TOWSON UNIVERSITY
OFFICE OF GRADUATE STUDIES

THE INFLUENCE OF HISTORICAL LAND USE ON THE SUCCESSIONAL DYNAMICS OF A SUBURBAN DECIDUOUS FOREST

by

Daniel B. Breen III

A thesis

Presented to the faculty of

Towson University

in partial fulfillment

of the requirements for the degree

Master of Science

Department of Biological Sciences

Towson University
Towson, Maryland 21252

May 2014

TOWSON UNIVERSITY
OFFICE OF GRADUATE STUDIES

THESIS APPROVAL PAGE

This is to certify that the thesis prepared by Daniel B. Breen III entitled "The influence of historical land use on the successional dynamics of a suburban deciduous forest" has been approved by the thesis committee as satisfactorily completing the thesis requirements for the degree of Master of Science.

Vanessa Beauchamp
Chair, Thesis Committee Signature Dr. Vanessa Beauchamp — 4/11/14 Date

Committee Member Signature Dr. Susan Gresens — April 11 2014 Date

Committee Member Signature Dr. Roland Roberts — Apr. 11, 2014 Date

Janet V. DeLany
Dean of Graduate Studies Signature Dr. Janet DeLany — April 16, 2014 Date

Acknowledgments

I would like to recognize my advisor, Dr. Vanessa Beauchamp, and my thesis committee members, Dr. Roland Roberts and Dr. Susan Gresens, for their guidance and support on this study. I am also grateful to the Middle Patuxent Environmental Foundation and Towson University's Department of Biological Sciences and Graduate Student Association for contributing funding for this research. In addition, I would like to acknowledge Cheryl Farfaras and Stephanie Koontz for access to their data; Dr. Paporn Thebpanya for instructing me in ArcGIS; Cody Kepner, Adele LeBrun, Matthew Moreland, Amber Epps, and Danielle Iuliucci for assistance with fieldwork and/or data entry; and the Howard County Department of Recreation and Parks, the Howard County GIS Division, the Columbia Archives, the Maryland State Archives, the U.S. Geological Survey, and the Natural Resource Conservation Service, from which I obtained historical and spatial data.

Abstract

The influence of historical land use on the successional dynamics of a suburban deciduous forest

Daniel B. Breen III

Length of time since agricultural abandonment, variations in topography and soil, and forest fragmentation associated with suburban development can influence the succession of a deciduous forest. I analyzed herbaceous and woody vegetation data collected at the forested Middle Patuxent Environmental Area (MPEA) in 2001, 2009, and 2012 to better understand succession in a suburban forest remnant and to investigate the effects of time since abandonment and variations in landscape on vegetation. Herbaceous vegetation fluctuated across decadal, interannual, and seasonal scales, with a decadal increase in major invasive species. Shrubs also experienced a greater abundance of invasive species across the decade, whereas the tree stratum better aligned with the expected trends of a deciduous forest. Though herbaceous plants and shrubs displayed some differential distributions reflective of time since abandonment, trees differed the most distinctly in accordance with agricultural legacy, proximity to suburban edges, and major soil nutrients.

Table of Contents

List of Tables vi

List of Figures viii

Chapter One — Successional trajectories of a suburban deciduous forest at the Middle Patuxent Environmental Area 1

Chapter Two — The influence of agricultural abandonment and the abiotic environment on the vegetation communities of a suburban deciduous forest 32

Tables 57

Figures 75

Literature Cited 88

Curriculum Vita 117

List of Tables

Table 1. Number of vascular plant taxa recorded in each sampling period. 57

Table 2. Measures of mean (±SE) beta diversity and mean (±SE) proportional effective species turnover for herbaceous vegetation, shrubs, and trees. 57

Table 3. Significant correlations between beta diversity of a) herbaceous species, b) shrubs, and c) trees and major environmental characteristics. 58

Table 4. Number of plots containing the most common: a) herbaceous species and the change in frequency at the decadal (2001–2012), interannual (2009–2012), and semiannual (June–September 2012) timeframes; b) shrub species and the change in frequency at the decadal (2001–2012) timeframe; and c) tree species and the change in frequency at the decadal (2001–2012) timeframe. Common species were defined as those present in ≥30 in at least one dataset. 61

Table 5. Mean temperature and precipitation in Howard County, Maryland during January, June, and September of the three survey years. 61

Table 6. Change in abundance of the most common understory vegetation, as represented by: a) mean coverage of herbaceous species and their change in coverage at the decadal (2001–2012), interannual (2009–2012), and semiannual (June–September 2012) timeframes; b) mean coverage of shrub species (≤1 m tall) and their change in coverage at the decadal (2001–2012) timeframe; and c) frequency of tree seedlings (≤1 m tall) and their change in frequency at the semiannual (June–September 2012) timeframe. Common species were defined as those present in ≥30 plots in at least one dataset. 63

Table 7. Number of common a) herbaceous morphospecies (n=23), b) shrubs (n=13), and c) trees (n=9) as grouped by plot turnover. Noted are whether a species exhibited a net increase, decrease, or constancy in its plot frequency during each of the three timeframes and whether such change involved a shift in distribution among individual plots. 65

Table 8. Number of a) common large shrubs (≥1 m tall) and b) mature trees (≥1 m tall) observed in 2001 and 2012 and their change in number. (* includes both generic *Rosa*, recorded only in 2001, and *Rosa multiflora*.) 66

Table 9. Change in number of common mature trees (>1 m tall) in each DBH class between 2001 and 2009–2012. 67

