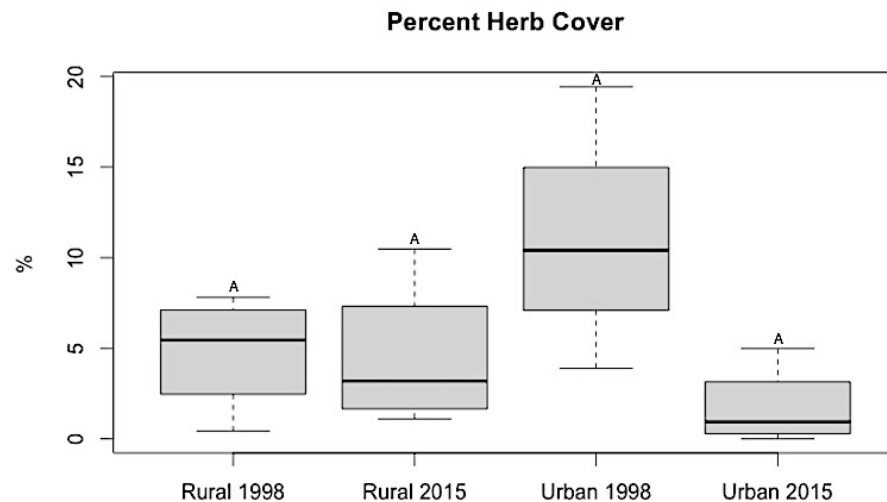


Figure 18. Box and whisker diagram of percent herb cover in urban and rural plots in Baltimore in 1998 and 2015. The upper and lower limits of each box indicate the 75<sup>th</sup> and 25<sup>th</sup> percentiles, respectively. The bar dissecting each box is the median value of that group ( $n = 4$ ). The upper and lower limits of the whiskers indicate the maximum and minimum values for that group. The same letters above each box and whisker plot represent no difference whereas distinct letters represent a statistically significant difference as determined by Welch-ANOVA with the Games-Howell *post hoc* test ( $p < 0.05$ ). F-value= 2.632,  $p$ -value = 0.140.

## Changes in Forest Community Composition

### *Exotic Species*

The overall proportion of exotic species was higher in the urban plots (Figure 19). In fact, two of the rural plots, Oregon Ridge Upslope 1 and Oregon Ridge Midslope 1, had no exotic species in 2015 (Figure 19). In the urban plots, exotic vines were found in every plot (Figure 19). Exotic trees and saplings were only found in Hillsdale 2 (Figure 19). Exotic species dominance was highest in the vine layer of both the urban and rural plots (Figure 19). The proportion of exotic seedlings has remained at zero in all plots (data not shown).

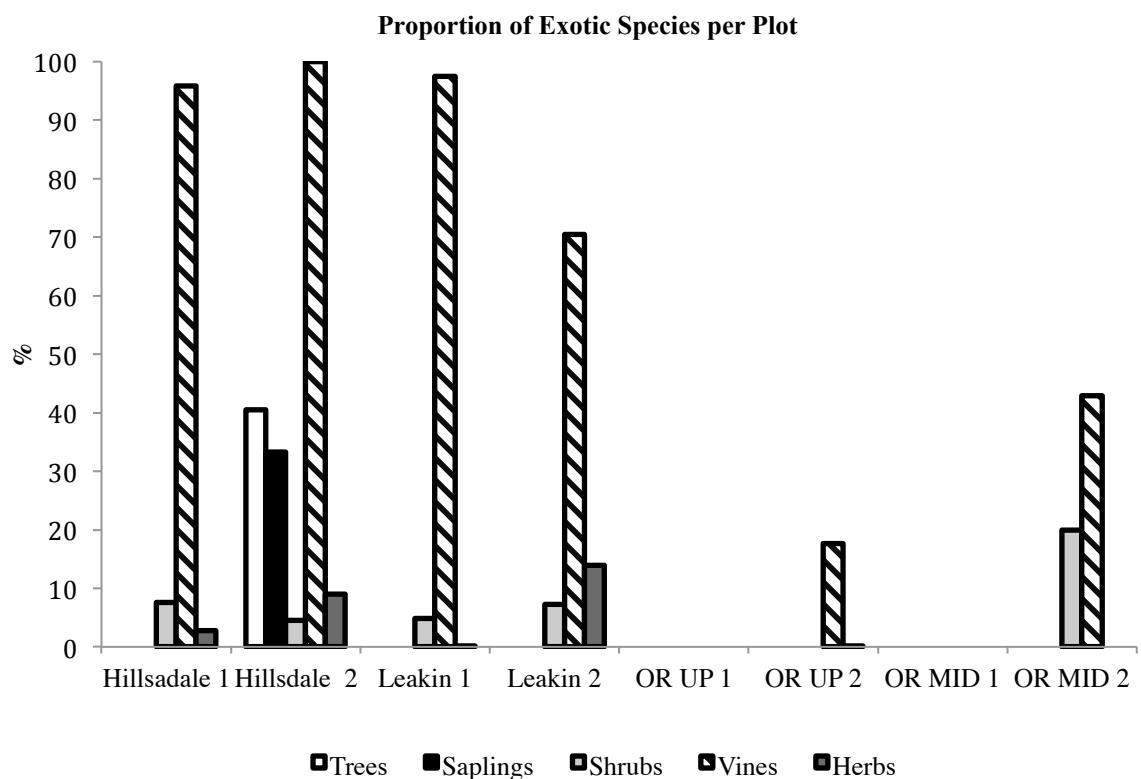


Figure 19. The proportion of exotic species within each forested Baltimore plot from 1998 to 2015 categorized by forest layer. Proportions were based on individuals for trees and saplings, and percent cover (cm) for shrubs, vines, and herbs. The first four plots listed on the x-axis are urban plots and the next four are rural plots.

### *Forest Community Composition and Diversity*

Non-metric multidimensional scaling (NMDS) based on sapling species shows that the urban and rural plots' sapling composition changed from 1998 to 2015 (Figure 20). This change is apparent in the shift of the 2015 convex hull polygons towards the positive end of both Axis 1 and Axis 2 relative to 1998 polygons. The shift between the 1998 and 2015 urban polygons is largely driven by species losses in Hillsdale 1, Leakin 1, and Leakin 2. For example, many of the species at low values on Axis 2 and between -0.5 and 0.5 on Axis 1 were lost to the urban 2015 sapling community. Hillsdale 2 experienced less compositional change than the other urban plots, resulting in a pivoting of the urban polygons in ordination space. Loss of sapling species in the rural plots shifted the rural 2015 polygon to positive values on Axis 2 relative to the rural 1998 polygon. The upward shifts of both the urban and rural plots in 2015 illustrate that the second axis is the gradient of species loss over time. The first axis is largely driven by the dissimilarity of Hillsdale 2 to all other urban and rural plots. The larger convex hulls of the urban groups signify more variation in urban sapling community than in rural sapling community (Figure 20). The reduction volume of the rural convex hulls over time illustrates that beta diversity of saplings has decreased in the rural plots. The similar shapes of the urban convex hulls illustrate a similar amount of beta diversity in the urban plots.

