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# Abundance and Distribution of Invasive Woody Shrub Mahonia bealei in the Metropolitan Atlanta Area

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**ABUNDANCE AND DISTRIBUTION OF INVASIVE WOODY SHRUB MAHONIA BEALEI IN THE METROPOLITAN ATLANTA AREA**

by

ADAM GREIM

Under the Direction of Lawrence Kiage, PhD

ABSTRACT

Woody invasive plants are a pernicious threat to the structure and function of ecosystems worldwide. However, due to the growing number of invasive species and the variable timeline of invasion, many invasive plants are unrecognized or underreported, leading to long-term ecological damage that is beyond the capability of cost-efficient management programs. *Mahonia bealei* is a woody shrub native to China that is invading the forests of the southeastern U.S. and is likely underreported. This study identified and mapped all occurrences of *Mahonia bealei* across 40 woodlots throughout DeKalb County, Georgia, and analyzed vital indicators in the habitats that may promote colonization and establishment. *M. bealei* was found in 90% of sample sites, frequently in large numbers within the forest interior. The high abundance of *M. bealei* combined with success in low-light environments indicates an aggressive and successful long-term invasion of the Southeastern Piedmont.

INDEX WORDS: Invasive species, *Mahonia bealei*, low-resource, woody, Piedmont, Georgia.

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ADAM GREIM

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| | |
|---|---|
| ALIPC | Alabama Invasive Plant Council |
| DCR | Department of Conservation |
| EDDMS | Early Detection and Distribution Mapping System |
| GAEPPC | Georgia Exotic Pest Plant Council |
| GIS | Geographic Information System |
| GPS | Global Positioning System |
| NAD | North American Datum |
| NCIPC | North Carolina Invasive Plant Council |
| KYEPPC | Kentucky Exotic Pest Plant Council |
| SCEPPC | South Carolina Exotic Pest Plant Council |
| TNIPC | Tennessee Invasive Plant Council |

# 1 INTRODUCTION

Biological invasions are a global phenomenon with consequences ranging from the endangerment of native ecosystems and biodiversity to wide-scale alteration of ecosystem services, including agriculture, forestry, nutrient cycling, water resources, pollination, recreation, and others (Castro-Diez et al. 2019; Downey and Richardson 2016; Lapin et al. 2019; Pejchar et al. 2009; Potgieter et al. 2018; Pyŝek et al. 2012; Vaz et al. 2019). Frequency of biological invasions have increased exponentially and are projected to continue rising as international trade grows and intensifies (Jean-Nicolas et al. 2017; Rejmanek 2014). Estimates of economic damages resulting from invasive species vary greatly due to the lack of a systemic empirical method of estimation, but figures in the U.S. range from $131 billion cumulatively to $128 billion annually (Pejchar et al. 2009). Biological invasions are widely considered to be the second most significant threat to biodiversity after habitat destruction, with many impacts still unknown (Simberloff et al. 2013).

Invasive plants constitute a major component of these impacts, but historically most research has been directed toward non-woody plants such as terrestrial grasses and aquatic vegetation (Webster et al. 2006). However, woody invaders, i.e. trees and shrubs, are increasingly recognized as a pernicious threat that is profoundly altering ecosystem structures throughout the world. The majority of invasive woody plants were introduced intentionally for horticulture or agroforestry, eventually establishing themselves in their new environment by virtue of the very traits that made them attractive (Richardson and Rejmanek 2011). *Mahonia bealei*, also known as leatherleaf mahonia, originates from China like many invasive plant species in the U.S. Southeast and has rapidly expanded its range after many years of relative quiet (Allen et al.

2006). As it continues its aggressive expansion, there is an increased need for documentation of its occurrence and research of its impacts on native ecosystems.

### 1.1 Impacts of Invasive Plants

When a species progresses from non-native to naturalized and finally to invasive is a matter of some debate. The Georgia Exotic Pest Plant Council (GAEPPC) defines an invasive plant species as "…any species, including its seeds, spores or other biological material capable of propagating that species, that is not native to that ecosystem; and whose introduction does or is likely to cause environmental harm" (GAEPPC 2018). Invasive plants can devastate native communities by reducing species richness and abundance, altering the genetic flow through hybridization, disrupting mutualisms such as pollination and dispersal, deteriorating the habitat through allelopathy, and fundamentally changing ecosystem structure and habitat (Downey and Richardson 2016; Pyŝek et al. 2012). They may also serve as a host and dispersal unit for other invasive species, including pathogens.

Environmental harm extends to the human sphere in the form of ecosystem service degradation, which by definition are services provided to humanity from the environment (de Groot et al. 2012). Changes in ecosystem function can lead to the loss or alteration of provisional ecosystem services such as agricultural and forest products, and regulating/recreational ecosystem services including water management (such as clean drinking water), climate stabilization (in the form of carbon sequestration), pollination of crops, pest control, erosion control, and culture/recreation (Pejchar et al. 2009; Liebhold et al. 2017). Often these potential threats will conflict with a plant's utility as an intentionally introduced resource (Richardson and Rejmanek 2011). These conflicts can be economic or cultural in nature; for example, California is thoroughly populated with invasive eucalyptus trees, which have dramatically altered native ecosystems and significantly contribute to wildfire hazard risk, but they have also become a cultural California icon (Simberloff et al. 2013). South Africa has a large number of intentionally introduced *Pinus* and *Acacia* tree species for economic production but has reckoned with the unforeseen consequences of groundwater depletion and the deterioration of grazing resources (Dickie et al. 2014). The total economic impact of invasive plants on ecosystem services has been called the "invisible tax" since it is not often included in the decision-making processes of policy (Pejchar et al. 2009).

## 1.2 Invasive Woody Plant Species

Invasive woody plants, in particular, are part of a larger invasive structure composed of other plant species as well as insects and diseases that alter the composition of native habitat (Webster et al. 2006). While long documented as alien in a number of environments, woody plants are only recently considered to be important invasive species and are now recognized among the most widespread and damaging of invasive organisms (Richardson and Rejmanek 2011). Indeed, 21 woody plant species are on the list of "100 of the World's Worst Invaders (Lowe et al. 2000; Rejmanek 2014). An updated database in 2014 records a total of 751 invasive woody plants, including 434 trees and 317 shrubs from 90 families (Rejmanek 2014). The regions that have been invaded by the most species of trees are the Pacific Islands (136 species), Southern Africa (118), Australia (116), and North America (98). Invasive shrub species are most numerous in North America (98), Australia (87), the Pacific Islands (71), and Europe (61). The sources of invasive trees are largely from Asia (122-146, depending on origination within Eurasia), Australia (81), and South America (81), whereas invasive shrubs originate from Asia

(103-118), Europe (68), and South America (54) (Rejmanek 2014). It should be noted that this inventory includes only plants documented as clearly invasive, as opposed to merely naturalized or present only in highly disturbed areas. Most of these plants were intentionally introduced, primarily as horticulture (62% of documented species), and to lesser extent forestry (13%), food (10%), and agroforestry (7%) (Richardson and Rejmanek 2011).

### 1.3 The Role of Horticulture

Horticulture undoubtedly plays a pivotal role in the introduction and dissemination of invasive plants. A remarkable 77% of all invasive woody plants in North America were introduced for horticulture, usually with minimal scrutiny concerning their environmental risks (Richardson and Rejmanek 2011). Numerous physiological traits that are prized by horticulturalists, such as ornamental displays of abundant fruit and a general resilience and adaptability, are excellent traits for an organism seeking to establish itself in a new environment. Furthermore, non-native plants are often genetically enhanced through selective breeding, additionally increasing their biological fitness. These plants are cultivated and protected from predation and other environmental threats, which provide them the opportunity to reach maturity and accumulate large stores of propagules. Cultivation typically occurs in nurseries, which are scattered across a landscape of fragmented natural habitat within an urban matrix (Richardson and Rejmanek 2011; Liebhold et al. 2017). Successful invasions will usually proceed from many smaller foci rather than a single large one, and nurseries along with residential plantings provide these, functioning as an ideal launch pad for dissemination and widespread colonization (Bartuszevige et al. 2006; Mack et al., 2000).

## 1.4 Competitive Advantages of Invasive Plants

Non-native plants that become invasive tend to share distinct physiological characteristics that provide a competitive advantage over native plants (van Kleunen et al. 2010). These can include a superior photosynthesis efficiency, water use efficiency, nitrogen use efficiency, faster growth rate, higher reproductive output, an ability to form homogenous stands to the exclusion of others, animal-dispersed seeds which promote widespread dispersal, and an overall hardiness and adaptability (Nunez-Mir et al. 2019; Rejmanek 2014; Webster et al. 2006). Notably, woody invasive plants from Asia have been found to be more successful in the United States than species introduced from North America to Asia in part due to their extended seasonal leaf phenology, enabling them to take better advantage of the growing season (Rejmanek 2014). Furthermore, plants outside of their native range experience less herbivory, described as the "enemy-release" hypothesis (van Kleunen et al. 2010).

Many plants, particularly shrubs, have the additional benefit of being aided in their dispersal by birds. Over 60% of invasive shrubs are bird dispersed, and long-distance dispersal events exponentially raise the likelihood and rate of successful expansion (Bonilla and Pringle 2015; Gosper et al. 2005; Nunez-Mir et al. 2019; Rojas et al. 2019). Invasive shrubs are more likely to have large stores of fruit, which attract birds, creating a mutualism between the birds and the invasive plants that facilitates the expansion. Birds may shift their foraging patterns to capitalize on the fruits of invasive plants, creating a positive feedback loop. This may occur at the expense of native plants, which would be negatively affected by the decrease in avian dispersal. Gosper et al. 2005 found that smaller seeds (< 15 mm) are more likely to be dispersed, and plants with more fruit production, i.e. large stores of propagules, experienced greater dispersal. In some instances, dispersal of invasive species is aided by non-native frugivorous avian species as was recently highlighted in New Caledonia (Thibault et al. 2018). A conspicuous display of fruit enhances the rate of dissemination, and non-native plants were often intentionally introduced to new regions because of this aesthetic property. The timing and longevity of invasive plant fruit production may influence the behavior of dispersers, which capitalize on enhanced fruit abundance or take advantage of early and/or late seasonal fruit. Disturbed habitats such as the forest gaps and edges of fragmented landscapes are especially amenable to invasive species and tend to have more rapid removal of fruits (Gosper et al. 2005).

### 1.5 Phases of Invasion

Biological invasions go through four spatiotemporal phases which are non-discrete and dependent upon the invasive species and environmental factors of the affected landscape. The temporal component of these phases plays an important role in the recognition and management of invasive species, which must occur in the early stages if the most damaging effects of invasion are to be avoided.

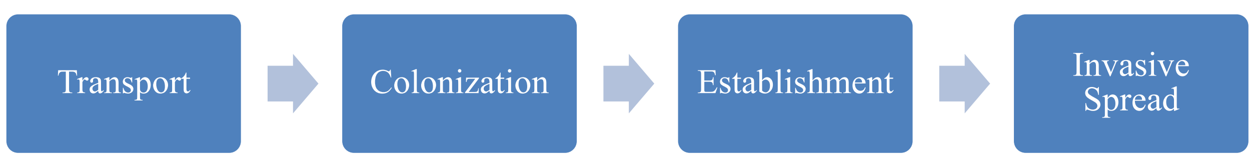



*Figure 1 Stages of invasion in simplified form*

Belying the reality of a nascent invasion is the common occurrence of a “lag-phase” (Figure 2), which occurs between establishment and invasive spread when small populations of non-native species adapt to their new environment (Theoharides and Dukes 2007). During this time a species is deemed unproblematic but may merely be awaiting environmental conditions that preclude a rapid, if not exponential, population increase (With 2004; Hobbs and Humphries 1995) (Figure 2.5.1). Documented lag phases generally last multiple decades, but are highly variable; for example, *Abultilon theophrasti*, commonly known as velvetleaf, was first introduced prior to 1700 in the United States, but only recently became an aggressive invader (Theoharides and Dukes 2007). The aggressively invasive plants of 2050 are currently being nurtured and unknowingly primed for exponential growth.