Table 10. Average deer browse of the most common: a) herbaceous species; b) small shrubs (<1 m); c) large shrubs (>1 m); and d) tree seedlings (<1 m) in 2001, 2009, and 2012. Common species were defined as those present in ≥30 in at least one dataset. 68

Table 11. Average environmental factors and environmental conditions of: a) herbaceous communities; b) shrub communities; and c) tree communities. Letters denote significant differences among groups, according to an ANOVA permutation procedure and post-hoc comparison of 95% confidence intervals. 70

Table 12. Spearman's correlations of the major environmental gradients with: a) abundance of herbaceous invasive species (all classified as shade-intolerant); b) abundance of major invasive shrubs (classified by shade tolerance); and c) frequency of lianas. 73

List of Figures

Figure 1. Layout of the current 99 long-term monitoring plots at the Middle Patuxent Environmental Area. 75

Figure 2. Sampling design of each 20 x 20 m plot, including eight 1 x 1 m subplots for understory vegetation sampling and four 2 x 4 m subplots for shrub sampling. 75

Figure 3. Mean (±SE) beta diversity of herbs, shrubs, and trees at the decadal (2001–2012) time scale. 76

Figure 4. NMDS results of a) herbaceous vegetation, b) shrubs, and c) trees, each at the decadal (2001–2012) timeframe. Major species correlations included: for herbaceous vegetation, the x-xis with *M. vimineum* (r = –0.74) and the y-axis with *P. indica/F. vesca* (r = 0.51), *Persicaria* (r = 0.38), and graminoids (r = 0.36); for shrubs, the x-axis with *L. benzoin* (r = –0.42) and *E. umbellata* (r = 0.88) and the y-axis with *L. benzoin* (r = 0.69), *R. multiflora* (r = 0.47), *V. acerifolium* (r = –0.54), and *Vaccinium* (r = –0.52); and for trees, the x-axis with *Prunus* (r = 0.50), *L. tulipifera* (r = 0.45), and *C. caroliniana* (r = –0.79) and the y-axis with *R. pseudoacacia* (r = 0.60), *Prunus* (r = 0.47), *L. tulipifera* (r = –0.56), and *F. grandifolia* (r = –0.51). 77

Figure 5. a) Forest cover and surrounding landscape at the MPEA in 1943, 1970, and 2011, with the MPEA's present-day boundary outlined in red, and b) each long-term monitoring plot's first known date of reforestation since 1943, also noting the boundary between the historical Doughoregan Manor and Discovery tracts. 79

Figure 6. Major landscape features of the MPEA, including: a) elevation, b) soil drainage classes, and c) soil types. 80

Figure 7. Variation in a) soil exchange capacity, b) phosphorus, c) sulfur, d) calcium, e) nitrate, and f) nitrogen throughout the MPEA's soils. 82

Figure 8. Spatial distributions throughout the MPEA in 2012 of the: a) herbaceous communities; b) shrub communities; and c) mature tree communities. 83

Figure 9. NMDS results displaying the distributions of long-term monitoring plots throughout species space and correlations with major environmental variables: a) herbaceous species, b) shrubs, and c) trees. 85

Figure 10. Distribution of the newly invasive *Oplismenus undulatifolius* (wavyleaf basketgrass) at the MPEA in 2012. 87

Figure 11. Number of seedlings per 8 m^2 sampled in each mature tree community. 87

Chapter One

Successional trajectories of a suburban deciduous forest at the Middle Patuxent Environmental Area

Abstract

Eastern deciduous forests experience succession as a directional change in which herbaceous plants, shrubs, shade-intolerant trees, and shade-tolerant trees sequentially succeed each other as the dominant vegetation type. Suburban forest remnants such as the Middle Patuxent Environmental Area (MPEA) in Maryland, USA represent a secondary successional habitat with disturbances that have frequently reset microhabitats to earlier successional stages. I analyzed herbaceous and woody vegetation data collected at the MPEA in 2001, 2009, and 2012 with the goals of better understanding succession in a suburban forest remnant and differentiating long-term succession from seasonal and interannual variation. My predictions were that there would be an increase of late-successional vegetation and a reduction of early-successional vegetation, that herbaceous species would exhibit greater change than woody species, and that the degree of herbaceous change would increase along with time between surveys. Beta diversity differed amongst herbaceous vegetation, shrubs, and trees ($p < 0.001$) and also increased along with time between herbaceous surveys. Herbaceous vegetation fluctuated across all three time scales and in no singular direction, but the most consistent decadal trend involved increases in the invasive species *Microstegium vimineum* and *Alliaria petiolata*. Higher abundances of invasive *Elaeagnus umbellata*, *Rosa multiflora*, and *Berbergis thunbergii* were the most evident changes in the shrub stratum. The tree stratum's more modest change was led by an increase of late-successional *Fagus grandifolia*, which aligned with expected successional trends.

Introduction

Succession, one of the most foundational concepts in ecology (Finegan 1984; Cadenasso et al. 2009), describes a directional change in the species composition and three-dimensional dynamics of a vegetation community over time (Clements 1916, 1949; Anderson 2007; Pickett et al. 2009). Secondary succession is commenced by a disturbance to an established plant community that reverts the environment to an earlier stage, initiating predictable stages in which herbaceous species, shrubs, shade-intolerant trees, and finally shade-tolerant trees sequentially replace each other as the dominant vegetation type (Miles 1979; Heiri et al. 2012; Oikonomakis & Ganatsas 2012). Though Clements's (1916) original paradigm defined succession as highly deterministic and proposed that all vegetation communities would eventually progress towards the stable and unchangeable climax community of an old-growth forest, it is now widely recognized that this view may represent more of an ideal pathway that in reality is much more nuanced and stochastic, as vegetation communities are constantly being modified under different environmental stressors (Pickett et al. 2001; Meiners et al. 2002; Bartha et al. 2003; Dahlstrom et al. 2010; Lebrija-Trejos et al. 2010).