In the shrub and vine layer, the processes driving the axes of the NMDS are less clear. The 2015 urban shrub and vine community is a subset of the urban 1998 shrub and vine community (Figure 21). For example, the species closest to Axis 2 and nearest to the urban 1998 convex hull polygon were not found or were less common in the urban plots

in 2015. However, species located between -1 and 0 of the first axis remained present in the urban plots between 1998 and 2015. The rural shrub and vine community changed dramatically from 1998 to 2015 (Figure 21). This shift is likely due to losses of the dominant shrubs found in the rural 1998 plots, with coinciding gains in exotic vine and shrub species. Rural and urban plots shared particular exotic species, explaining the shift downward in the rural 2015 polygon. However, the shift of the rural 2015 polygon away from the second axis was likely driven by the single isolated species furthest from the second axis. This species only occurred within the rural plots in 2015, thus making those plots more dissimilar than the rural 1998 plots. The large amount of space between the rural 1998 and 2015 polygons shows that the magnitude of shrub and vine compositional change over time was greater in the rural plots than the urban plots.

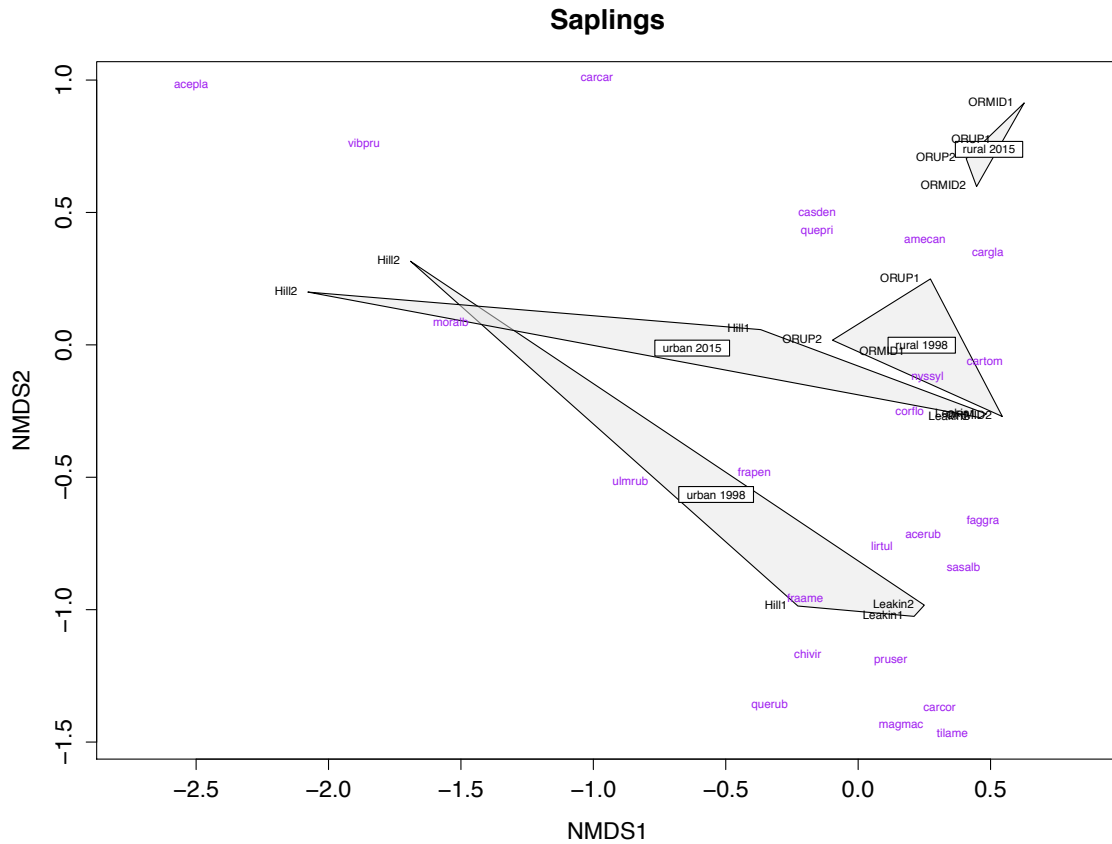


Figure 20. Non-metric multidimensional scaling (NMDS) of the sapling community composition in forested Baltimore plots in 1998 and 2015 plotted within ordination space. Shaded convex hulls envelop the urban and rural plots in 1998 and 2015. Plot points within the NMDS are based on Bray-Curtis distance, calculated using abundance data for 24 species. The distance between the points represents compositional similarity, with closer points being more similar than points further apart. Stress score = 0.133, procrustes: rmse= 0.0001075085, max residual= 0.001313793.