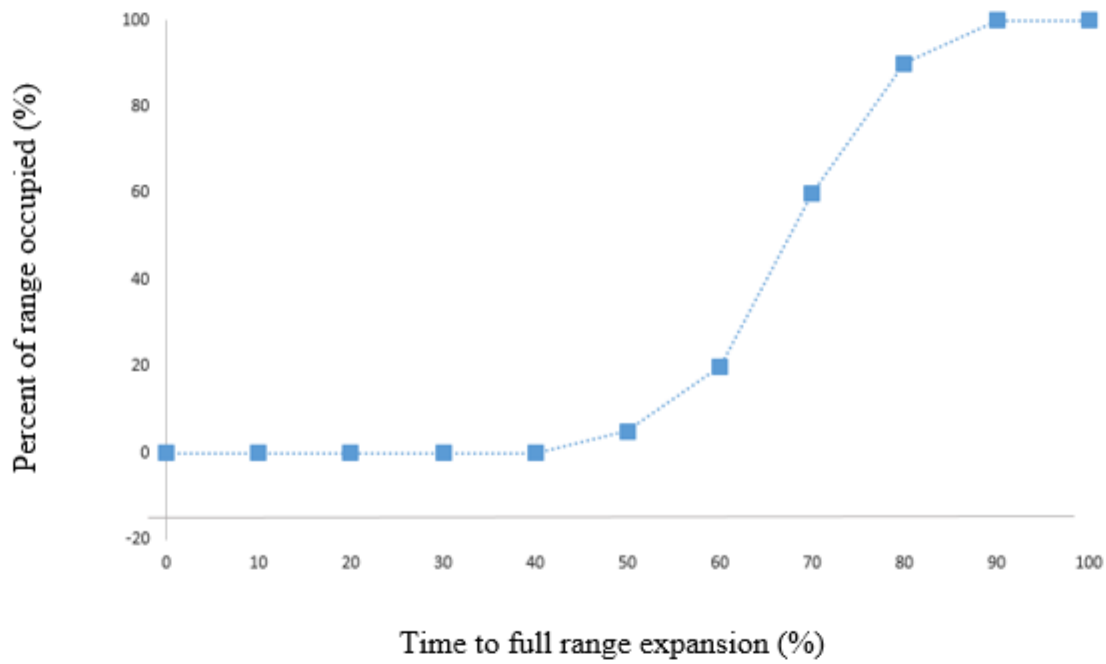



*Figure 2 Lag phase - typical establishment curve of invasive plants (simplified from Hobbs and Humphries 1995). A species' invasive status may be unknown until a large percent of available range is occupied, at which point management is costly or impossible.*

### 1.6 Simultaneous Invasions

The majority of prior studies have taken a single-species approach on the effects of invasive plants on native species and generally concluded that invasive plants do not directly cause native extinctions. These determinations are likely premature and do not consider the complex temporal and non-linear aspects of extinction trajectories and the thresholds at which they occur (Figure 2.6.1). 43% of native plant species are threatened by more than one invasive plant, and in certain circumstances, more than ten invasive species. The thresholds that determine native plant vulnerability vary considerably – in some cases, invasive plants that cover as little as 15% to 20% of a local area cause reduction in native species density, and the risk of

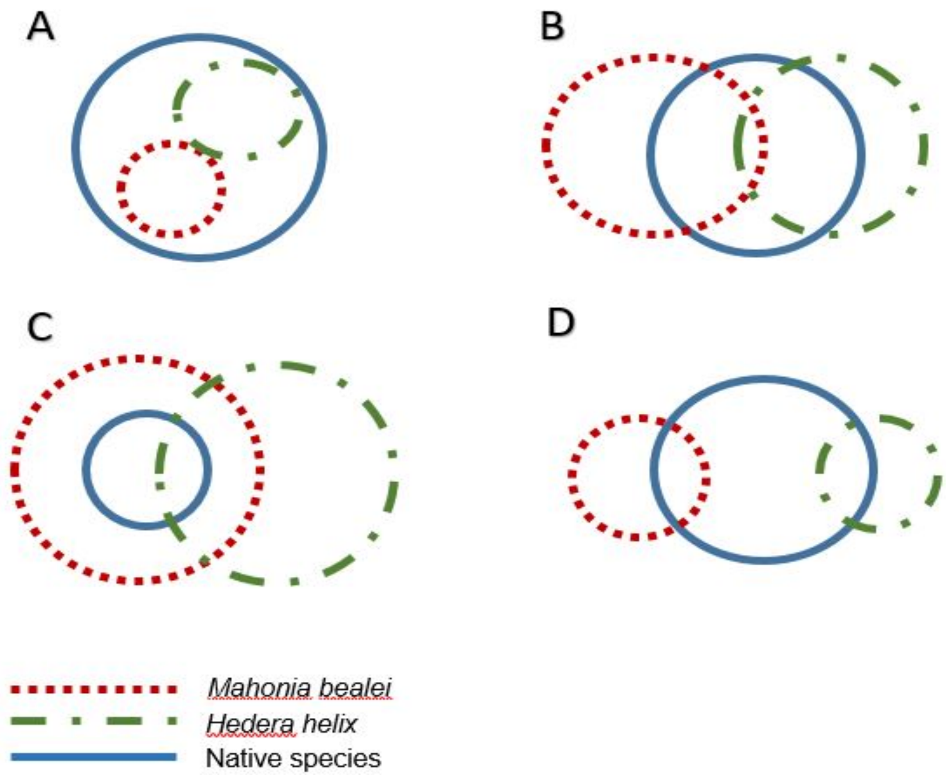



*Figure 3 Possible distributions of native species (solid line) and coinciding invasive species* Mahonia bealei *and* Hedera helix *(dotted lines).*

further reductions increase with the duration of the invasion. The cumulative effect of multiple invasive species, while not likely to cause the extinction of a widespread native species, may cause local extirpations or significant population declines of varying chronology. Long term data is largely absent, and the most sensitive species may be eliminated long before the responsible invasion is documented, creating a sampling bias that underrepresents the ecological deterioration (Downey and Richardson 2016).

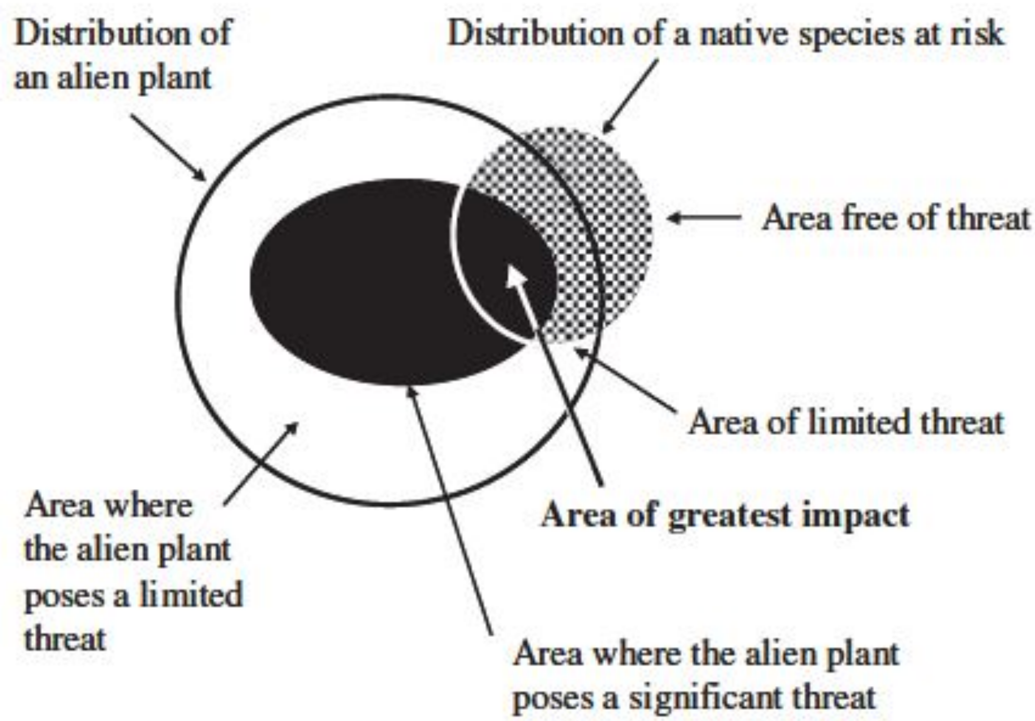



*Figure 4 Potential area of greatest threat to native species. Effects of invasive species are highly specific to individual species, with the magnitude of threat dependent on the extent of conflict in space or resources (Downey and Richardson 2016).*

## 1.7 The Southern Piedmont and the Role of Landscape in Invasion Success

Metropolitan Atlanta is in the larger physiographic region of the Southern Piedmont, a forested region between the Atlantic coastal plain and the Appalachian Mountains. The Piedmont is characterized by rapid urbanization resulting in increased habitat destruction and landscape fragmentation, leaving behind a large proportion of edge habitat relative to undisturbed forests (Allen et al. 2006). Edge habitat is characterized by high levels of environmental disturbance (Figure 2.7.1), especially in urbanizing areas, and are universally recognized as being strongly correlated with increased invasive species density and invasion success (Allen et al. 2006; Vilà and Ibáñez 2011). Recruitment and colonization have the highest chance of success when more than 20% of the landscape has been disturbed, as is typical of urban sprawl (With 2004). The highly tolerant and adaptable plant species that become invasive often take advantage of corridors where disturbance is more common. These corridors include roads and edges of developing areas, although natural features such as creeks and rivers are also known to have a higher proportion of naturalized species (Duguay et al. 2007; Pennington et al. 2010). The corridors serve as conduits for dispersion and have greater resource availability, primarily sunlight (Dillon et al. 2018). The most successful invaders in the southern Piedmont include kudzu (*Pueraria montana*), tree-of-heaven (*Ailanthus altissima*), Chinese wisteria (*Wisteria sinesis*), Japanese honeysuckle (*Lonicera japonica*), and others, often in competition for the same space.