Temperate deciduous forests in the eastern United States can be expected to undergo secondary succession in a predictable manner. After an initial abandonment of agriculture, old fields become dominated by an influx of ruderal herbs and graminoids characterized by their high growth and dispersal rates, relatively smaller sizes, intolerance of shade, and periods of dormancy (Van Breugel et al. 2007; Fridley & Wright 2012). Exotic annuals often thrive better than native ruderals at this early stage (Meiners et al. 2002; Tognetti et al. 2010). Common woody species subsequently come to dominate an old field within 10 to 20 years and may include the shrub *Rosa multiflora* and the trees *Acer negundo* and *Prunus serotina* (Myster &

Pickett 1990; D'Orangeville et al. 2011). After a longer timeframe of 15 to 45 years, these early colonizers may be joined and perhaps outcompeted by such shrubs as *Lonicera, Rubus,* and *Viburnum* (Copenheaver 2008) and mid-successional trees along the lines of *Liriodendron tulipifera,* whose sun-tolerant seedlings allow the species to colonize gaps in the canopy layer and form a regrowth forest (Abrams & Copenheaver 1999; Hart et al. 2008). Herbaceous vegetation in the forest understory consequently becomes less abundant and shifts in species composition to shade-tolerant forbs (Bellemare et al. 2005). The annual invasive grass *Microstegium vimineum,* which is prolific throughout the Mid-Atlantic region, has an advantage over many early-successional herbs in its modest shade tolerance, allowing this weed to encroach into forest edges and below canopy gaps that have yet to be recolonized by trees (Flory & Clay 2010; Cheplick & Fox 2011; Duguay & Farfaras 2011).

Late-successional species are disproportionately woody and more commonly exhibit lower dispersal and growth rates, larger sizes, longer life spans, and shade-tolerance. By a century after abandonment, many prior agricultural lands have become indistinguishable from forests that have never been cleared (Flinn & Marks 2007) and support a mature deciduous forest dominated by the trees *Fagus grandifolia, Quercus rubra,* and *Carya glabra* (Copenheaver 2008; Busby et al. 2009; Abrams & Steiner 2013). Though *F. grandifolia* is shade-tolerant (Busby et al. 2008), canopy gaps generated by natural disturbances allow for the continued recruitment of shade-intolerant species and persistent dominance of *Quercus* and *Carya,* both of which are more moderately tolerant of shade but relatively long-lived (Bolton & D'Amato 2011; Richards & Hart 2011; Vepakomma et al. 2012; Cowden et al. 2014). As natural fire regimes have all but ceased in the eastern United States, the shorter-lived but shade-tolerant *Acer rubrum* has become increasingly prolific in eastern forests (Hall & Motzkin 2002; Flinn & Marks 2007; Hanberry

2013; Thompson et al. 2013), whereas *Quercus rubra* and other fire-adapted trees have declined (Abrams & Copenheaver 1999; McCarthy et al. 2001; Johnson & Abrams 2009; Cowden et al. 2014).

Suburban forest remnants face a number of altered dynamics that can impede the expected secondary succession of a temperate deciduous forest. Forest fragmentation instigates dual negative effects not only by reducing a woodland's overall area but also by creating a higher proportion of sensitive edge habitats, which experience greater fluctuations in microclimates (Meffe & Carroll 1994; Zhou et al. 2011; Schulz & Gray 2013), are more prone to liana invasion (Ladwig & Meiners 2010; Brudvrig & Damschen 2011), can pose a physical barrier for seed dispersal (Cadenasso & Pickett 2001; Devlaeminck et al. 2005; Komuro & Koike 2005), and provide increased habitat for ruderals (Koncz et al. 2011; Čepelová & Münzbergová 2012). Uncontrolled deer populations in scattered forest refugia can decimate understory vegetation, particularly woody seedlings, and thus stall the development of a more mature forest (Côté et al. 2004; Aronson & Handel 2011; Bressette et al. 2012; Beauchamp et al. 2013). Fragmented suburban forests also tend to support higher proportions of escaped ornamental plants and other invasive species (Reichard & White 2001; McKinney 2004; Duguay et al. 2007; Gavier-Pizarro et al. 2010). For example, throughout a forest remnant in the Boston suburbs, Hamlin et al. (2012) found the proportion of invasive species to have increased in conjunction with twentieth-century suburbanization — expanding from 16% in 1895 to 35% in 2011 — and also noted that 75% of invasive species have persisted from 1895 to 2011, compared with a lower 62% of native species.

Secondary succession may be studied comprehensively through the establishment of permanent vegetation plots in undisturbed environments that are intended to be monitored across

decades or even centuries (Phillips 1959; Bakker et al. 1996; Pickett et al. 2001; Wilson et al. 2004). For instance, the Buell-Small Successional Study, the longest North American study of post-agricultural secondary succession, was established on the New Jersey Piedmont in 1956 and has produced a wealth of data concerning the spatio-temporal dynamics of vegetation throughout abandoned agricultural fields (Meiners et al. 2002; Bartha et al. 2003; Meiners et al. 2009; Ladwig & Meiners 2010). Among the practical applications of this line of long-term research are prioritizing restoration efforts and understanding the extent that passive vegetation recovery can succeed on its own without intervention, neither of which would be discernible from looking at only a single time slice (Pickett et al. 2001; Young et al. 2005; Cadenasso et al. 2009; Hobbs et al. 2011).