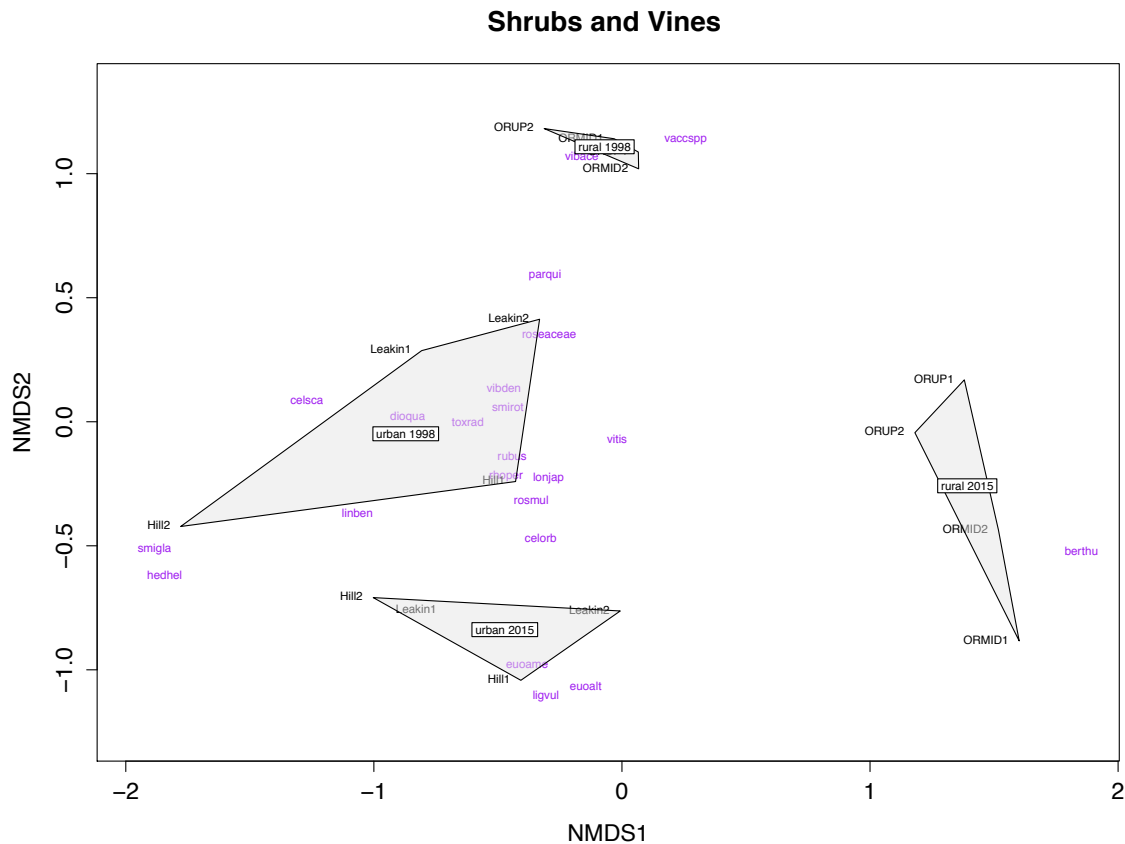


Figure 21. Non-metric multidimensional scaling (NMDS) of the shrub and vine community composition in forested Baltimore plots in 1998 and 2015 plotted within ordination space. Shaded convex hulls envelop the urban and rural plots in 1998 and 2015. Plot points within the NMDS are based on Bray-Curtis distance, calculated using abundance data for 22 taxa. The distance between the points represents compositional similarity, with closer points being more similar than points further apart. Stress score = 0.104, procrustes: rmse=3.203644e-06, max residual= 8.709903e-06.

### *Alpha and Beta Diversity*

The urban plots had more total species than the rural plots in 1998 and 2015 (Table 6). The total number of species reduced by six in the rural plots and by four in the urban plots (Table 6). The total number in the rural plots was an outcome of a loss of 11 species and a gain of 5 species since 1998 (Table 6). In the urban plots, 20 species were lost and 16 species were gained (Table 6). Greater loss and gain in species in the urban plots yielded a beta turnover nearly double that of the rural value (Table 6).

Alpha diversity was significantly lower in the rural plots as compared to the urban plots in both 2015 ( $p$ -value=0.001) and in 1998 ( $p$ -value=0.044) (Table 6). From 1998 to 2015, there was no significant change in alpha diversity within rural plots ( $p$ -value=0.083) or urban plots ( $p$ -value=0.981) (Table 6). By contrast, beta diversity significantly declined from 1998 to 2015 in the rural plots ( $p$ -value=0.036) but not in the urban plots ( $p$ -value=0.999) (Table 6). Beta diversity in the urban plots did not differ between 1998 and 2015 ( $p$ -value=0.999) (Table 6).

Table 6. Diversity metrics for all species in urban and rural plots in Baltimore in 1998 and 2015. Total species ( $\gamma$ ) is the sum total of all species within a group ( $n=4$ ). Alpha diversity ( $\alpha$ ) is the mean species richness per group. Beta diversity ( $\beta$ ) is the average pair-wise comparison of the inverse of the Jaccard similarity index within each group. Species lost and species gained were summed per group. Turnover since 1998 ( $\beta\tau$ ) is the absolute value of species lost and gained divided by the product of alpha and two (Grace & McCune 2002). The same letters for values in the columns of alpha and beta diversity represent no difference whereas distinct letters represent a statistically significant difference as determined by ANOVA with Tukey's *post hoc* test ( $p < 0.05$ ). Alpha diversity,  $p$ -value = 0.0003 (F-value =15.15) and beta diversity,  $p$ -value= 0.013, (F-Value=4.652).

Group	Total Species ( $\gamma$ )	Alpha Diversity ( $\alpha$ )	Beta Diversity ( $\beta$ )	Species Lost Since 1998	Species Gained Since 1998	Turnover Since 1998 ( $\beta\tau$ )
Urban 1998	73	41 $\pm$ 3.08 <sup>A</sup>	0.42 $\pm$ 0.06 <sup>A</sup>			
Rural 1998	46	30.75 $\pm$ 0.63 <sup>B</sup>	0.57 $\pm$ 0.03 <sup>B</sup>			
Urban 2015	69	39.5 $\pm$ 2.87 <sup>A</sup>	0.42 $\pm$ 0.03 <sup>A</sup>	20	16	0.44
Rural 2015	40	21.75 $\pm$ 2.39 <sup>B</sup>	0.43 $\pm$ 0.03 <sup>A</sup>	11	5	0.26

## Chapter Four: Discussion

### Summary of the Findings

In this study, I found significant differences both between the urban and rural plots and within plot-types over time. The major temporal changes were in the sapling, shrub, and seedling layers, whereas the tree and herb layers remained similar. The abundance of saplings greatly declined due to mortality in both the urban and the rural plots. Eight sapling species were lost altogether from the plots. The sapling species that were retained in the plots tended to have greater basal area and were more shade tolerant than those present in 1998. Total shrub and seedling cover declined in the rural plots, but not in the urban plots. In the urban plots, all species decreased in relative abundance from 1998 to 2015 with the exception of *Lindera benzoin*, which increased from 63% to 91%. As in 1998, the amount of vine cover in 2015 was greater in the urban plots. Invasive vines, shrubs, and herbs were found in two of the rural plots in 2015, whereas none were reported in the rural plots in 1998. Tree abundance and the proportion of herb cover were similar between the urban and rural plots in both surveys. Alpha diversity was higher in the urban plots in both survey years. Beta diversity decreased in the rural plots, resulting in no difference in beta diversity between the urban and rural plots in 2015. The amount of species turnover within the urban plots was nearly 41% greater than the turn over of the rural plots.