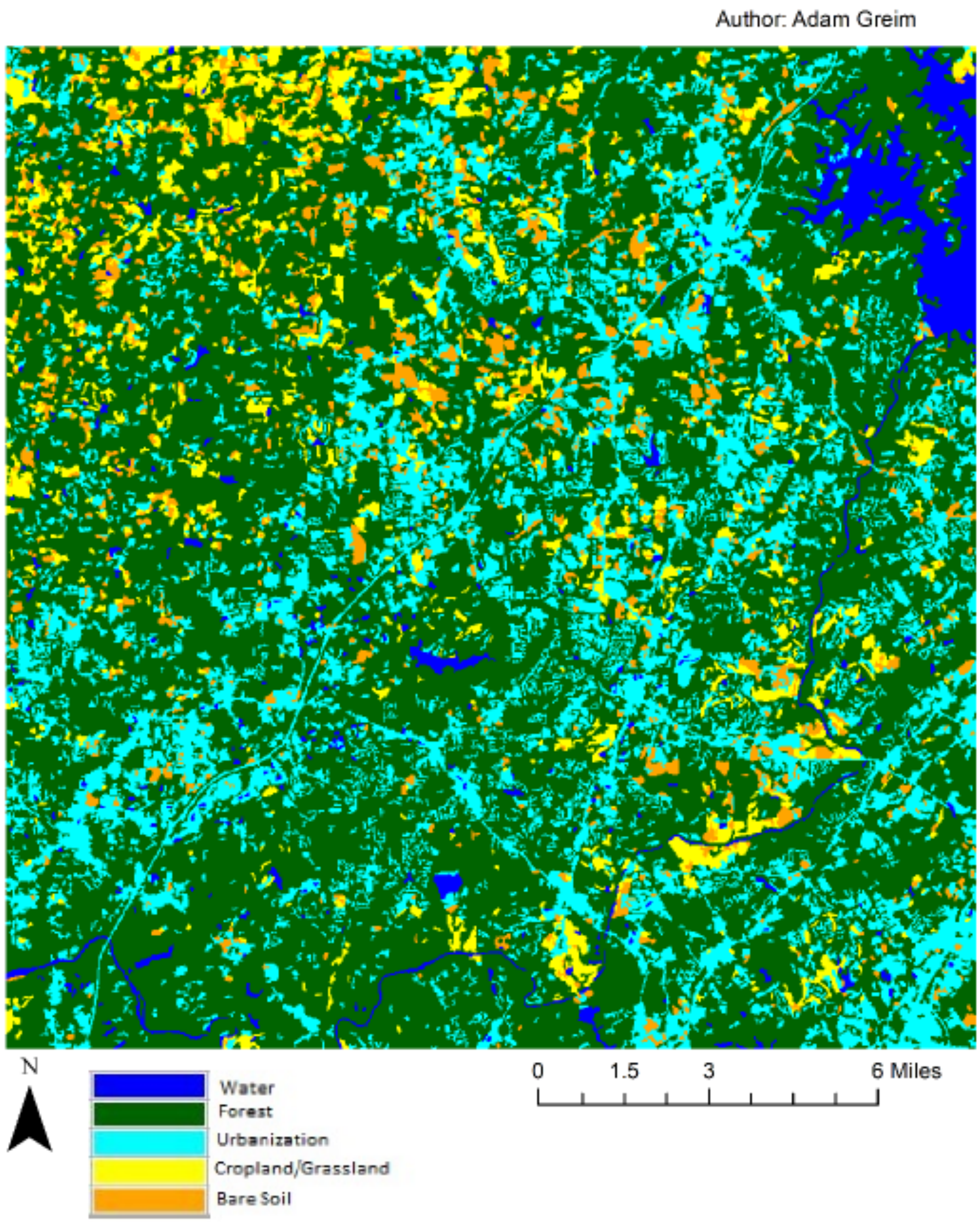



*Figure 5 Land cover analysis of a section of Metropolitan Atlanta*

## 1.8 Urban Forests

Forest fragments within an urban landscape, such as those that define the Atlanta metropolitan region, have more introduced plant species than other types of landscapes, as well as higher proportions of introduced species compared to native communities (Duguay et al. 2007; Hawthorne et al. 2015; Pennington et al. 2010). Urban forest fragments are important refuges for native biodiversity and are typically the last significant remaining areas of natural habitat in the immediate region. Mature forests may have greater biotic resistance thanks to greater biodiversity, and this in turn supports herbivores that suppress invader population (Dillon et al. 2018; Liebhold et al. 2017). However, they may also act as stepping stones for both invasive species and non-native species that are in the lag phase of invasion (Hawthorne et al. 2015). The greater the fragmentation, which results in smaller and more isolated patches, and the longer period of time they have been fragmented, the greater the extinction rate of native flora (Downey and Richardson 2016). With (2004) concluded that there is likely a threshold of disturbance above which invasion is much more likely, and also a threshold of biodiversity above which invasion is much less likely. In a particular ecosystem, there may be a critical biodiversity threshold, when the introduction of a single additional species can result in "a cascade of extinctions among indigenous species." Thus, urban forests maintain a balance between their ecological value and their role in the success of colonization and spread of non-native species.

## 1.9 Invasions in Low-Resource Environments

Most focus on invasive ecology has been on early successional traits as the predicator of invasion success, leading to conclusions that closed-canopy forests are especially resistant to invasion (Martin et al. 2009). However, recent research indicates that resource efficiency traits more typical of late successional species allows non-native plants to invade low-resource environments, especially those found in the interior of the deciduous forests of eastern North America (Martin et al. 2010; Liebhold et al. 2017). Invasive plants exhibit greater photosynthetic energy-use efficiency and marginally greater photosynthetic nitrogen use efficiency, the extent of which is magnified over the duration of leaf lifespan (Heberling and Fridley, 2013). This essentially amounts to greater productivity per unit leaf investment and is especially pronounced for invasive woody species such as *Mahonia bealei* from central and east Asia that are able to make greater relative carbon gains in autumn, capitalizing on a temporal niche that native species have not utilized. Funk and Vitousek (2007) found that across a broad taxonomic spectrum, invasive plants are more efficient in carbon assimilation per unit of resource and often have thicker leaves with a longer leaf lifespan than the native community.

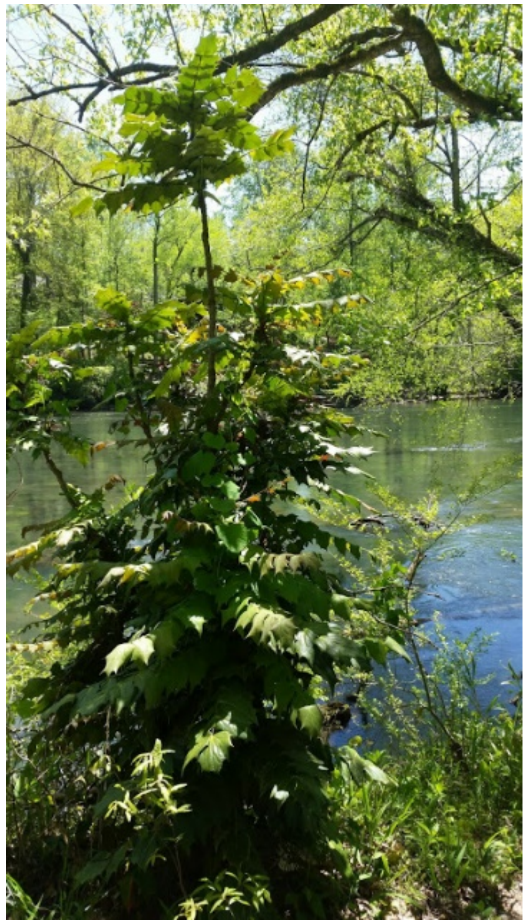


*Figure 6 Mahonia bealei in Chattahoochee National Recreation Area*

### *1.10 Mahonia bealei*

*Mahonia bealei*, also known as leatherleaf mahonia, from the family Berberidaceae, originates from the temperate region of east China and is an established ornamental in the Southeastern United States. A clonal shrub, *M. bealei* can grow up to four meters tall and one to two meters wide in a multi-stem structure, with pinnately compound spiny leaflets (Allen et al. 2006). The flowers are bright yellow, and it has large and plentiful blue berries that remain throughout the summer, both of which account for its popularity as an ornamental, although it also has utility in landscaping as a barrier plant due to its spiny evergreen leaflets. The flowers attract pollinators and the fruit is popular with birds and potentially other fauna, which serve as the primary dispersal mechanism. *M. bealei* fruits in winter, and in early spring bird activity increases; hence, *M. bealei* may have a competitive edge against most native shrubs which have yet to produce fruit. It prefers moderately moist, well-drained soil in partial to full shade, but it is tolerant of drought, dense clay soils, and full sun, making *M. bealei* a fairly adaptable species.

The invasive categorization of *Mahonia bealei* is hazy, with each respective Exotic Pest Plant Council (EPPC) per state (or equivalent) using a different categorization system. In the Southeast, states have somewhat conflicting recommendations, with Virginia and Florida not listing *M. bealei* as invasive at all, South Carolina listing it as “Alert” (the lowest level threat out of four, citing a need for “more distribution information”), Tennessee listing it as “Emerging” (rather than Established), Kentucky listing it as a “Moderate” threat (second lowest threat level out of four), and Alabama with the most cautious classification (Category 2 out of 3), but with no recommended management strategies (Virginia Department of Conservation and Recreation 2014, South Carolina Environmental Pest Plant Council 2014, Tennessee Invasive Plant Council 2018, Kentucky Environmental Pest Plant Council 2013, Alabama Invasive Plant Council 2007, North Carolina Invasive Plant Council 2019). In Georgia, it is categorized by the GAEPPC as a Category 3 invasive (on a scale of 1 to 4, the latter being the least severe), i.e. an “exotic plant that is a minor problem in Georgia natural areas, or is not yet known to be a problem in Georgia but is known to be a problem in adjacent states” (GAEPPC 2018) (Table 2.10.1).

*Table 1 Number of Invasive Plants by Category per the Georgia Exotic Pest Plant Council (GAEPPC 2018)*

| Category | Number of species |
|---|---|
| 1 | 20 |
| 1 Alert | 8 |
| 2 | 31 |
| 3 | 49 |
| 4 | 42 |

**Category 1** - Exotic plant that is a serious problem in Georgia natural areas by extensively invading native plant communities and displacing native species. (e.g. kudzu, Chinese privet).

**Category 1 Alert** - Exotic plant that is a not yet a serious problem in Georgia natural areas, but that has significant potential to become a serious problem.

**Category 2** - Exotic plant that is a moderate problem in Georgia natural areas through invading native plant communities and displacing native species, but to a lesser degree than category 1 species.

**Category 3** - Exotic plant that is a minor problem in Georgia natural areas, or is not yet known to be a problem in Georgia but is known to be a problem in adjacent states.

**Category 4** - Exotic plant that is naturalized in Georgia but generally does not pose a problem in Georgia natural areas or a potentially invasive plant in need of additional information to determine its true status.

### 1.11 Previous Studies of *Mahonia bealei* Occurrence in the Southeast and Analogs

A 2006 study in suburban areas in South Carolina randomly sampled 15 woodlots (defined as "forest islands embedded within an urban matrix") to assess the invasion of *M. bealei* and found that 87% of the woodlots surveyed had been invaded (Allen et al. 2006). The occurrence of *M. bealei* at the 15 sites ranged from 0 to 291 individuals, with a mean of 47 and a median of 14, and notably, individuals were not restricted to the edge of the woodlots but were found up to 61 meters in the forest interior. This dispersal pattern indicates that *M. bealei* not only capitalizes on disturbed areas for establishment but also that disturbed areas serve as conduits for invasion deep into natural habitats, where it can flourish and displace native plants. By estimating the age of the plants, Allen et al. 2006 was able to gauge the intensity of the invasion and determined that rapid population growth can be expected, and the invasion was in the early stages of aggressive expansion.

A 2012 comprehensive vascular plant inventory of several parks adjacent to metro Atlanta's Chattachoochee River found few occurrences of *M. bealei*, all of which were in disturbed areas, and categorized the species as "rare", in agreement with GAEPPC's Category 3 status (Zomlefer et al. 2012) (Figure 2.11.1).

*Figure 7* Mahonia bealei *with fruit partially eaten by birds. Birds provide* M. bealei *with long-distance dispersal opportunities that greatly increase chances of new colonies, creating multiple foci that create successful invasion.*

Additional studies of close relatives of *M. bealei* indicate similar invasive abilities. *Mahonia aquifolium*, native to the western United States and widely invasive in Europe, grew larger in terms of stem length, number of leaves, and above-ground biomass than either of the two native European *Mahonia* species. Ross et al. 2009 determined that the selection of breeders as well as intentional hybridization have led to enhanced physiological fitness, a situation markedly similar to *M. bealei* in the U.S. Another shrub, *Berberis thunbergii*, also a member of Berberidacaeae, native to Japan and East Asia, is a well-documented invader of eastern U.S. forests (Ehrenfeld 1997).