Comparatively few studies have attempted to distinguish changes in suburban deciduous forests that are truly indicative of succession and those that simply reflect short-term variations in temperature, precipitation, and ongoing human disturbances (Chaideftou et al. 2012). In this study, I analyzed vegetation sampled in permanent monitoring plots across decadal, interannual, and seasonal timeframes. My goals were to gain a broad understanding of the temporal dynamics in control of succession throughout a suburban forest remnant, to verify whether my observed temporal patterns aligned with the expected successional trajectories of a typical eastern deciduous forest, and to strengthen land management decisions by better discerning actual succession from short-term floral variations. My major predictions were that the most notable changes across the decade would involve an increase of late-successional vegetation and a reduction of early-successional vegetation. I also predicted that the magnitude of change in herbaceous vegetation would increase along with time between survey periods and that herbaceous species would experience a greater degree of change than woody species.

Additionally, I expected that succession would occur at differential rates in relation to variation in such factors as time since reforestation, canopy openness, proximity to forest edges or canopy gaps, and the initial presence of invasive species, with the most disturbed habitats being identified as at greatest risk of invasive species colonization.

Materials and Methods

Study Area

Situated on the Piedmont physiographic province, the Middle Patuxent Environmental Area (MPEA) is located in Howard County, Maryland near the suburban communities of Columbia and Clarksville, roughly 40 km southwest of Baltimore and 60 km north of Washington, D.C. (lat 39°12’35’’N, long 76°54’27’’W). Today, the MPEA encompasses 413 ha of secondary successional forest as well as a few managed meadows and riparian habitats near the Middle Patuxent River, which completely bisects the property. Collaboratively managed by the Howard County Department of Recreation and Parks and the non-profit Middle Patuxent Environmental Foundation, the MPEA’s mission is centered on natural resource conservation, environmental education, research, and passive recreation. Previously cleared and utilized for agriculture beginning in the eighteenth century, the MPEA has since reverted to forest at staggered rates and has remained undisturbed since being set aside for conservation in the mid 1960s. Over the next 35 years, a few periodic studies were conducted at the MPEA that have provided some baseline data on vegetation (Carlson et al. 1971; Connor et al. 1971). The MPEA offers a prime opportunity to study secondary succession at the interface of an isolated forest and suburbia, and recent vegetation surveys at the MPEA in the early twenty-first century allow for robust successional analyses with ongoing data that continue to be collected.

Data Collection (2001)

In 2001, Schwierjohann and Farfaras (unpubl. data) established 110 20 x 20 m (0.04 ha) long-term monitoring plots spaced 150 m apart east to west and 250 m apart north to south to collect ongoing data to develop an adaptive management plan (Fig. 1). Each plot was marked with a center tree, from which a 10 m transect extended in each cardinal direction (Fig. 2). An initial dataset of herbaceous species, shrubs, and trees was collected over the course of that summer between June and September. Two 1 x 1 m quadrats were placed on each transect between 4–5 m and 9–10 m to sample the percent coverage of all herbaceous and woody species constituting the ground layer of less than 1 m tall (Daubenmire 1959). Members of Poaceae, Cyperaceae, and Juncaceae, aside from the invasive grass *Microstegium vimineum*, were broadly grouped together as graminoids during this initial year. The diameter at breast height (DBH) of all large shrubs (> 1m tall) and trees was estimated throughout the entire 0.04 ha plot at 1.37 m high using the following size classes: 1 = 0–13.2 cm, 2 = 13.3–27.6 cm, 3 = 27.7–42 cm, 4 = 42.1–56.4 cm, and 5 > 56.5 cm. Deer browse was also recorded using the codes: 1 = 0%, 2 = 1–5%, 3 = 6–15%, 4 = 16–30%, 5 = 31-50%, 6 = 51–75%, and 7 = 76–100%.

Data Collection (2009)

A problem with the initial 2001 dataset was that its early-summer and late-summer sample units could not be properly compared with each other because of the high degree of temporal variation that herbaceous vegetation, particularly noxious invasives such as *M. vimineum* and *Alliaria petiolata* of which control is crucial to the MPEA's management of natural resources, experiences throughout the summer (Cypher et al. 1988; Smith et al. 2007). Deer browse tends to increase seasonally as well (Williams & Ward 2006). Consequently, Koontz (2011) and Beauchamp re-sampled all of the permanent plots in June 2009 to control for

this semiannual variation that was present in the original 2001 dataset, as well as to gather data for long-term successional comparisons. Herbaceous plants were surveyed in each 1 x 1 m quadrat as in 2001; however, all herbaceous species, including graminoids, were classified to the species level whenever possible. The DBH of all mature trees throughout the entire plot was again recorded but was measured specifically, rather than aggregating into size classes. Shrubs were also sampled in 2009, but under a different methodology than in 2001 and these data are not used in this analysis. Soil samples were gathered from each corner of the four 1 x 1 m quadrats positioned at 4–5 m along each transect, using a tulip bulb planter extended to a depth of 12–15 cm (Koontz 2011; Beauchamp et al. 2013). Each plot's samples were then consolidated and sent to Brookside Labs in Knoxville, OH, where they underwent soil chemistry analyses to determine the soil pH (McLean 1982); the percentage of organic matter (Schulte & Hopkins 1986); the concentrations of nutrients including nitrate, nitrogen release, phosphorus, calcium, and sulfur; and the percentages of sand, silt, and clay.