### Species Composition

The two species recruited into the tree layer in this study (*Nyssa sylvatica* and *Acer rubrum*) are noted in other research as the predominating species contributing to regeneration (Abrams 1990; Nowacki & Abrams, 2008; McGarvey *et al.* 2013; Desprez



*et al.* 2014). These reports argue that *Acer rubrum* and *Nyssa sylvatica* have particular success in expanding their ranges and abundances because they are adapted to understory environments and they are habitat generalists (Abrams 1998; Desprez *et al.* 2014). In the sapling layer, *Nyssa sylvatica* had the highest retention in both the urban and rural plots. It is suggested that the trend towards shade tolerant species is driven by reductions in canopy disturbance (Nowack & Abrams 2008; Hanberry *et al.* 2012; Hutchinson *et al.* 2012).

Canopy cover in this study remained relatively unchanged since 1998. Limited canopy openness coincided with no representation of *Quercus* spp. or *Liriodendron tulipifera* in the sapling layer. *Quercus* spp. and *Liriodendron tulipifera*, the two most common trees in 1998 and 2015, are shade-intolerant (Burns & Honkala 1990). The relatively closed canopy environment may have contributed to the decline in *Quercus* spp. and *Liriodendron tulipifera* regeneration. However, Cowell *et al.* (2010) reported that canopy gaps were only marginally associated with *Quercus* spp. survival, suggesting that light availability alone was not enough to maintain *Quercus* spp. dominance. The absence of *Quercus* spp. and *Liriodendron tulipifera* from the sapling layer indicates that the tree layer will look quite different in the next century. Forests in Baltimore will be dominated by *Nyssa sylvatica* and *Acer rubrum* unless there are large disturbances that open forest canopies.

Canopy cover was estimated at around 85% in both the rural and urban plots. This assessment is similar to the 90% canopy cover reported in the health assessment of Oregon Ridge in 2007 (Baltimore County EPS, 2007), suggesting that there have been few disturbances to the canopy in the rural or urban plots. Closed canopies can reduce

survivorship of gap-phase species and shade intolerant species (Augspurger 1984). Although these species can often persist as seedlings, they will not grow appreciably in shaded conditions (Augspurger 1984). Many of the sapling species in my study with the largest declines are considered shade intolerant (*Fraxinus americana*, *Prunus serotina*, *Sassafras albidum*, and *Carya cordiformis*) (Burns & Honkala 1990). Still, the most common seedlings in 2015 were *Prunus serotina* in the rural plots and *Fraxinus americana* in the urban plots. If a canopy disturbance occurs, *Prunus serotina* and *Fraxinus americana* may show a resurgence in the plots.

Stromayer & Warren (1997) proposed that deer browsing shifts understory vegetation to an alternative stable state that is resistant to the regeneration of previously reported dominant species. This shift is clearly demonstrated in the shrub layer. Shrub cover plummeted in the rural plots, whereas shrub cover in the urban plots remained stable. However, *Lindera benzoin*, the shrub species that represented 91% of the urban shrub layer, is a species avoided by deer due to the biochemical defenses of its leaves and twigs (Rawinski 2008). A study in Washington, D.C., reported that deer negatively impacted all major woody species with the exception of *Lindera benzoin* and *Fagus grandifolia* (Rawinski 2008). Similarly, in my study, *Fagus grandifolia* retention and recruitment was observed in the urban plots, but not in the rural plots.

Recruitment and retention of sapling species was low in all plots. Unpalatable understory species appeared more commonly than palatable species. Interestingly, *Carya tomentosa* recruitment was observed in both the urban and rural plots and it is both palatable to deer and intolerant of shade (McCarthy 1994). McGarvey et al. (2013) also found the successful regeneration of *Carya tomentosa* in a deer exclusion study in

Virginia. The apparent resilience of this species may be an interesting area of future research.

The vine layer had the highest percentage of exotic species of all forest layers. The Groffman et al. (2006) study reported similar findings, with exotic vines more common in urban areas. Interestingly, the invasive vine, *Celastrus orbiculatus* declined in relative abundance between survey years in the urban plots. Declines in *Celastrus orbiculatus* abundance have also been reported in another study (Rossell et al. 2007), which attributed the reduction to deer browsing. With the exception of vines, exotic species represented a relatively small proportion of the community composition in the urban and rural plots. There were, however, more exotic species in the urban plots than in the rural plots. This finding is consistent with other studies that report higher exotic species richness in urban forests (Kowarik 2003; McDonnell & Hahs 2008). Although uncommon, three new exotic species were found in the rural plots: *Microstegium vimineum*, a highly invasive grass, and *Rosa multiflora* and *Berberis thunbergii*, two particularly aggressive invasive shrubs. If left unmanaged, these invasive species are capable of inhibiting native species recruitment (Oswalt et al. 2007).

Disease and infestations may have influenced tree and sapling regeneration in the plots. Major losses of *Fraxinus americana* and *Cornus florida* saplings in both the urban and rural plots suggest that infestations (e.g. emerald ash borer) and disease (e.g. dogwood anthracnose) have contributed to species loss (United States Department of Agriculture 2015). Gypsy moths were reported in eight stands at Oregon Ridge Park, with complete defoliation and subsequent death in one stand in 2006 (Baltimore County EPS, 2007). Although the rural plots were not located in the affected stands, it is possible

that gypsy moth infestation-related stress and death reduced acorn production and thus oak regeneration throughout the park.

### **Forest Structure**

Changes were apparent in several forest strata. Groffman et al. (2006) described all of the plots as well developed at every layer in 1998. In 2015, however, much of the vegetation below the canopy level had decreased in abundance and cover, and saplings were a minor structural component of the plots. Although there were fewer saplings in both the urban and the rural plots in 2015, the magnitude of reduction was far greater in the urban plots. With mean density of urban saplings nearly two thirds greater than rural saplings in 1998, the potential for loss was larger in the urban plots.

From my field observations, deer regularly visited the plots, browsing extensively. Deer browsing typically focuses on plant individuals within the ungulate's reach, such as herbs, seedlings, shrubs, and saplings. Overbrowsing results in forest stands devoid of understory plants and overrepresented by mature trees (Tilghman 1989; Stromayer & Warren 1997; Côté et al 2004). Because of their immense impact on forest density and structure, deer are considered a keystone herbivore (Rooney 2001). It may be that deer had reduced saplings in the rural plots prior to 1998, and deer populations have since expanded into urban plots, decimating saplings in those areas as well. It is unknown whether the deer population occurs at similar densities in Baltimore City and Baltimore County. Personal correspondence with Maryland State deer scientist Brian Eyeler has revealed that overabundant deer are an increasing concern in Baltimore City.