### 1.12 Current Documentation

Currently, there is a distinct lack of documentation of *M. bealei* in Georgia. Various county governments and state government organizations have, at most, recorded it as being present in the area, and most local resource management agencies do not specifically recommend removal, instead directing resources toward the removal of better documented invasive species, i.e. Categories 1, 1 Alert, and 2, per the GAEPPC. Mapping of *M. bealei* by any centralized authority does not currently exist – the only documentation of its occurrence is through crowd-sourced applications, primarily Early Detection and Distribution Mapping System (EDDMS), a University of Georgia-developed online platform that allows the public to record instances of invasive plants with GPS coordinates and pictures, which are then verified by an official naturalist. A less reliable but more popular platform is iNaturalist, a broad application that allows the public to record instances of any animal or plant species, with no regard for invasion status, and little to no review process. During a five-month period in 2019, observations in Georgia on iNaturalist increased 213%, from 82 in May to 175 in October. In the same period, observations on EDDMS increased has 258%, from 24 verified sightings to 62 (iNaturalist.org, eddmaps.org).

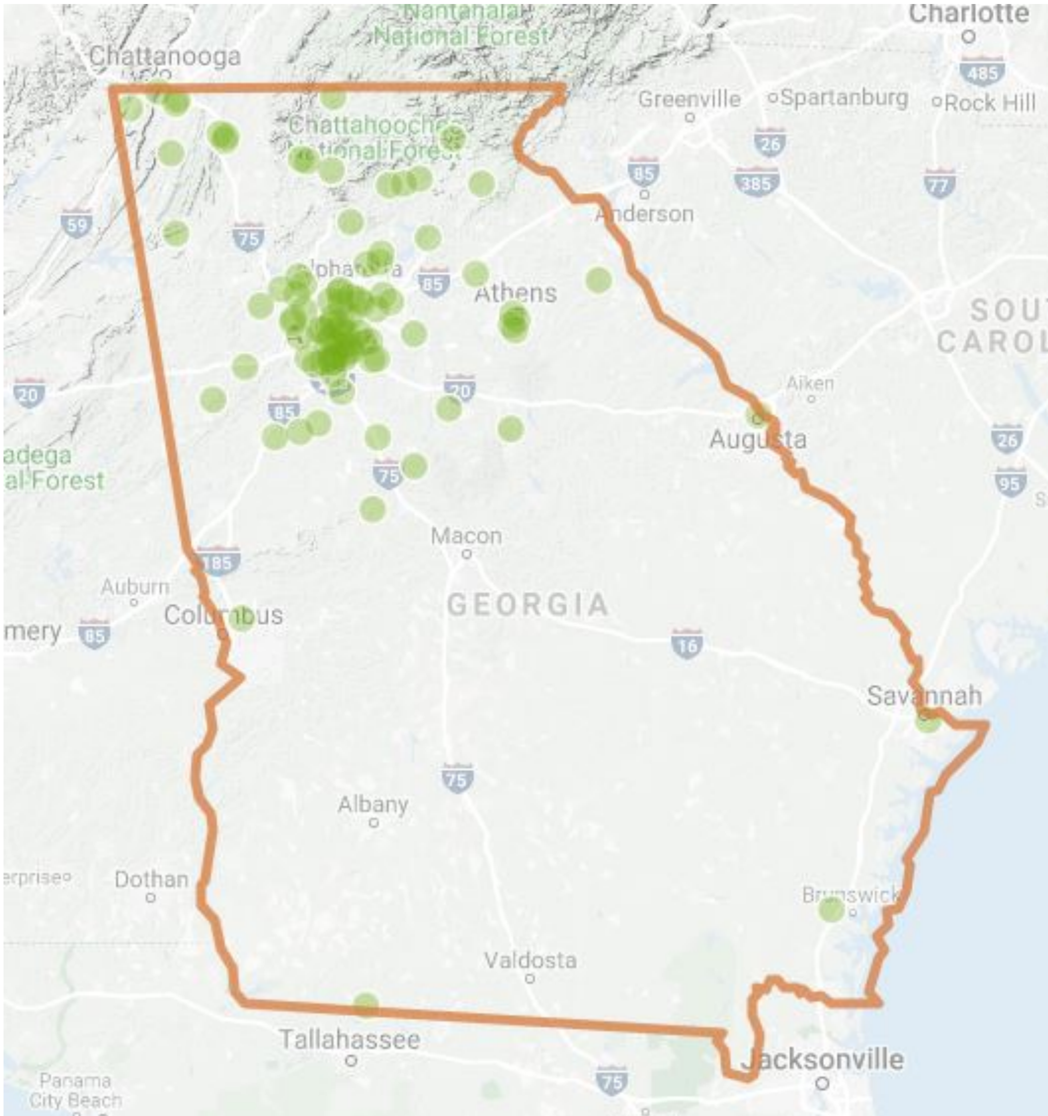



*Figure 8 Observations of M. bealei total 175 on iNaturalist, October 2019 (iNaturalist.org)*

### 1.13 Study Objective

The few existing studies of *M. bealei* and its close relatives' invasion potential indicate that there is a significant risk of rapid and widespread invasion. There cannot be an effective invasive species management strategy without sufficient documentation of the extent and intensity of the invasion. The costs associated with invasive plant management rise enormously with widespread occurrence, therefore the optimal time to manage or eradicate invasive plants is as soon as their invasive status is recognized. Such management efforts are largely done by a variety of natural resource agencies with limited funds, therefore prudent allocation of resources is imperative for the mitigation or eradication of invasive plants. Robust documentation of the occurrence *Mahonia bealei* would allow local, state, and national groups to effectively prioritize their invasive species management, and also provide useful data to contribute to the understanding of the status and implications of invasive plants on a regional and global level on our changing planet. The goal of this study is to investigate the spread of *Mahonia bealei* in forest fragments that define the urbanizing landscapes of the physiographic region of the Southern Piedmont of Georgia. The study will also seek to provide possible mitigation strategies for control of woody invasive species based on best management practices. This study intends to answer the questions:

1. How abundant and widespread is *Mahonia bealei* in the metropolitan Atlanta area?
2. What pattern of invasion does it display?
3. Which vegetation communities are most vulnerable to invasion by *Mahonia bealei*?
4. What mitigation measures could be adopted to tame the spread of *Mahonia bealei*?

# 2 METHODS

## 2.1 Sample Site Selection

Forty woodlots were randomly selected from a database containing 364 GPS coordinates within accessible woodlots located within the limits of DeKalb County, Georgia, USA. DeKalb County is one of the twelve counties that compose Metropolitan Atlanta, roughly 8,000 square miles of north Georgia. Many areas of the county are developing rapidly and exhibit the ecological effects of recently fragmented forests, and others are fairly stable suburbs that contain protected green spaces including parks and urban forests. DeKalb County contains every major forest type that is found in the region (primarily oak-pine-hickory, pine-oak, and mesic forests) amid a wide spectrum of urbanization density. The selection of forty woodlots ensured an accurate sample of the urbanizing southern Piedmont with a population that provided statistical robustness, producing results that can be extrapolated across the region as a whole.

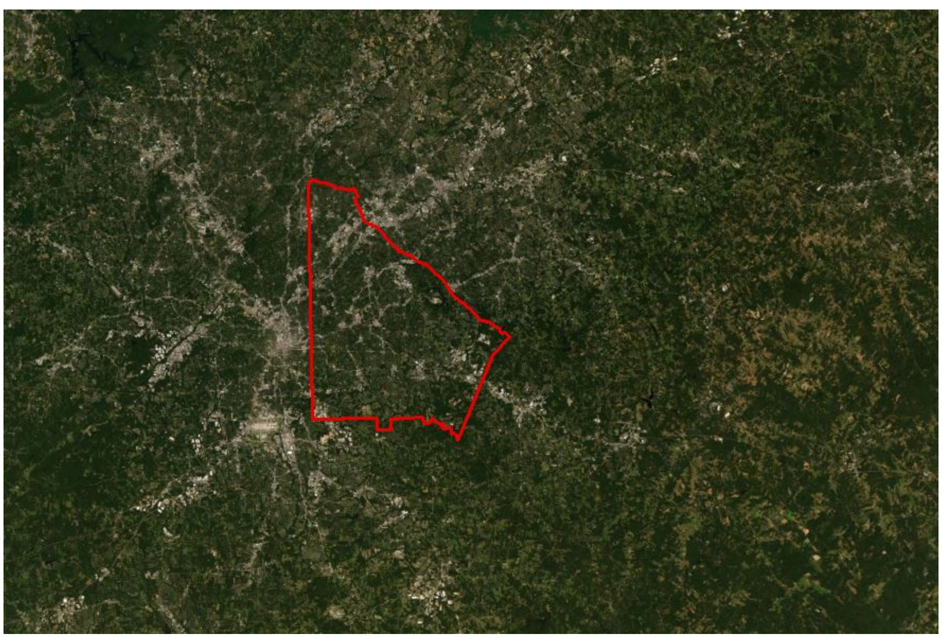


*Figure 9 DeKalb County within the Atlanta Metropolitan area.*

Woodlots are essentially forest islands, defined as fragments of native forest habitat that are predominantly surrounded by non-forest habitat, such as infrastructure (roads, buildings, other impervious areas), fields (agricultural and recreational), water bodies, and bare soil (typically lots under development). Lot size was determined by using Esri's ArcGIS 10.6 with a combination of the available World Imagery (2017) and Open Streetmap basemaps in the NAD 1983 StatePlane Georgia West (Meters) projection. Due to the fragmented and *ad-hoc* nature of regional planning in DeKalb County, the shape of each woodlot is generally irregular, and was measured to include all substantial forest land, while excluding landscaped areas such as residential backyards. Narrow lobes of tree canopy (~ 5 to 15 meters) that branched off significantly from the mass of the woodlot were not included in the measurement.

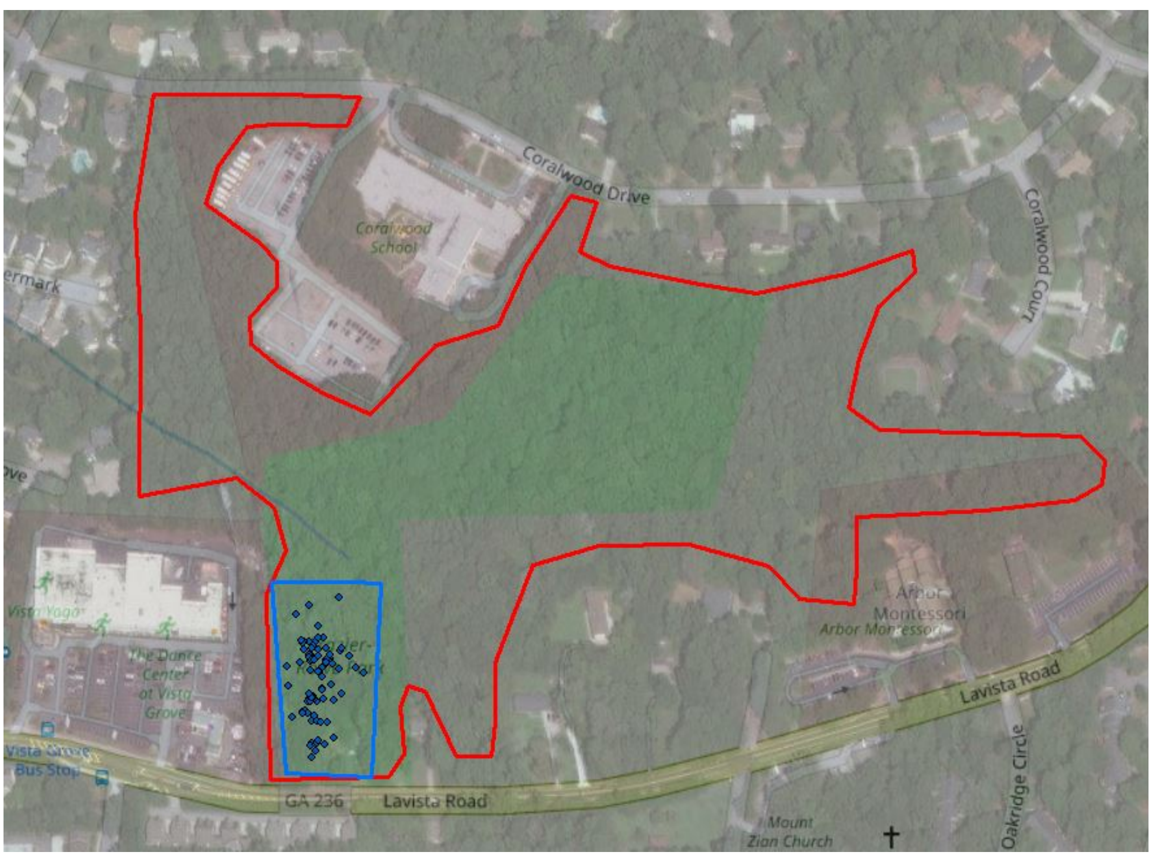



*Figure 10 Example of sample site and encompassing woodlot (Frazier Rowe Park)*

The sample sites within each woodlot were chosen primarily in regard to edge inclusion, accessibility, and ease of measurement. Typically, the perimeter of a sample site was established by measuring the length of the edge of any non-forested area, such as a parking lot, football field, paved walking trail, or creek, using either a 90 m tape measure or pacing off an appropriate distance. Once the initial side of the site polygon was established, the remaining sides were estimated within the forest interior, using natural edges such as streams or walking trails where possible. When needed, as in areas with a thick understory, orange flagging was tied to trees to demarcate the site area. The sample site area varied from 3,631 to 8,901 $m^2$ – an estimation gleaned from GIS measurement.