Data Collection (2012)

The 2009 sampling had its own disadvantages in that it did not cover any late-summer herbaceous species dynamics and its exclusively early-summer timeframe prevented any long-term comparisons from being made with the more than half of plots that were originally sampled during the late summer of 2001. To control for semiannual variation and obtain data for successional analyses with these latter plots, I collected two additional herbaceous datasets of all of the plots, first in the early summer from June 4, 2012 to July 6, 2012 and again during the late summer from August 21, 2012 to September 23, 2012. Ground-layer vegetation was sampled using the same methodology as in 2001.

Large shrubs greater than 1 m tall were sampled using a different methodology than in 2001, as it was deemed unfeasible to survey larger woody species either in the small 1 x 1 m quadrats or by measuring the DBH of a typical shrub with multiple stems (Phillips 1959; Brockerhoff et al. 2008*b*; Koontz 2011; Wiser et al. 2011). The percent coverage of shrubs greater than 1 m in height and percent coverage of deer browse were recorded in four larger, 2 x 4 m quadrats placed on each transect at 6–8 m (Wiser et al. 2011; Beauchamp unpubl. data). Within the entire plot, all shrubs greater than 1 m in height were tallied, but their DBH was not measured. Woody deer browse was again recorded as well. Mature trees over 1.5 m tall were not sampled in 2012 because they were not expected to have changed significantly since the 2009 sampling; however, the number of tree saplings 1 to 1.5 m tall, though not their DBH, was recorded in 2012, as this size class had been missed in previous years. The percent coverage and number of individual tree seedlings, defined as tree species less than 1m tall, were surveyed along with their deer browse in the eight 1 x 1 m quadrats during both sampling periods in 2012.

Environmental variables including the percent coverage of total understory vegetation, bare soil, leaf litter, woody debris, rocks, and water were also recorded during both sampling periods in 2012. Leaf litter depth was measured at three diagonal points starting at the quadrat's bottom left corner. These environmental data were subsequently averaged for each plot. To assess canopy cover and transmitted light, a single set of four photographs was taken between the two sampling periods in July to August 2012 using a DSLR camera equipped with a hemispherical lens. The camera was positioned along each transect at 7 m, attached to a level tripod at 1.4 m high. Canopy photographs were taken on overcast days to prevent bright sun from distorting the measure of light intensity. Average values of canopy openness and transmitted light were subsequently derived using the software programs SideLook and Gap Light Analyzer.

Weather data concerning average temperature and precipitation during each sampling period and the preceding winter and spring were obtained from NOAA.

Herbaceous and woody species were identified using Weakley (2012), Brown and Brown (1972, 1984), Newcomb (1977), Del Tredici (2010), Uva et al. (1997), Hitchcock (1971), and the results of previous MPEA plant surveys as detailed in Beauchamp et al. (2013). Additional visits were made to the MPEA in the spring and early summer of 2013 to verify the identifications of any spring ephemerals, particularly members of Poaceae, Cyperaceae, and Juncaceae, that were not in flower during either of the 2012 sampling periods. By 2012, 11 plots had been removed from the study because over half of the plot had either eroded into the river, stretched onto a managed meadow no longer being influenced by succession, or extended onto inaccessible private property, thereby reducing the number of plots to 99.

Data Analysis

Herbaceous vegetation was analyzed across three separate time scales. The two semiannual datasets sampled in 2012 were compared with each other to assess phenological variations within a single growing season and to identify any major differences in vegetation composition between the early summer and the late summer. Comparisons between the June 2009 and June 2012 datasets were also conducted to identify interannual variations in vegetation that may result from yearly differences in temperature or precipitation, as well as from any interobserver inconsistencies. To investigate the bigger picture of decadal successional patterns at the MPEA, which can be better discerned from other sources of variation after identifying any distinctly semiannual and interannual differences, the original 2001 dataset was compared with a composite 2012 dataset comprised of plots sampled in whichever of the two timeframes was

consistent with their original 2001 survey — 44 plots in the early summer and 55 in the late summer. Shrubs and trees were analyzed from a decadal standpoint only.

Species distributions were comprehensively analyzed using both presence/absence data and abundance data. Common species were defined as species present in 30 or more plots. Abundance was assessed using the mean percent coverage for herbs and small shrubs (<1 m tall) and the number of individuals per plot for large shrubs (>1 m tall) and mature trees (>1 m tall). An importance value (IV) was calculated for the shrub and tree taxa that incorporated data on both frequency and abundance. For shrubs, relative abundance was calculated from coverage in the 1 x 1 m quadrats for the small shrub stratum (<1 m) and, for the large shrub stratum (>1 m), either by the number of quadrats occupied for the 2001 dataset or by coverage in the 2 x 4 m quadrats for the 2012 dataset. Shrub relative frequency was determined for the small shrub stratum by the number of 1 x 1 m quadrats occupied and for the large shrub stratum by the number of individuals in the whole plot. Tree IVs were calculated for each plot as the relative average of frequency and basal area. Tree saplings (1–1.5 m) that were sampled in 2012 were combined with the mature tree data collected in 2009 to comprise a more recent dataset on trees greater than 1 m in height to be compared with the original 2001 dataset of trees over 1 m tall. To account for the number of tree seedlings being recorded over a smaller area than the number of mature trees, the total ground area of 8 m^2 sampled for seedlings out of a whole plot's 400 m^2 that was sampled for mature trees was factored into any comparisons among the different tree strata.