In contrast to sapling abundance, seedling cover did not decline in the urban plots. Deer may not have a significant impact on seedling abundance. For instance, McGarvey

et al. (2013) found that deer in Virginia had no significant impact on seedling abundance or composition. Similarly, Rooney (2001) showed that deer browsing has a greater impact on sapling abundance than on seedling abundance. Although the relatively stable amount of seedling cover in the urban plots may support these findings, the decline in rural seedling cover does not. Deer may have browsed on the seedling layer in the rural plots because there were few other sources of reachable vegetation. Saplings, shrubs, and vines may not be as limited in the urban plots, leaving seedlings largely ignored by deer. If browsing affects seedlings, which are close to the ground, it is perplexing that herb cover did not decline in the rural plots as well. Intensive herb browsing has been reported in numerous other studies (Horsely *et al.* 2003; McGraw & Furedi 2005, Royo *et al.* 2010). It may be that the herbaceous species in this study are less palatable than in other studies.

One of the more dramatic findings was the decline in rural shrub cover from 1998 to 2015 (Figure 13) during which time the urban plots declined only slightly. The most common rural shrub, *Viburnum acerifolium*, was reported in other studies to be preferentially browsed by deer (Kribel *et al.* 2011). The reduction of *Viburnum acerifolium* in the rural and urban plots suggests that deer browsing on this species is likely. Despite *Viburnum acerifolium* being nearly extirpated from the urban plots, overall shrub cover remained relatively unchanged. Importantly, only one shrub species dominated the urban plots, *Lindera Benzoin*. This shrub is known to be unpalatable and often avoided by deer (Rawinski 2008). Although guided in different manners, the structure of the shrub layer in the urban and rural plots seem influenced by the browsing preferences of deer.

Few differences were found in the structure of the tree layers in the plots. In addition to presenting a structural barrier for deer browsing, mature trees are generally long-lived and more resilient to disturbance than understory species. After reaching maturity, above-ground tree growth declines (Gower et al. 1996). Therefore, it is not surprising that structural changes have not occurred in the tree layer. Canopy cover also did not change between 1998 and 2015, suggesting minimal disturbances to the canopy. When canopy disturbance is low, the opportunity for many understory species that rely on periodic breaks in the canopy to survive is reduced (Runkle 1982; Brokaw 1987). Canopy cover may therefore contribute to the decline in many shade-intolerant understory plants. If canopy cover were the primary driver of understory plant density, however, we would expect to see higher relative abundances of shade tolerant species. Instead, there are reductions of nearly every species except those that are large or unpalatable to deer.

### **Diversity**

The urban plots had higher alpha diversity in both survey years. Urban forests often experience naturalization of escaped exotic species (Kowarik 2003; McDonnell & Hahs 2008). Exotic species introduction commonly increases alpha diversity (Schwartz *et al.* 2006; McKinney 2008). Still, non-native species in this study were a minimal proportion of the plant community. The higher alpha diversities of the urban plots may be better explained by widespread loss of species from the rural plots, rather than a gain in exotic species in the urban plots. Further, if species introductions remain lower in the rural plots, diversity is likely to remain higher in the urban plots.

Although many environmental factors likely contribute to species loss in the plots, indicator species suggest that deer browsing and canopy closure may be the primary drivers. A decline in biodiversity as a result of intense browsing on palatable species has been reported in other studies (Begley-Miller *et al.* 2014; Rooney & Waller 2003; Côté *et al.* 2004). Under closed canopy conditions, losses of shade intolerant species have been observed (Augspurger 1984) due to the inhibition of seed germination (Vázquez-Yanes *et al.* 1990) and reduced seedling survival (Wright 2002). It can be hypothesized that species loss due to deer browsing and canopy closure explain the lower alpha diversities in the rural plots. Whereas canopy in the urban plots had a similar amount of closure compared to the rural plots, a consistent alpha diversity in the urban plots suggests canopy cover alone is not driving species diversity in the plots.

Beta diversity decreased in the rural plots, but alpha diversity remained unchanged. These findings suggest that a species lost in the rural plots was unique to an individual plot, whereas species gained or retained was similar across all rural plots. Although many species were lost in the urban plots, species introduction was high. This turnover trend maintained alpha and beta diversities in the urban plots, suggesting specific species were unanimously lost or gained in the urban plots.

The high turnover found in the urban plots may suggest that urban forests are more dynamic and therefore more resilient than rural forests. It has been proposed that small isolated forest fragments may be hyper-dynamic due to high species turnover from species loss coupled with influxes of species migrating from forest edges (Laurance 2002). I suggest a similar hyper-dynamic pattern occurred in the urban plots. Higher exposure to novel species, as is common in urban areas, may allow urban forests to

maintain diversity despite deer, disease, and fire suppression. Other studies have shown that moderate levels of urbanization can facilitate biodiversity loss as well as gain (Schwartz *et al.* 2006; McKinney 2008). The ability of an ecosystem to be structurally resilient due to high amounts of turnover suggests a functional role for diversity (Folke *et al.* 2004). With the exception of saplings, biomass was more stable and biodiversity was greater within the urban plots. These results suggest that urban forests may be better able to adapt to environmental stress.

### **Review of the Experimental Design**

In plant community ecology, there has been a shift towards studies that focus on trait-based functional and phylogenetic diversity and away from composition-based studies (McGill *et al.* 2006; Kraft & Ackerly 2010; Cadotte *et al.* 2011). Such functional and phylogenetic studies have had difficulty explaining community structure due to the differential effect of ecological and evolutionary processes on phylogenetic signals (Cavender-Bares *et al.* 2009) and the phenotypic variability of traits between assemblages (Violle *et al.* 2012). I argue that there remains great value in understanding the abundance and distribution of species. Urban vegetation provides many important ecosystem services (Grove *et al.* 2006; McDonnell *et al.* 2008; Niemelä 2014), and to preserve these services, more composition-based studies are needed. For example, the filtering effects of habitat fragmentation and urban environmental conditions on the composition of plants are poorly understood (Williams *et al.* 2009).

Species composition is an integrative response variable of community assemblages (Dray *et al.* 2012) that is sensitive to local environmental conditions (Argawal *et al.* 2007). For instance, floristic data have been extremely useful in assessing



the expansion of exotic plant species in urban systems (McKinney 2006; Williams *et al.* 2009; Trentanovi *et al.* 2013). Without understanding prior species composition in a community, it is not possible to quantify the rate or direction of change. Further, it can be difficult to make distinctions between the effects of natural and anthropogenic change on species diversity and abundance, as communities naturally have different amounts of floristic variability (Margurran *et al.* 2010). To make a well-founded assessment of change within the biodiversity of a community, long-term research is needed.