## 2.2 Variables

In addition to the primary factor of abundance, three secondary variables were included through observation – disturbance, ground cover, and canopy cover. Each was evaluated using a 1 to 5-point scale, with 5 being the most intense.

Disturbance was assessed on observed primarily on anthropogenic disturbance, past and present. This included the presence and proximity of extensively trafficked roads and any trails or other signs of regular human presence within the park, such as the number of trails and their perceived amount of use (paved or dirt), evidence of park maintenance, and discarded trash or intentional dumping sites. Evidence of hydrological disturbance, common in urbanizing areas with a high proportion of impermeable surface area including erosion, scouring, waterlines, and sediment deposition, was also factored as disturbance. A sample site with a score of 5 in disturbance, for instance, may be adjacent to a busy road or railroad, may be intersected with several footpaths, and may be subjected to higher levels of noise and wind.

Ground cover was assessed by the extent of the herbaceous layer, including grasses, herbs, and woody vines.  Ground cover throughout the site often varied considerably by density, and was averaged out to give a general estimation.  Both the coverage and the dominant species was observed.  All forests in the Piedmont contain an herbaceous layer of some kind, therefore a 1 on the scale indicates ground coverage that would be found in the bottom quintile of sample sites, and a 5 would be in the upper quintile and characterized by a heavy herbaceous layer that virtually covers the entire sample site.

Canopy was assessed by both the extent of observed canopy coverage in the growing season and shade as a function of canopy coverage including any present understory.  As all sites were located within woodlots, a score of 1 amounted to canopy coverage of roughly 60%+, with a score of 5 amounting to 95%+.

### 2.3 Data Collection

Between May and September 2019, information was collected on the invasion of *Mahonia bealei* by surveying each of the 40 sample sites, and using a Garmin GPS 60CSx to create waypoints of each occurrence found.  Each waypoint consisted of latitude and longitude coordinates, elevation, and time of collection.  The GPS coordinates were then uploaded and mapped into GIS, and the woodlots and sample sites were also mapped.  The seven variables (Abundance, Elevation, Ground Cover, Disturbance, Canopy, Size of Sample Site, and Woodlot Size), were then tested for bivariate correlation.

| ID | lat | lon | Elevation | Location | cmt |
|---|---|---|---|---|---|
| 1 | 33.75255221 | -84.28580213 | 295.9693604 | Dearborn Park | 17-MAY-19 4:55:16PM |
| 2 | 33.75255522 | -84.28588998 | 302.9388428 | Dearborn Park | 17-MAY-19 4:56:54PM |
| 3 | 33.75258909 | -84.28583331 | 302.458252 | Dearborn Park | 17-MAY-19 4:57:46PM |
| 4 | 33.7524989 | -84.28588863 | 298.1323242 | Dearborn Park | 17-MAY-19 5:01:22PM |
| 5 | 33.75256369 | -84.2858142 | 297.4112549 | Dearborn Park | 17-MAY-19 5:01:56PM |
| 6 | 33.75256092 | -84.28569761 | 294.7677002 | Dearborn Park | 17-MAY-19 5:07:17PM |
| 7 | 33.7526719 | -84.28600657 | 292.6047363 | Dearborn Park | 17-MAY-19 5:14:32PM |
| 8 | 33.75250502 | -84.28618728 | 292.8450928 | Dearborn Park | 17-MAY-19 5:17:27PM |
| 9 | 33.76526739 | -84.33659353 | 302.2178955 | Candler Park | 18-MAY-19 2:27:38PM |
| 10 | 33.76556762 | -84.33644911 | 310.1486816 | Candler Park | 18-MAY-19 3:00:34PM |
| 11 | 33.81542642 | -84.27533102 | 314.4744873 | Laurel Ridge Elementary | 18-MAY-19 3:55:56PM |
| 12 | 33.8153395 | -84.27531737 | 314.4744873 | Laurel Ridge Elementary | 18-MAY-19 3:56:09PM |
| 13 | 33.81523746 | -84.27532647 | 313.9938965 | Laurel Ridge Elementary | 18-MAY-19 3:56:16PM |
| 14 | 33.81517699 | -84.27530828 | 313.9938965 | Laurel Ridge Elementary | 18-MAY-19 3:56:20PM |
| 15 | 33.81514675 | -84.27533557 | 314.2342529 | Laurel Ridge Elementary | 18-MAY-19 3:56:23PM |
| 16 | 33.81534554 | -84.27447476 | 313.5133057 | Laurel Ridge Elementary | 18-MAY-19 3:57:09PM |

*Figure 11 Sample of collected waypoints*

# 3 RESULTS

## 3.1 Variable Analyses

36 out of the 40 sample sites (Figure 4.1.1), or 90%, contained the presence of at least one *Mahonia bealei* specimen, with a total of 1,874 plants across all sites, a mean of 46.9, and a median of 9. Presence ranged from 1 to 336 in the 36 sites, with six sites containing between 50 and 100 plants, and four sites exceeding 200. Elevation averaged 294m for all plants, ground cover for all sites averaged 3 on the five-point scale, disturbance averaged 2.75, and canopy extent averaged 3.8. Density of plant abundance per sample site area averaged one plant per 1,011 $m^2$, with the highest density measuring one plant per 17 $m^2$ .

The average sample site measured roughly 5,700 $m^2$, and the encompassing woodlots measured 163,025 $m^2$; however, this included one outlier measuring 1,864,301 $m^2$. Discarding this outlier, the average woodlot size was 119,587 $m^2$.

The most significant correlations between abundance and the six variables (elevation, ground cover, disturbance, canopy, sample site size, and woodlot size) were disturbance ($r = -0.38$ at $p<0.01$), and canopy ($r = 0.272$ at $p < 0.05$).

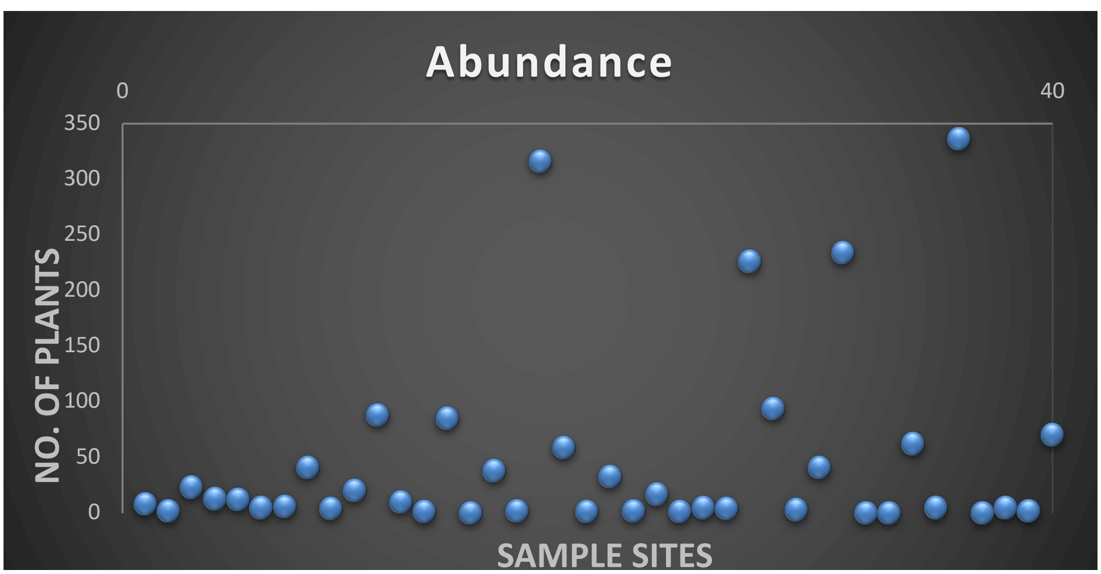



*Figure 12 Abundance of* Mahonia bealei *per sample site*

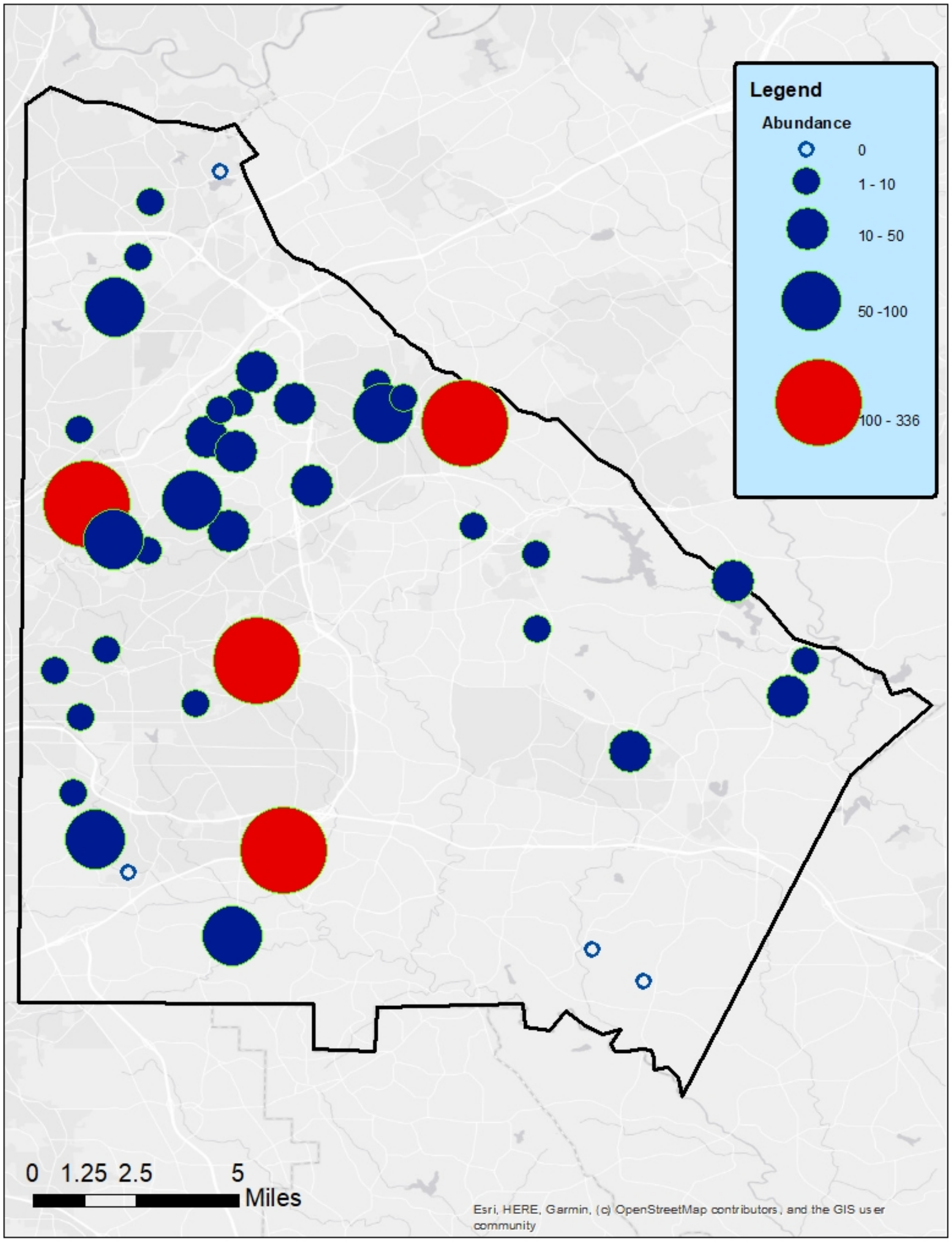



*Figure 13 Sample sites by plant abundance*

Table 2 Variable Analysis

| Variable | R Value | Sig. (1-tailed) |
|---|---|---|
| Elevation | -0.085 | 0.311 |
| Ground Cover | 0.190 | 0.124 |
| Disturbance | -0.380** | 0.008 |
| Canopy | 0.272* | 0.047 |
| Sample Site Size | 0.212 | 0.980 |
| Woodlot Size | 0.047 | 0.387 |