To investigate whether species may be migrating into different plots at different successional stages while retaining a similar total number of plots — a process that would be masked when only examining net changes in frequency — I defined the additional metric of plot

turnover as the ratio of a species' newly colonized plots to its total change in plot frequency between datasets. Herbaceous importance values (IVs) were also derived as the mean of coverage and frequency throughout a plot's 8 quadrats, and a paired *t*-test was then conducted using these herbaceous IVs to discern any significant differences in specific plots between sampling periods at each of the three scales of comparison.

Alpha, beta, and gamma diversity have long been employed to describe vegetation since Whittaker (1960) first developed these three components of species diversity. While alpha diversity and gamma diversity are essentially the same concept applied at different scales, respectively reporting an inventory of the sample unit and of the greater landscape, beta diversity represents a very different idea, that of the gradient of change among sample units throughout space and/or time (Whittaker 1960; McCune & Grace 2002; Jurasinski et al. 2009). Beta diversity can be depicted in a number of ways, and recent literature has criticized the inconsistencies in which beta diversity is utilized in vegetation studies (Jurasinski et al. 2009; Moreno & Rodriguez 2010; Tuomisto 2010*a–c*, 2011; Semeniuk & Cresswell 2013). To more thoroughly analyze vegetation succession at the MPEA, I incorporated two metrics of species change into my analyses. First, beta diversity was calculated in the R package vegan (R Development Core Team 2013) with the vegdist function, using a Sorensen distance measure. My second metric of species compositional change, proportional effective species turnover, has been utilized in a similar study of forest understory vegetation (Chaideftu et al. 2012) and was calculated as:

$$\beta_y = 1 - Sy/S_a$$

with S_y being the species richness of dataset *y* and S_a the cumulative species richness of all datasets (Tuomisto 2010*b*).

Multivariate analysis is a widespread approach to studying the relationships between vegetation species composition and land management (Chytry et al. 2002; Cooper et al. 2006; Oliver et al. 2013; Peters et al. 2013), and non-metric multidimensional scaling (NMDS) is one of the most common and robust ordination techniques applied to vegetation studies (Clarke 1993; McCune & Grace 2002; Austin 2013; Salako et al. 2013). I conducted an NMDS in PC-ORD version 5.10 (McCune & Mefford 2013) to visualize successional shifts. These ordinations were performed using herbaceous coverage and shrub and tree IVs. The NMDS settings in each analysis included a Sorensen distance measure, the slow-and-thorough autopilot mode, 250 runs with real data, a maximum of 500 iterations, and a random starting configuration. Ordination results were assessed using the criteria of McCune and Grace (2002) that included a target mean final stress of less than 20, preferably between 10 and 15. The Pearson's (r) correlation coefficients were used to identify the species most correlated with each axis.

Results

Throughout all of the plant surveys at the MPEA, a total of 436 vascular plant taxa spanning 277 genera and 106 families has been recorded (Table 1). This tally comprises 295 herbaceous taxa, 55 of which are graminoids, as well as 57 shrubs, 68 trees, and 16 lianas/vines. Exclusively within the long-term monitoring plots that were surveyed in 2001, 2009, and 2012 as part of this study, there were 322 taxa comprised of 41 shrubs, 51 trees, 15 lianas/vines, and 167 herbaceous taxa, including 48 graminoids.

When most graminoid species and the genera *Galium, Geum, Oxalis, Potentilla/ Fragaria, Solidago,* and *Viola* were each consolidated as a single morphospecies for uniformity in analysis among survey periods, there were 148 herbaceous taxa spanning 60 families. The most represented herbaceous families were Asteraceae (14 morphospecies), Lamiaceae (11

morphospecies), Fabaceae (9 morphospecies), and Polygonaceae (8 morphospecies). Though graminoids were combined for analysis, there have been 27 species in Poaceae, 18 species in Cyperaceae, and three species in Juncaceae identified at the MPEA in this study. The greatest number of herbaceous morphospecies was observed in 2012, though both of the earlier datasets had more morphospecies than either of the separate 2012 datasets. Fifty-one herbaceous morphospecies were present in all four datasets. The 2009 survey added 25 new morphospecies, while 28 morphospecies were tallied for the first time in 2012. The numbers of morphospecies unique to a single dataset included 23 in 2001, 15 in 2009, 7 in the early summer of 2012, and 11 in the late summer of 2012.

Among shrubs, a total of 57 species, plus eight woody liana species and the liana genus *Vitis*, have been cumulatively identified, and 41 shrubs and eight lianas were noted as present in the long-term monitoring plots in at least one sampling year. Thirty-three shrub morphospecies spanning 13 families were incorporated into this analysis, with the genera *Clematis* (1 species and generic), *Crataegus* (generic), *Rubus* (5 species), *Smilax* (2 species), *Vaccinium* (4 species), and *Vitis* (generic) each consolidated. There were multiple morphospecies in Rosaceae, Adoxaceae, Caprifoliaceae, and Celastraceae. All but one morphospecies was initially recorded in 2001, and 20 of them remained present in 2012.

Lastly, there have been 68 tree species in 23 families identified throughout the MPEA. The most represented family is Fagaceae (15 species), followed by Juglandaceae (8 species) and Sapindaceae (6 species). Fifty-one of these species have been observed in the long-term monitoring plots of this study. For analysis, 29 tree morphospecies were utilized, including the consolidated genera of *Carya* (6 species), *Fraxinus* (2 species), *Prunus* (3 species), *Quercus* (12

species), and *Ulmus* (3 species). Twenty-four of these morphospecies were recorded in both periods of sampling, one was recorded only in 2001, and four were tallied only in 2009–2012.