Long-term plots are powerful tools for detecting change in ecological systems. Repeated sampling of an area provides unique insights that cannot be achieved through other sampling methods. For example, in this study, species turnover in the urban plots was nearly twice that of the rural plots. Turnover has important implications for the resilience of ecosystems (Allen *et al.* 2005). This insight into the dynamics of urban and rural forests would not have been found if only a single survey had been conducted. An obvious reason long-term research has not been adopted for all investigations of ecological change over time is that such research can be costly and time-consuming (Gardner *et al.* 2007). There are additional challenges for studies that have the means for long-term research. Over time, methodology changes and it can be difficult to decide whether to continue with the established long-term design or switch to a new design (Margurran *et al.* 2010).

In this study, I collected data as described in the initial 1998 survey to ensure comparability with the data previously gathered. Limitations of this design include low sample size that limits power to detect change, inconsistent methods across layers that preclude the use of robust methods for community analysis, and ambiguous methods that

increase the chance of sampling error. Going forward, I would suggest that future researchers consider adding plots to increase statistical power. By converting all measures to abundances of individuals per the appropriate unit area, consistent sampling of individual abundances can be achieved, allowing for the use of more robust methods to assess community composition (Chao *et al.* 2005). I also suggest the adoption and use of field tools that reduce the need for biased estimation and streamline data collection. For example, canopy cover could be measured using a specialized digital camera rather than visual gauge. Although future changes to the sampling design will in some ways limit the comparability of data between the new and previous studies, these changes would help ensure unambiguous collection protocols and improve data quality (Margurran *et al.* 2010).

### **Future Research**

There has been much speculation throughout this study about the effect of deer browsing on vegetation structure and composition within the plots. A further study is needed to quantify the relative effect of deer browsing in urban forests, in the manner of such studies conducted in wildland forests (Tilghman 1989; Hanberry *et al.* 2012; McGarvey *et al.* 2013). Deer browsing studies commonly use exclosure designs to determine the relative impact of deer on vegetation (Graham 1958; Horsely *et al.* 2003; McGarvey *et al.* 2013). I would suggest using a similar exclusion design, but in urban and rural sites. If deer are reducing sapling abundance and diversity in urban and rural forests, regeneration may increase if deer are excluded. Results of such a study would have the potential to provide local municipalities with valuable information on how and where to focus population control of deer and forest conservation efforts in urban areas.

Another direction of future study could explore the link between taxonomic diversity and functional traits. In my study, I found much higher species turnover in the urban plots relative to the rural plots. It would be valuable to know if the species lost and gained had any shared traits. Similar studies have compared the homogenization of species to trait convergence in temperate and tropical forests (Swenson *et al.*, 2012, Tobias & Monika 2012; Sonnier *et al.* 2014). None of these studies, however, had long-term turnover data to evaluate the dynamics of change in forested ecosystems. Using data from my study, a future project could evaluate how species turnover compares to functional turnover in urban and rural forests. Results of such research could provide novel insights into the various ways diversity can change over time and how these changes relate to species vulnerability and resilience.

## **Conclusion**

Human-induced disturbances have increasingly shaped forest communities surrounding the Chesapeake Bay since the arrival of European colonizers (Sprague *et al.* 2006; Brush 2009). The resulting decrease in frequency, extent, and magnitude of forest fires, increase in deer populations, and introduction of invasive species, pests, and pathogens have continuously altered Maryland forests. However, there is a potential difference in the magnitudes of change in urban and rural areas. In this study, I used forest structure, composition, and diversity to evaluate the relative influence of urban and rural land-use context on forest vegetation. Using long-term data, I was able to compare the dynamics of change within urban and rural plots.

Alpha diversity was lower in the rural plots as compared to the urban plots in both surveys. Since 1998, the rural plots have experienced a decline in beta diversity,

providing evidence that the community composition has homogenized within the rural plots. Structural analyses show that most of the rural understory layers have decreased in abundance since 1998. Despite a modified environment, alpha and beta diversities remained unchanged in the urban plots due to a high level of species turnover. Saplings were greatly reduced, whereas the remaining forest layers were structurally similar. In both the urban and rural plots, compositional comparisons show that shade tolerant and unpalatable species had higher retention and in some cases increased in abundance. These results suggest that deer browsing and canopy cover may be influencing species assemblages.

Species loss in the sapling layer and species turnover supported my hypothesis that compositional change would be greater in the urban plots. Contrary to my expectations, the herb and shrub layers were neither structurally altered nor highly invaded in the urban plots. I also expected to observe a decline in deciduous hardwood species and an increase in deciduous soft wood species in both the urban and rural plots. My findings generally supported this hypothesis with the exception of one anomalous hardwood species. The overall findings of this study provide evidence that urban forests may be more resilient to disturbance than rural forests. My findings suggest that the major factors influencing species abundance and distribution within the plots were deer browsing and canopy cover. Therefore, I suggest that land managers evaluate the extent of deer browsing in Baltimore area forests and implement deer population control plans. Without such measures, the structure and diversity of rural forests may continue to decline.

## Appendix 1 Species List

### TREES

#### Code

ACEPLA  
ACERUB  
AILALT  
CARCAR  
CARGLA  
CAROVA  
CARTOM  
CERCAN  
CHIVIR  
CORFLO  
FAGGRA  
FRAPEN  
LIRTUL  
NYSSYL  
PRUAVI  
PRUSER  
PRUSRL  
QUEALB  
QUECOC  
QUEMAR  
QUEMON  
QUERUB  
QUEVEL  
SASALB  
ULMRUB

#### Scientific name

*Acer platanoides* L.  
*Acer rubrum* L.  
*Ailanthus altissima* (Mill.) Swingle  
*Carpinus caroliniana* Walter  
*Carya glabra* (Mill.) Sweet  
*Carya ovata* (Mill.) K. Koch  
*Carya tomentosa* (Lam.) Nutt.  
*Cercis canadensis* L.  
*Chionanthus virginicus* L.  
*Cornus florida* L.  
*Fagus grandifolia* Ehrh.  
*Fraxinus pennsylvanica* Marshall  
*Liriodendron tulipifera* L.  
*Nyssa sylvatica* Marshall  
*Prunus avium* (L.) L.  
*Prunus serotina* Ehrh.  
*Prunus serrulata* Lindl.  
*Quercus alba* L.  
*Quercus coccinea* Münchh.  
*Quercus marilandica* Münchh.  
*Quercus montana* Willd.  
*Quercus rubra* L.  
*Quercus velutina* Lam.  
*Sassafras albidum* (Nutt.) Nees  
*Ulmus rubra* Muhl.