** Correlation is significant at the 0.01 level (1-tailed)

* Correlation is significant at the 0.05 level (1-tailed)

## 3.2 Woodlot Evaluation

The woodlots were mostly composed of dry to dry mesic oak-pine-hickory forests, and mesic to submesic forests, with many also containing riparian zones with perennial, intermittent, and ephemeral streams, and their adjacent floodplains. Dominant tree species included white oak (*Quercus alba*), black oak (*Quercus velutina*), southern red oak (*Quercus falcata*), water oak (*Quercus nigra*), pignut hickory (*Carya glabra*), mockernut hickory (*Carya tomentosa*), sweetgum (*Liquidambar styraciflua*), tulip poplar (*Liriodendron tulipifera*), red maple (*Acer *rubrum*), and loblolly pine (*Pinus taeda*). Topography ranged from flat to steeply sloped areas (~30 degrees, maximum), often due to hydrological features, primarily perennial, intermittent, and ephemeral streams. Soil types were primarily various types of sandy loam (see Appendix A). Woodlots were often public parks or adjacent to public schools; others were adjacent or proximate to churches, historic districts and sites, and community gardens. Several sites were undeveloped land that is not currently in use. Three sites, located in the more urbanized parts of DeKalb County, were designated nature parks, e.g. Kirkwood Urban Park. These are notable because all three exhibited clear evidence of some invasive species management, either in the past or ongoing. One site, Briarlake Forest Park, had a pile of freshly culled *M. bealei*; another, Mary Scott Nature Park, had multiple invasive species flagged for removal. Multiple healthy and unmarked *M. bealei* plants were still found at all of these sites, further demonstrating resilience and fecundity.

*Figure 14 Cut stems of Mahonia bealei as invasive species control*


*Figure 15 Active removal of invasive plants at one sample site*

# 4 DISCUSSION

## 4.1 Disturbance

*Mahonia bealei* had a significant negative correlation ($r = -0.38$ at $p < 0.01$) with disturbance. Disturbance is greatest at the edges of habitats, especially within urban and urbanizing matrices, though smaller disturbances such as hiking trails within forest fragments and may also potentially impact dispersal. The data suggests that *M. bealei* prefers late-successional forests, i.e., climax communities, which are unable to form in the presence of the regular disturbances that typify edge communities and therefore are found in the interior of woodlots. Disturbed areas have considerably more sunlight, and while *M. bealei* can tolerate bright sunlight and was found along edges, these were typically isolated cases that did not constitute the majority of substantial colonies. It seems likely that it is outcompeted by early successional plants, native and non-native, including the most intensely invasive plants in

Georgia such as kudzu (*Pueraria* sp.), Japanese honeysuckle (*Lonicera japonica*), wisteria (*Wisteria* sp.), and tree-of-heaven (*Ailanthus altissuma*). It is also possible that frequently disturbed areas inhibit the presence of animal species that contribute to the dispersal of *M. bealei*. These results echo those found in Clemson by Allen et al. (2006), where *M. bealei* was found up to 61 m in the interior of woodlots, away from any notable disturbance. Ehrenfield (1997) found that *Mahonia bealei* relative Japanese barberry (*Berberis thunbergii*) had spread away from forest edges and roads into the forest interior.

## 4.2 Ground Cover

Ground cover in the form of an herbaceous layer did not have a significant correlation with abundance of *M. bealei* (r = 0.190). Although leaf litter was not considered, the heavy leaf litter that is typical of deciduous hardwood forests was present in a large majority of sites with high abundance; this is likely due in part to the contributions made to soil quality in the form of nutrients and moisture retention. *M. bealei* was least likely to be found in pine forests, which create acidic soil conditions and less vegetative ground cover. The most common species in the herbaceous layer was, by far, *Hedera helix*, or English ivy, another invasive plant which frequently coincided with *M. bealei*. *Hedera helix* is an evergreen vine that grows in thick mats that allow no direct sunlight to penetrate, yet *M. bealei* germinates and grows quite well in this environment. This is possibly due to *Hedera helix* keeping the ground moist, although the relationship is likely commensal, as *M. bealei* has no observed benefit for *Hedera helix*. The deleterious effects of *H. helix* on the native herbaceous layer is well-documented, and thus the ability of *M. bealei* to thrive in coincidence is testament of its shade-tolerance and general adaptability (Biggerstaff et al. 2007).

Many sites contained populations of invasive Chinese privet (*Ligustrum sinese*), which is also known to create homogenous stands, but privet was found primarily in slightly lower elevations, such as the floodplains of intermittent streams, so while *M. bealei* was often found nearby, they were not in competition. Extensively invasive Japanese stiltgrass, (*Microstegium vimineum)*, was also present in numerous sites, and occasionally occupied areas outside floodplains where *M. bealei* was abundant, but there does not appear to be a relationship between the two, antagonistic or otherwise. Allen et al. (2007) also noted heavy presence of *H. helix* and *Lingustrum sinese,* among other invasive species, but concluded that the interactions among them were unclear. There was a strong negative correlation with the most notorious invasive plant, kudzu, and other early successional invasive plants such as Japanese honeysuckle and tree-of-heaven. In fact, despite its reputation for remarkable invasion success, kudzu was found in only one of the 40 sites, further implicating the unique role *M. bealei* has by invading the most established native communities.

*Figure 16* M. bealei *with* Hedera helix

### 4.3 Canopy

Canopy cover was found to have a significant correlation with *M. bealei* abundance ($r = 0.272$ at $p < 0.05$). Georgia Piedmont climax communities tend to have the largest canopy extent (90%+), and *M. bealei* was found in abundance in some of the most extensively shaded areas in the woodlots, from both the canopy and often an understory as well. Areas with less canopy coverage were usually dominated by pines, i.e. early successional forests, and were less populated with *M. bealei.* Allen et al. (2006) also found that *M. bealei* flourished in woodlots with well over 90% canopy cover.

### 4.4 Invasion of Forest Interior

Like most invasive plants, *Mahonia bealei* is highly adaptable and can be observed in the frequently disturbed environments that characterize a fragmented urban landscape. However, the largest populations were found in the interior of each sample site rather than along the edges. This further indicates that avian dispersal is a more significant factor than a preference for disturbed areas. This mode of dispersal provides *M. bealei* with an expeditious and comprehensive dispersal pattern. Most importantly, *M. bealei* is able to establish and flourish in the climax communities of the Georgia Piedmont. Invasion of these communities indicates an enormous potential for continuing widespread invasion and the resulting alteration of natural communities and ecosystem services. In fact, *M. bealei* likely poses a greater threat to more ecologically valuable habitats, i.e. the late successional forests, and less of a threat to the secondary successional habitats where the more well-known invasive plants have taken root.

Recent research has highlighted the potential importance of shade tolerance and high resource use efficiency in invasive plants, asserting that survivorship in low-light environments is essential for successional long-term establishment in forest communities, and *M. bealei* has shown that it thrives in low-light conditions (Martin et al. 2010). As an evergreen, *M. bealei* is also able to capitalize on the increased amounts of sunlight during the winter months in the deciduous climax communities, compounding its competitive edge, whereas the decreased canopies found in early successional pine forests do not provide this advantage.

*M. bealei* is exceedingly well-adapted to shade and is able to germinate and grow directly out of a heavy herbaceous layer in areas with already extensive canopies. It was found less often and in smaller numbers in pine forests, which indicates *M. bealei*'s preference for established forest communities, which have moist, rich soil, more extensive ground cover, and higher canopy coverage. However, *M. bealei* was still found in some capacity in the majority of pine forest woodlots.

### 4.5 Major Colonies

The greatest plant abundances occurred in oak-hickory or oak-hickory-pine forests, in or closely proximate to riparian corridors that contained rich, moist, well-drained soil. The colonies occurred above the high-water mark and outside of evident scouring and erosional processes, but still within the greater drainage area, on sloped areas between 10 and 30 degrees. *M. bealei* was never in the floodplain. Exposed topographical ridges also displayed reduced populations, likely due to reduced amounts of quality soil and increased wind disturbance. However, sloped areas often had high plant densities, with colonies that more often spread horizontally along topographic contours than vertically. The highest plant densities occurred with a high number of seedlings (< 1-year-old) relative to mature plants. The seedlings, concurrently with large numbers of plants in all life stages (evidenced by the presence of new annual growth and the overall sizes of the plants), provided conclusive evidence of a thriving colony in the midst of expansion. Invasive woody species that are able to regenerate under their own canopy are more likely to self-perpetuating, and unlikely to be supplanted by native communities without active management (McAlpine et al. 2018).

### 4.6 Implication of *Mahonia bealei* Presence

The high percentage of plant occurrence across woodlot samples indicates that abundance is widespread in DeKalb County, and likely also across the entire Piedmont ecoregion in Georgia. *M. bealei* has a demonstrated ability to survive in all major habitat types that can be found in the region and can flourish in the environmentally valuable forest fragments that remain within urban sprawl. The presence of each invasive *M. bealei* potentially displaces native species, and large colonies may modify the ecological structure and integrity of the woodlot as well as any ecosystem services. Comparatively little research has been done into the implications of invasions in the interior of undisturbed established forest communities, since low-light environments are thought to be less vulnerable to invasive plants; however, the early-successional traits of well-documented invasive plants typically promote establishment along the edges of mature forest communities, and those that penetrate deeper into the forests may not succeed on a longer timeline as secondary succession by native plant communities ultimately displaces the invaders that are not well-suited for low-light conditions. *M. bealei* has demonstrated not only a tolerance, but a proclivity to thrive in the low-light conditions that characterize the most ecologically valuable forest remnants. The rapid dispersal combined with a high likelihood of long-term invasion success strongly encourages further study and active management, and therefore should be elevated to a Category 2 invasive plant per the GAEPPC.

## 4.7 Potential Mitigation Methods

The most important approach to managing invasive plants is prevention, as extensive invasions are often unmanageable. This can be achieved by encouraging the use of native species for horticulture and placing stringent limitations on certain families of plants that are known to be invasive in parts of the world, especially east Asia. The reduction of exotic horticulture would significantly slow the rate of new invasive plants, and slow nascent invasions by reducing propagule pressure.