Beta Diversity

Beta diversity at the decadal scale was significantly different among herbaceous vegetation, shrubs, and trees ($p < 0.001$), and both this metric and proportional effective species turnover tended to decrease as growth habit longevity increased (Fig. 3; Table 2). Herbaceous beta diversity increased significantly ($p < 0.01$) along with length of time between replicates. In contrast, proportional effective species turnover was significantly highest in September 2012 ($p < 0.01$) and indistinguishable amongst the other three datasets. When examining its relationship with environmental characteristics, herbaceous beta diversity was in all three timeframes negatively correlated with total vegetation coverage, species richness, native species coverage, exotic species coverage, and coverage of *M. vimineum* and was positively correlated with depth and coverage of leaf litter (Table 3a). At only the two shorter scales, beta diversity had positive correlations with elevation, distance to a riparian habitat, soil organic matter, nitrogen, sulfur, and nitrate and negative correlations with exotic species richness and coverage of *Arisaema triphyllum, Persicaria, Polystichum acrostichoides,* and *Viola.* There were no significant correlations between herbaceous beta diversity and either canopy openness, distance to forest edge, or time since reforestation.

For the shrubs, proportional effective species turnover differed notably between 2001 and 2012, with the former year having a higher share of unique shrub species. Less common species in eight native genera disappeared completely: *Cephalanthus occidentalis, Corylus americana, Hamamelis virginiana, Kalmia latifolia, Maclura pomifera, Malus,* and *Staphylea trifolia.* Shrub beta diversity had significant positive correlations with overall species richness, native species

richness, distance to forest edge, leaf litter depth, and coverage of *Berberis thunbergii* and *Rubus*; it was negatively correlated with time since reforestation and *Lindera benzoin* coverage (Table 3b). In contrast, there was a higher proportion of unique tree species in 2012 than there were shrubs in that latter year. Tree beta diversity was positively correlated with species richness and length of time since reforestation and negatively correlated with tree density (Table 3c).

Herbaceous Species

Species present in over 30 plots in all of the four survey periods were considered the most common species. Twelve herbaceous morphospecies were consistently defined as common: *Alliaria petiolata*, *Arisaema triphyllum*, *Circaea canadensis*, *Galium*, graminoids, *Microstegium vimineum*, *Parthenocissus quinquefolia*, *Persicaria*, *Polystichum acrostichoides*, *Potentilla indica/ Fragaria vesca*, *Sanicula canadensis*, and *Viola* (Table 4a). Most of these common herbs are perennials, though *M. vimineum*, *Galium*, *Persicaria*, and *A. petiolata* are annuals. In terms of origin, *M. vimineum*, *P. indica*, *Persicaria*, and *A. petiolata* are exotic species, and both *M. vimineum* (Rauschert et al. 2010; Anderson et al. 2013) and *A. petiolata* (Lankau 2013; Waller & Maas 2013) are regarded as particularly problematic invasive weeds.

The most striking expansions in plot frequency at the decadal scale involved invasive *A. petiolata* and the understory herbs *P. acrostichoides* and *P. indica/ F. vesca*. Fewer changes in frequency occurred across the two shorter timeframes, and the most common herbs actually exhibited a greater degree of change seasonally than they did interannually. Between 2009 and 2012, the prolifically distributed *M. vimineum* and *P. indica/ F. vesca* gained in frequency. Weather variations between 2009 and 2012 were also noteworthy in that the former year had higher than average rainfall while the latter was preceded by an uncharacteristically mild winter (Table 5). In contrast, the greatest changes in frequency throughout the summer of 2012 involved

reductions of spring ephemerals such as *A. triphyllum*, *Viola*, and the less frequent *Podophyllum peltatum*. *Oplismenus undulatifolius*, a less common species but one that is worth mentioning because it is a relatively recent invasive weed to have colonized Maryland, was absent from the MPEA in 2001 but present in 3 plots in 2009 and 12 plots in 2012, increasingly so in the late summer when this perennial has reached its seed-producing stage.

When examining herbaceous abundance, most of the common species declined in their mean coverage throughout all three timeframes (Table 6a). Decadally, *M. vimineum* exhibited a steep dropoff from its initially highest mean coverage, but this formidable riparian invader still managed to rank highest in coverage during both of the 2012 survey periods even with its decline. Graminoids trailed *M. vimineum* in both of these respects, while *A. petiolata* had the largest decadal increase in coverage. At the interannual scale, graminoids displayed the only major increase in coverage. Seasonally, an increase of the summer-emergent *M. vimineum* and a reduction of the early-summer annual *A. petiolata* far exceeded the magnitude of all other changes in abundance.

Despite net decreases in occupancy, nearly all common herbs still exhibited some shifts to previously unoccupied plots, especially at the decadal and interannual scales (Table 7a). Incorporating both frequency and abundance, the significantly higher importances of *A. petiolata* ($p < 0.01$) between 2001 and 2012 involved considerable shifts to previously unoccupied plots. *M. vimineum* displayed relatively high decadal turnover without a significant per-plot change in importance, in contrast to *P. acrostichoides*'s significant increase with little turnover ($p < 0.01$). The interannual increases in *M. vimineum* ($p < 0.01$) and graminoids ($p < 0.01$) were also significant and involved some degree of plot turnover. Throughout 2012, the drastic seasonal declines of *P. quinquefolia*, *A. triphyllum*, and *Viola* involved little or no plot turnover, unlike the

significant seasonal shifts in importance of both *A. petiolata* ($p < 0.01$) and *M. vimineum* ($p < 0.01$).