#### Common name

Norway maple  
Red maple  
Tree of heaven  
American hornbeam  
Pignut hickory  
Shagbark hickory  
Mockernut hickory  
Eastern redbud  
White fringetree  
Flowering dogwood  
American beech  
Green ash  
Tulip poplar  
Blackgum  
Sweet cherry  
Black cherry  
Japanese flowering cherry  
White oak  
Scarlet oak  
Blackjack oak  
Chestnut oak  
Northern red oak  
Black oak  
Sassafras  
Slippery elm

#### Plots

H2  
L1, L2, O1, O2, O3, O4, H1, H2  
H2  
O2, O4  
L1, O1, O2, O3, O4, H1  
O1, O3  
L1, L2, O1, O4, H1  
H2  
L1  
L1, L2, O1, O2, O3, H1, H2  
L1, L2, O2, H1  
H1, H2  
L1, L2, O1, O2, O3, O4, H1, H2  
L2, O1, O2, O3, O4, H1, H2  
H2  
L1, H1, H2  
H2  
L1, L2, O1, O2, O3, O4, H1, H2  
H1  
O1  
O1, O3, O4  
L1, L2, O1, O2, O4, H1  
L1, L2, O1, O2, O3, O4, H2  
L1, L2, O3  
H1, H2

### SAPLINGS

#### Code

ACEPLA

#### Scientific name

*Acer platanoides* L.

#### Common name

Norway maple

#### Plots

H2

ACERUB	<i>Acer rubrum</i> L.	Red maple	L1, L2, O1, O3, H1
AMECAN	<i>Amelanchier canadensis</i> (L.) Medik.	Canadian serviceberry	O2, O4
CARCAR	<i>Carpinus caroliniana</i> Walter	American hornbeam	O1, O4
CARGLA	<i>Carya glabra</i> (Mill.) Sweet	Pignut hickory	L2, O1, O2, O3, H1
CARTOM	<i>Carya tomentosa</i> (Lam.) Nutt.	Mockernut hickory	L2, O1, O3, H1
CHIVIR	<i>Chionanthus virginicus</i> L.	White fringetree	L1, H1
CORFLO	<i>Cornus florida</i> L.	Flowering dogwood	L2, O2, O3, H1
FAGGRA	<i>Fagus grandifolia</i> Ehrh.	American beech	L1, L2
FRAAME	<i>Fraxinus americana</i> L.	White ash	L1
FRAPEN	<i>Fraxinus pennsylvanica</i> Marshall	Green ash	L2, H1, H2
LIRTUL	<i>Liriodendron tulipifera</i> L.	Tulip poplar	O2
NYSSYL	<i>Nyssa sylvatica</i> Marshall	Blackgum	L1, L2, O1, O2, O3, O4, H1
PRUSER	<i>Prunus serotina</i> Ehrh.	Black cherry	L1, L2, H1
SASALB	<i>Sassafras albidum</i> (Nutt.) Nees	Sassafras	L2, O2
ULMRUB	<i>Ulmus rubra</i> Muhl.	Slippery elm	H1
VIBPRU	<i>Viburnum prunifolium</i> L.	Blackhaw	H1, H2

## SEEDLINGS

Code	Scientific name	Common name	Plots
ACERUB	<i>Acer rubrum</i> L.	Red maple	L1, L2, O1, O2, O3, O4, H1
AILALT	<i>Ailanthus altissima</i> (Mill.) Swingle	Tree of heaven	L1
AMEARB	<i>Amelanchier arborea</i> (Michx. f.) Fernald	Common serviceberry	O2, O4, H1
AMECAN	<i>Amelanchier canadensis</i> (L.) Medik.	Canadian serviceberry	O1, O2, O4, H1
CARCAR	<i>Carpinus caroliniana</i> Walter	American hornbeam	O2, O4
CARCOR	<i>Carya cordiformis</i> (Wangenh.) K. Koch	Bitternut hickory	L1, H2
CARGLA	<i>Carya glabra</i> (Mill.) Sweet	Pignut hickory	L1, O1, O3
CARSPP	<i>Carya</i> sp.	Hickory	L1, O2, O3, O4, H1
CARTOM	<i>Carya tomentosa</i> (Lam.) Nutt.	Mockernut hickory	L1, L2
CHIVIR	<i>Chionanthus virginicus</i> L.	White fringetree	L2
FAGGRA	<i>Fagus grandifolia</i> Ehrh.	American beech	L1, L2, O4, H1
FRAAME	<i>Fraxinus americana</i> L.	White ash	L1, O4
FRAPEN	<i>Fraxinus pennsylvanica</i> Marshall	Green ash	L1
FRASPP	<i>Fraxinus</i> sp.	Ash	L2, H1, H2
LIRTUL	<i>Liriodendron tulipifera</i> L.	Tuliptree	L1, L2, O1, O2, O3, O4, H1
NYSSYL	<i>Nyssa sylvatica</i> Marshall	Blackgum	L2, O1, O3, O4, H1, H2

PRUSER	<i>Prunus serotina</i> Ehrh.	Black cherry	L2, H1
QUEALB	<i>Quercus alba</i> L.	White oak	L1, L2, O3, H1, H2
QUEMON	<i>Quercus montana</i> Willd.	Chestnut oak	O3, O4
QUERUB	<i>Quercus rubra</i> L.	Northern red oak	L1, O4
QUEVEL	<i>Quercus velutina</i> Lam.	Black oak	O3, O4
SASALB	<i>Sassafras albidum</i> (Nutt.) Nees	Sassafras	L2, O2, O3
ULMRUB	<i>Ulmus rubra</i> Muhl.	Slippery elm	H1

## SHRUBS

Code	Scientific name	Common name	Plots
BERTHU	<i>Berberis thunbergii</i> DC.	Japanese barberry	L2, O4
EUOALT	<i>Euonymus alatus</i> (Thunb.) Siebold	Burningbush	O1, H1
EUOAME	<i>Euonymus americanus</i> L.	Bursting-heart	O1, H1
EUOSPP	<i>Euonymus</i> sp.		O1
GAYBAC	<i>Gaylussacia baccata</i> (Wangenh.) K. Koch	Black huckleberry	O4
ILEOPA	<i>Ilex opaca</i> Aiton	American holly	H1
LIGVUL	<i>Ligustrum vulgare</i> L.	European privet	H1, H2
LINBEN	<i>Lindera benzoin</i> (L.) Blume	Northern spicebush	L1, L2, H1, H2
RHOPER	<i>Rhododendron periclymenoides</i> (Michx.) Shinnars	Pink azalea	H1
ROSMUL	<i>Rosa multiflora</i> Thunb.	Multiflora rose	L1, L2, O4, H1
ROSSPP	<i>Rosaceae</i> sp.		L1, O1, O4, H1, H2
RUBFLA	<i>Rubus flagellaris</i> Willd.	Northern dewberry	H1
RUBPEN	<i>Rubus pensilvanicus</i> Poir.	Pennsylvania blackberry	L2, H1
RUBPHO	<i>Rubus phoenicolasius</i> Maxim.	Wine raspberry	L1, L2, O2, H2
VACANG	<i>Vaccinium angustifolium</i> Aiton	Lowbush blueberry	L2
VACCOR	<i>Vaccinium corymbosum</i> L.	Highbush blueberry	L2, O1, O2, O3, O4
VACPAL	<i>Vaccinium pallidum</i> Aiton	Blue Ridge blueberry	O1, O2, O3, O4
VACSPP	<i>Vaccinium</i> sp.		O4
VIBACE	<i>Viburnum acerifolium</i> L.	Mapleleaf viburnum	L1, L2, O1, O2, O3, O4
VIBDEN	<i>Viburnum dentatum</i> L.	Southern arrowwood	L2, O4, H1, H2