For invasions already underway, early detection and rapid response is imperative. Regular surveying and monitoring by state and federal management agencies provide the most authoritative and comprehensive data, but crowd-sourced GPS reporting through applications such as EDDMaps and iNatural can also provide a cost-effective method to monitor the rate and locations of invasions, particularly in urban forests and parks (Hawthorne et al. 2015). Where *M. bealei* is known to be spreading, mechanical treatments would be most effective, as the thick waxy cuticle of the evergreen leaves is more resistance to the more common herbicides such as glyphosate. Webster et al. 2006 recommends for wood invasive plants, such as *M. bealei*, to start control activities from the less heavily invaded areas and work back towards the more heavily invaded areas.

## 4.8 Impacts of Research

This case study of the invasive spread of a woody shrub into a region's most ecologically rich and established native habitats has serious regional and global implications. *Mahonia bealei* is a convincing indicator of the increase in Asian-originated woody species that have invaded the interior of the expansive deciduous forests of eastern North America. The number of non-native plants that are adapted to low-light conditions is likely to rise as international trade increases, while many other species may already be present and just now emerging from the lag phase of a long-term invasive establishment, but yet to be recognized. The nature of late-successional invasions is long-term success in the most valuable natural habitats, in contrast with early-successional invasions. This study provides more contrary evidence to the paradigm that climax communities are largely resistant to invasion. The continuing displacement of native species, disruption of local ecosystem processes, and the decline of ecosystem service quality are to be expected in the future without a serious and well-resourced effort to understand and manage biological invasions.

**REFERENCES**

Allen, C. R., Garmestani, A. S., Labram, J. A., Peck, A. E., & Prevost, L. B. (2006). When Landscaping Goes Bad: The Incipient Invasion of Mahonia bealei in the Southeastern United States. *Biological Invasions; Dordrecht*, *8*(2), 169–176.

Bartuszevige, A. M., D. L. Gorchov, and L. Raab. “The Relative Importance of Landscape and Community Features in the Invasion of an Exotic Shrub in a Fragmented Landscape.” *Ecography* 29, no. 2 (April 2006): 213–22.

Biggerstaff, Matthew S., and Christopher W. Beck. “Effects of Method of English Ivy Removal and Seed Addition on Regeneration of Vegetation in a Southeastern Piedmont Forest.” *American Midland Naturalist* 158, no. 1 (July 2007): 206–20.

Bonilla, N. O., & Pringle, E. G. (2015). Contagious seed dispersal and the spread of avian-dispersed exotic plants. *Biological Invasions*, *17*(12), 3409–3418.

Castro-Diez, P., Vaz, A.S., Silva, J.S., Loo, M., Alonso, A., Aponte, C., Bayon, A., Bellingham, P.J., Chiuffo, M.C., DiManno, N., Julian, K., Kandert, S., La Porta, N., Marchante, H., Maule, H.G., Mayfield, M.M., Metcalfe, D., Monteverdi, M.C., Nunez, M.A., Ostertag, R., Parker, I.M., Peltzer, D.A., Potgieter, L.J., Raymundo, M., Rayome, D., Reisman-Berman, O., Richardson, D.M., Roos, R.E., Saldana, A., Shackleton, R.T., Torres, A., Trudgen, M., Urban, J., Vicente, J.R., Vila, M., Ylioja, T., Zenni, R.D. and Godoy, O. (2019) Global effects of non-native tree species on multiple ecosystem services. Biological Reviews 94(4), 1477-1501.

de Groot, R. S., Alkemade, R., Braat, L., Hein, L., & Willemen, L. (2010). Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. *Ecological Complexity*, *7*(3), 260–272.

Dickie, I. A., Bennett, B. M., Burrows, L. E., Nunez, M. A., Peltzer, D. A., Porte, A., … van Wilgen, B. W. (2014). Conflicting values: ecosystem services and invasive tree management. *Biological Invasions*, *16*(3), 705–719.

Dillon, Whalen W., Deah Lieurance, Drew T. Hiatt, Keith Clay, and S. Luke Flory. "Native and Invasive Woody Species Differentially Respond to Forest Edges and Forest Successional Age." *Forests* 9, no. 7 (July 2018): 381.

Downey, P. O., & Richardson, D. M. (2016). Alien plant invasions and native plant extinctions: a six-threshold framework. *AoB PLANTS*, *8*.

Duguay, S., Eigenbrod, F., & Fahrig, L. (2007). Effects of surrounding urbanization on non-native flora in small forest patches. *Landscape Ecology*, *22*(4), 589–599.

Early Detection & Distribution Mapping System. https://www.eddmaps.org/distribution/viewmap.cfm?sub=6889

Ehrenfeld, J. G. "Invasion of Deciduous Forest Preserves in the New York Metropolitan Region by Japanese Barberry (Berberis Thunbergii DC)." *Journal of the Torrey Botanical Society* 124, no. 2 (June 1997): 210–15.

Georgia Exotic Pest Plant Council. https://www.gaeppc.org/list/

Gosper, C. R., Stansbury, C. D., & Vivian-Smith, G. (2005). Seed Dispersal of Fleshy-Fruited Invasive Plants by Birds: Contributing Factors and Management Options. *Diversity and Distributions*, *11*(6), 549–558.

Funk, Jennifer L., and Peter M. Vitousek. "Resource-Use Efficiency and Plant Invasion in Low-Resource Systems." *Nature* 446, no. 7139 (April 26, 2007): 1079–81.

Hawthorne, T. L., Elmore, V., Strong, A., Bennett-Martin, P., Finnie, J., Parkman, J., … Reed, J. (2015). Mapping non-native invasive species and accessibility in an urban forest: A case study of participatory mapping and citizen science in Atlanta, Georgia. *Applied Geography*, *56*, 187–198.

Heberling, J. Mason, and Jason D. Fridley. "Invaders Do Not Require High Resource Levels to Maintain Physiological Advantages in a Temperate Deciduous Forest." *Ecology* 97, no. 4 (April 2016): 874–84.

iNaturalist.org. https://www.inaturalist.org/taxa/165077-Mahonia-bealei

Jean-Nicolas, B., Marie-Christine, P., Nicolas, K., Agnes, H. and Serge, M. (2017) Spatiotemporal trends for exotic species in French freshwater ecosystems: where are we now? Hydrobiologia 785(1), 293-305.

Lapin, K., Oettel, J., Steiner, H., Langmaier, M., Sustic, D., Starlinger, F., Kindermann, G. and Frank, G. (2019) Invasive alien plant species in unmanaged forest reserves, Austria. Neobiota (48), 71-96.

Liebhold, A. M., Brockerhoff, E. G., Kalisz, S., Nuñez, M. A., Wardle, D. A., & Wingfield, M. J. (2017). Biological invasions in forest ecosystems. *Biological Invasions*, *19*(11), 3437–3458.

Martin, Patrick H., Charles D. Canham, and Richard K. Kobe. "Divergence from the Growth-Survival Trade-off and Extreme High Growth Rates Drive Patterns of Exotic Tree Invasions in Closed-Canopy Forests." *Journal of Ecology* 98, no. 4 (2010): 778–89.

Martin, Patrick H., Charles D. Canham, and Peter L. Marks. "Why Forests Appear Resistant to Exotic Plant Invasions: Intentional Introductions, Stand Dynamics, and the Role of Shade Tolerance." *Frontiers in Ecology and the Environment* 7, no. 3 (April 2009): 142–49.

Nunez-Mir, G.C., Guo, Q.F., Rejmanek, M., Iannone, B.V. and Fei, S.L. (2019) Predicting invasiveness of exotic woody species using a traits-based framework. *Ecology* 100(10): 11.

North Carolina State Extension. https://plants.ces.ncsu.edu/plants/all/mahonia-bealei/

Pejchar, L., & Mooney, H. A. (2009). Invasive species, ecosystem services and human well-being. *Trends in Ecology & Evolution*, *24*(9), 497–504.

Pennington, Derric N., James R. Hansel, and David L. Gorchov. "Urbanization and Riparian Forest Woody Communities: Diversity, Composition, and Structure within a Metropolitan Landscape." *Biological Conservation* 143, no. 1 (January 2010): 182–94.

Potgieter, L.J., Gaertner, M., Irlich, U.M., O'Farrell, P.J., Stafford, L., Vogt, H. and Richardson, D.M. (2018) Managing Urban Plant Invasions: a Multi-Criteria Prioritization Approach. Environmental Management 62(6), 1168-1185.

Pyšek, P., Jarošík, V., Hulme, P. E., Pergl, J., Hejda, M., Schaffner, U., & Vilà, M. (2012). A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology*, *18*(5), 1725–1737.

Rejmanek, M. (2014). Invasive trees and shrubs: where do they come from and what we should expect in the future? *Biological Invasions*, *16*(3), 483–498.

Richardson, D. M., & Rejmanek, M. (2011). Trees and shrubs as invasive alien species - a global review. *Diversity and Distributions*, *17*(5), 788–809.

Rojas, T. N., Gallo, M.C.F., Vergara-Tabares, D.L., Nazaro, M.G., Zampini, I.C., Isla, M.I. and Blendinger, P.G. (2019). "Being popular or freak: how alien plants integrate into native plant-frugivore networks." *Biological Invasions* **21**(8): 2589-2598.

Ross, C. A., Faust, D., & Auge, H. (2009). Mahonia invasions in different habitats: local adaptation or general-purpose genotypes? *Biological Invasions*, *11*(2), 441–452.

Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., … Vila, M. (2013). Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution*, *28*(1), 58–66.

Theoharides, K. A., & Dukes, J. S. (2007). Plant Invasion across Space and Time: Factors Affecting Nonindigenous Species Success during Four Stages of Invasion. *The New Phytologist*, *176*(2), 256–273.

Thibault, M., Masse, F., Pujapujane, A., Lannuzel, G., Bordez, L., Potter, M.A., Fogliani, B., Vidal, E. and Brescia, F. (2018) "Liaisons dangereuses": The invasive red-vented bulbul (Pycnonotus cafer), a disperser of exotic plant species in New Caledonia. Ecology and Evolution 8(18), 9259-9269.

van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, *13*(2), 235–245.

Vaz, A.S., Goncalves, J.F., Pereira, P., Santarem, F., Vicente, J.R. and Honrado, J.P. (2019) Earth observation and social media: Evaluating the spatiotemporal contribution of non-native trees to cultural ecosystem services. Remote Sensing of Environment 230, 12.

Webster, C. R., Jenkins, M. A., & Jose, S. (2006). Woody Invaders and the Challenges They Pose to Forest Ecosystems in the Eastern United States. *Journal of Forestry; Bethesda*, *104*(7), 366–374.

With, K. A. (2004). Assessing the Risk of Invasive Spread in Fragmented Landscapes. *Risk Analysis*, *24*(4), 803–815.

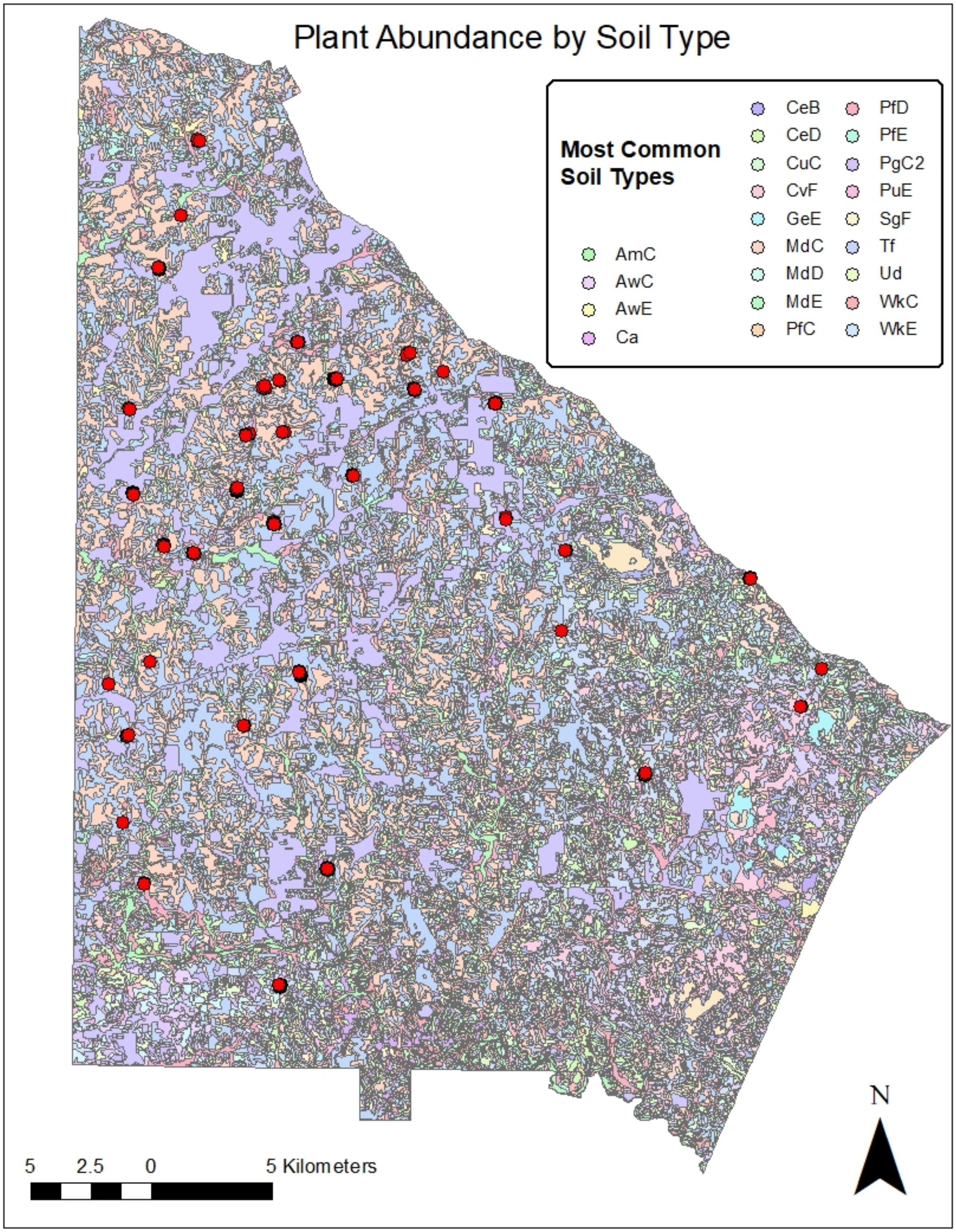
Zomlefer, W. B., Giannasi, D. E., Reynolds, A., & Heiman, K. (2012). Vascular Plant Flora of Chattahoochee River National Recreation Area, a Conservation Corridor from the Buford Dam to Atlanta, Georgia. *Rhodora*, *114*(957), 50–102.

# APPENDICES

## Appendix A Plant Abundance by Soil Type

Below is a map of soil types in DeKalb County, with plant locations included to illustrate the types of soil most commonly found in areas of high *Mahonia bealei* abundance. The data indicates that *M. bealei* is found in higher abundance in sandy loam soils, even when accounting for the dominant soil types of the sample site. For instance, soil type PfE (Pacolet sandy loam, 15 to 30 percent slopes) constitutes 13.88% of the soil found in the sample sites but contains 19.76% of all *Mahonia bealei*. Much of the sample site soils were classified under various Urban categories, e.g. Ud is “Urban land”, but nearly all other soils where *Mahonia bealei* was found were types of sandy loam.

*Appendix A.1 Map of Soil Type and Plant Abundance*



*Appendix A.2 Plant Abundance per Type of Soil and Dominant Soil Types per Sample Site*

| Soil Type | # of Plants | Percentage |
|---|---|---|
| PuE | 481 | 25.90% |
| PfE | 367 | 19.76% |
| Ud | 291 | 15.67% |
| MdC | 122 | 6.57% |
| MdD | 112 | 6.03% |
| MdE | 112 | 6.03% |
| CuC | 60 | 3.23% |
| PfC | 59 | 3.18% |
| WkE | 59 | 3.18% |
| SgF | 55 | 2.96% |
| Ca | 50 | 2.69% |

| Soil Type | Area (m2) | Percentage |
|---|---|---|
| PfE | 45944 | 13.88% |
| PuE | 42954 | 12.98% |
| PfC | 39267 | 11.87% |
| Ca | 35633 | 10.77% |
| CuC | 26071 | 7.88% |
| Ud | 22627 | 6.84% |
| Tf | 15399 | 4.65% |
| PfD | 13015 | 3.93% |
| MdE | 9986 | 3.02% |
| GeE | 9495 | 2.87% |
| AwE | 7564 | 2.29% |
| MdC | 7244 | 2.19% |
| AwC | 6877 | 2.08% |

# Appendix B Complete Site Data

| Latitude | Longitude | Site Location | Site No. | Abundance | Avg Elevation | Ground Cover | Disturbance | Canopy | Site Size | Woodlot Size | nsity (area/plants) m2 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 33.753610 | -84.287500 | Dearborn Park | 1 | 8 | 297.1 | 5 | 3 | 4 | 4,628 | 146,318 | 579 |
| 33.765400 | -84.337008 | Candler Park | 2 | 2 | 306.2 | 2 | 4 | 2 | 3,636 | 23,986 | 1,818 |
| 33.814711 | -84.275798 | Laurel Ridge Elementary | 3 | 23 | 312.6 | 1 | 5 | 2 | 5,149 | 9,189 | 224 |
| 33.848300 | -84.283500 | Lakeside High School | 4 | 13 | 292.4 | 5 | 2 | 5 | 6,310 | 119,853 | 485 |
| 33.830703 | -84.246170 | John's Homestead | 5 | 12 | 314.3 | 3 | 1 | 4 | 5,222 | 128,164 | 435 |
| 33.866978 | -84.223455 | Henderson Park | 6 | 5 | 324.4 | 2 | 3 | 4 | 4,949 | 160,203 | 990 |
| 33.860460 | -84.271969 | Hawthorne Elementary | 7 | 6 | 304.6 | 4 | 4 | 5 | 6,471 | 22,911 | 1,079 |
| 33.859654 | -84.252161 | St. Bede's Church | 8 | 41 | 293.1 | 4 | 1 | 4 | 6,563 | 21,968 | 160 |
| 33.857480 | -84.278563 | Mary Scott Nature Park | 9 | 4 | 308.7 | 2 | 5 | 4 | 8,901 | 53,200 | 2,225 |
| 33.842779 | -84.272946 | Briarlake Forest Park | 10 | 20 | 326.8 | 4 | 3 | 3 | 6,205 | 59,836 | 310 |
| 33.825644 | -84.288741 | Frazier-Rowe Park | 11 | 88 | 308.1 | 2 | 5 | 4 | 7,171 | 100,270 | 81 |
| 33.807703 | -84.304105 | Mason Mill Park | 12 | 10 | 296.3 | 2 | 3 | 3 | 4,517 | 130,370 | 452 |
| 33.722096 | -84.330853 | 1757 Mary Dell Dr | 13 | 1 | 309.2 | 4 | 3 | 5 | 3,657 | 12,105 | 3,657 |
| 33.705912 | -84.322869 | McNair High School | 14 | 85 | 268.1 | 5 | 1 | 4 | 5,377 | 296,511 | 63 |
| 33.693847 | -84.311193 | Gresham Park Baseball | 15 | 0 | | 1 | 3 | 1 | 5,475 | 235,671 | 0 |
| 33.736940 | -84.133890 | Redan Recreation Center | 16 | 38 | 282.6 | 2 | 4 | 4 | 6,078 | 68,494 | 160 |
| 33.850680 | -84.328745 | Briarwood Park | 17 | 2 | 271.1 | 5 | 3 | 5 | 4,460 | 25,615 | 2,230 |
| 33.824160 | -84.326166 | Elwyn John Sanctuary | 18 | 316 | 277.3 | 4 | 1 | 5 | 5,368 | 113,365 | 17 |
| 33.811737 | -84.316430 | W.D. Thompson Park | 19 | 59 | 279.5 | 2 | 3 | 5 | 6,558 | 142,327 | 111 |
| 33.772919 | -84.319034 | Deepdene Park | 20 | 1 | 306.8 | 3 | 5 | 4 | 6,917 | 74,753 | 6,917 |
| 33.75643 | -84.07777 | Rock Chapel Church | 21 | 33 | 301.9 | 1 | 1 | 3 | 4,055 | 19,552 | 123 |
| 33.76885 | -84.07179 | Stronghold Church | 22 | 2 | 242 | 1 | 1 | 3 | 6,287 | 479,006 | 3,144 |
| 33.79718 | -84.09752 | N. Deshon Rd | 23 | 17 | 270.7 | 4 | 1 | 4 | 7,812 | 182,594 | 460 |
| 33.780280 | -84.166670 | Wade-Walker Park | 24 | 1 | 297.4 | 3 | 3 | 5 | 5,734 | 51,802 | 5,734 |
| 33.806376 | -84.167191 | Stone Mountain trail | 25 | 5 | 312.8 | 1 | 1 | 4 | 3,631 | 97,141 | 726 |
| 33.816470 | -84.189100 | Stone Mill Elementary | 26 | 4 | 312.4 | 5 | 3 | 5 | 5,188 | 117,218 | 1,297 |
| 33.852871 | -84.192009 | Mountain West Church | 27 | 226 | 327.7 | 4 | 1 | 5 | 7,992 | 383,061 | 35 |
| 33.856364 | -84.221322 | St. Andrews Church | 28 | 94 | 338.6 | 5 | 1 | 4 | 7,418 | 23,192 | 79 |
| 33.862176 | -84.213651 | Kelley Cofer Park | 29 | 3 | 328.4 | 2 | 3 | 3 | 5,228 | 38,042 | 1,743 |
| 33.871258 | -84.265826 | Mercer | 30 | 41 | 285 | 1 | 5 | 2 | 6,399 | 38,974 | 156 |
| 33.701940 | -84.256110 | Exchange Park | 31 | 234 | 268.7 | 1 | 1 | 3 | 5,089 | 107,984 | 22 |
| 33.666960 | -84.147200 | Evans Mill trail | 32 | 0 | | 3 | 3 | 3 | 4,854 | 1,864,301 | 0 |
| 33.655593 | -84.128951 | Klondike Park | 33 | 0 | | 1 | 2 | 4 | 4,952 | 629,315 | 0 |
| 33.671490 | -84.274300 | Fork Creek Mountain Park | 34 | 62 | 258.1 | 4 | 1 | 4 | 5,837 | 260,469 | 94 |
| 33.748991 | -84.328190 | Kirkwood Urban Park | 35 | 5 | 296.1 | 4 | 5 | 4 | 6,137 | 41,592 | 1,227 |
| 33.768890 | -84.265560 | Avondale Historic District | 36 | 336 | 304.2 | 5 | 2 | 5 | 6,315 | 27,352 | 19 |
| 33.942238 | -84.278945 | Windwood Hollow Park | 37 | 0 | | 2 | 3 | 3 | 4,648 | 38,050 | 0 |
| 33.931108 | -84.303363 | Brook Park Run | 38 | 5 | 300.6 | 3 | 4 | 4 | 6,107 | 25,026 | 1,221 |
| 33.911690 | -84.307771 | Chamblee First United Church | 39 | 2 | 289.4 | 5 | 4 | 3 | 4,546 | 56,434 | 2,273 |
| 33.893937 | -84.315920 | Keswick Park | 40 | 70 | 297.6 | 3 | 3 | 5 | 6,147 | 101,990 | 88 |

| Abundance | |
|---|---|
| Median | 9 |
| Mean | 47 |
| Total | 1,874 |
| Avg Woodlot | |
| 163025 m2 | |
| Avg Site | |
| 5700 m2 | |
| Average Elevation | |
| 294.6m | |
| Average Density | |
| 1 plant per 1,011 m2 | |