## VINES

Code	Scientific name	Common name	Plots
CELORB	<i>Celastrus orbiculatus</i> Thunb.	Oriental bittersweet	L1, L2, O1, O3, O4, H1, H2

DIOVIL	<i>Dioscorea villosa</i> L.	Wild yam	L1, L2, H1, H2
HEDHEL	<i>Hedera helix</i> L.	English ivy	L1, L2, H1, H2
LONJAP	<i>Lonicera japonica</i> Thunb.	Japanese honeysuckle	L1, L2, O2, O4, H1, H2
MITREP	<i>Mitchella repens</i> L.	Partridgeberry	L1, O1, O2, O4, H1, H2
PARQUI	<i>Parthenocissus quinquefolia</i> (L.) Planch.	Virginia creeper	L1, L2, O2, O3, O4, H1, H2
SMIROT	<i>Smilax rotundifolia</i> L.	Roundleaf greenbrier	O2, O4, H1, H2
TOXRAD	<i>Toxicodendron radicans</i> (L.) Kuntze	Eastern poison ivy	L1, L2, O2, O4, H1, H2
VITAES	<i>Vitis aestivalis</i> Michx.	Summer grape	L2, O1
VITRIP	<i>Vitis riparia</i> Michx.	Riverbank grape	L1, L2, O3, H1, H2
VITSPP	<i>Vitis</i> sp.	Grape	O1

## HERBS

Code	Scientific name	Common name	Plots
ALLPET	<i>Alliaria petiolata</i> (M. Bieb.) Cav.&Grande	Garlic mustard	H1, H2
ARITRI	<i>Arisaema triphyllum</i> (L.) Schott	Jack in the pulpit	L1, L2, H1, H2
ATRSP	<i>Atrichum</i> sp.	Moss	O2
BOTVIR	<i>Botrychium virginianum</i> (L.) Sw.	Rattlesnake fern	L1
CARAMP	<i>Carex amphibola</i> Steud.	Eastern narrowleaf sedge	O4
CARBLA	<i>Carex blanda</i> Dewey	Eastern woodland sedge	L1, L2
CIRLUT	<i>Circaea lutetiana</i> L.	Broadleaf enchanter's nightshade	L1, L2, H2
CONSP	<i>Convolvulaceae</i> sp.		H2
CYNVIR	<i>Cynoglossum virginianum</i> L.	Wild comfrey	O4
DESNUD	<i>Desmodium nudiflorum</i> (L.) DC.	Nakedflower ticktrefoil	L1, L2, O1, O2, O3, H2
DUCIND	<i>Duchesnea indica</i> (Andrews) Teschem.	Indian strawberry	H2
EREHIE	<i>Erechtites hieraciifolius</i> (L.) Raf. ex DC.	American burnweed	O4, H1
ERIANN	<i>Erigeron annuus</i> (L.) Pers.	Eastern daisy fleabane	O2
EURDIV	<i>Eurybia divaricate</i> (L.) G.L. Nesom	White wood aster	L1, H1
EUTPUR	<i>Eutrochium purpureum</i> (L.) E.E. Lamont	Sweetscented joe pye weed	L1, H1
FABSPP	<i>Fabaceae</i> sp.		O4
GALCIR	<i>Galium circaezans</i> Michx.	Licorice bedstraw	O1, O2, O4, H1
GERSP	<i>Geranium</i> sp.		H1
GEUCAN	<i>Geum canadense</i> Jacq.	White avens	H2
HACVIR	<i>Hackelia virginiana</i> (L.) I.M. Johnst.	Beggarslice	L1, H2
KUMSTR	<i>Kummerowia striata</i> (Thunb.) Schindl.	Japanese clover	L1
LYCVIR	<i>Lycopus virginicus</i> L.	Virginia water horehound	L2, O4
			MEDVIR



MEDVIR	<i>Medeola virginiana</i> L.	Indian cucumber	O2, O4
MICVIM	<i>Microstegium vimineum</i> (Trin.) A. Camus	Nepalese browntop	L1, L2, O2
MONUNI	<i>Monotropa uniflora</i> L.	Indianpipe	O4
NABSPP	<i>Nabalus</i> sp.		L1
PHEHEX	<i>Phegopteris hexagonoptera</i> (Michx.) Fée	Broad beechfern	L1, H2
POASPP	<i>Poaceae</i> sp.	Mayapple	O4, H1
PODPEL	<i>Podophyllum peltatum</i> L.	Oriental lady's thumb	L1, L2, O4
POLCES	<i>Polygonum cespitosum</i> Blume var. <i>longisetum</i> (Bruijn) A.N. Steward	Solomon's seal	L1, O4
POLSPP	<i>Polygonatum</i> sp.		L1
RUBPEN	<i>Rubus pubescens</i> Raf.	Dwarf red blackberry	H2
SOLCAE	<i>Solidago caesia</i> L.	Wreath goldenrod	L1, H1
THADIO	<i>Thalictrum diocicum</i> L.	Early meadow-rue	H2
UVUSES	<i>Uvularia sessilifolia</i> L.	Sessileleaf bellwort	L2, H1
VIOHIR	<i>Viola hirsutula</i> Brainerd	Southern woodland violet	O2
VIOSPP	<i>Viola</i> sp.		O1, O3, H1

Appendix 1. Plant species list organized by forest layer.

**LEGEND**

L1- Leakin 1  
L2- Leakin 2  
O1- Oregon Ridge Upslope 1  
O2- Oregon Ridge Upslope 2  
O3- Oregon Ridge Midslope 1  
O4- Oregon Ridge Midslope 2  
H1- Hillsdale 1  
H2- Hillsdale 2

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