NMDS results for the longest of these three herbaceous comparisons produced a slightly higher than desirable mean final stress of 21.10 that explained 65.7% of the variance (Fig. 4a). The decadal trajectories in this short-lived stratum veered in all directions from the NMDS configuration's origin with no single overarching trend in their movements. The horizontal axis, of which plots shifted in both positive and negative directions, was most correlated with *M. vimineum* ($r = –0.74$). Major correlations with the ordination's vertical axis, which featured slightly more plot shifts in a positive bearing, included *P. indica/ F. vesca* ($r = 0.51$), *Persicaria* ($r = 0.38$), graminoids ($r = 0.36$), *M. vimineum* ($r = 0.33$), and *A. petiolata* ($r = 0.32$).

Shrubs

In the shrub stratum, the exotics *Lonicera japonica, Celastrus orbiculatus,* and *Rosa multiflora* and the native *Lindera benzoin* exceeded 90 plots in frequency (Table 4b). Among the other most common shrubs were *Rubus,* the exotics *Elaeagnus umbellata* and *Berberis thunbergii,* and the natives *Smilax* and *Viburnum prunifolium*. Nearly all of the common shrubs increased in frequency by greater than 10 plots. Some of the most alarming increases in frequency concerned the invasive shrubs *B. thunbergii, C. orbiculatus,* and *E. umbellata*. The greatest degree of plot turnover was exhibited by *Rubus,* contrasting with the expanded ranges of prolific *L. benzoin, B. thunbergii, E, umbellata,* and *R. multiflora* being accompanied by very minimal turnover among established plots (Table 7b).

The most abundant small shrubs (<1 m tall) in both years were *L. benzoin, L. japonica,* and *R. multiflora* (Table 5b). *Berberis thunbergii, R. multiflora,* and *Rubus* expanded the most in small shrub abundance between surveys. Among large shrubs (>1 m tall), an initial total of 4088

individuals in 2001 had increased to 6044 by 2012 (Table 8a). Most large shrubs exhibited a decadal increase in number, aside from the three *Viburnum* species. The number of large *E. umbellata* individuals more than doubled, *R. multiflora* nearly doubled as well, and *B. thunbergii* increased at an even greater magnitude but still lagged far behind these other two invasive shrubs in total number. *Lindera benzoin* was the most abundant large shrub in 2001 and became more numerous in 2012, but it was surpassed overwhelmingly by *E. umbellata* and to a lesser degree by *R. multiflora*.

The NMDS configuration performed on shrub importance values produced an attractive three-dimensional solution with a mean final stress of 16.79, explaining 82.0% of the variance (Fig. 4b). The shifts of plots throughout species space were largely directed both upwards and rightwards. This pattern was most overwhelmingly correlated with an increase in *E. umbellata* ($r_{\text{x-axis}} = 0.88$), in addition to decent increases in *L. benzoin* ($r_{\text{y-axis}} = 0.69$) and *R. multiflora* ($r_{\text{y-axis}} = 0.47$) and declines in both *V. acerifolium* ($r_{\text{y-axis}} = -0.54$), and *Vaccinium* ($r_{\text{y-axis}} = -0.52$).

Trees

Nine common tree morphospecies were observed in greater than 30 plots in both survey periods (Table 4c). The three most common trees were *Liriodendron tulipifera, Acer rubrum,* and *Cornus florida*, and other common morphospecies included *Nyssa sylvatica, Quercus, Carya, Carpinus caroliniana, Prunus,* and *Fagus grandifolia.* Most trees either declined in frequency or increased only slightly, and the greatest decreases were those displayed by *Prunus, C. florida, A. rubrum,* and *Quercus.* A majority of trees that declined in frequency still colonized some new plots (Table 7c). There were 4339 mature trees (>1 m tall) in 2001 and a reduced 3501 in 2009–2012 (Table 8b). *Carpinus caroliniana* and *L. tulipifera* boasted the most individuals, both with little plot turnover. *Fagus grandifolia*'s increased occupancy was mostly in newly

colonized plots. The most dramatic decline over the decade was *C. florida*'s. The NMDS of mature trees resulted in a mean final stress of 18.59 that explained 81.6% of the variance (Fig. 4c). Of the three major growth habits, the tree stratum's replicates displayed the least pronounced shifts in species space between 2001 and 2012. Most changes in position were in a downward direction that was correlated with reduced *Robinia pseudoacacia* ($r_{\text{y-axis}} = 0.60$) and a greater importance of both *L. tulipifera* ($r_{\text{y-axis}} = -0.56$) and *F. grandifolia* ($r_{\text{y-axis}} = -0.51$).

Over 70% of trees in both survey periods were in the smallest DBH class of 0–13.2 cm (Table 9). Though this lowest range comprised a heterogeneous mixture of species, it fully encompassed the sapling height category of 1–1.5 m tall that was in 2012 overwhelmingly dominated by *F. grandifolia* with 112 of the 214 individuals. Distantly following *F. grandifolia* in this latter respect were *C. caroliniana* with 36 saplings and *A. negundo* with 32. *Fagus grandifolia* was also the only common species to increase in its number of overall individuals between 2001 and 2012. Only 40% of plots contained one or more saplings in 2012, and comparatively fewer saplings were observed than either tree seedlings (<1 m tall), mature trees, or large shrubs in this same height range. Decadally, most DBH classes decreased in membership except for the highest class of >56.5 cm, of which *L. tulipifera* had the most individuals maturing into this greatest category. The two highest DBH classes were restricted almost entirely to *L. tulipifera, Quercus,* and *Carya.*

Tree seedlings were analyzed from a seasonal rather than a decadal perspective. There were 2826 individual seedlings observed in the early summer of 2012 and a reduced 1972 seedlings present in the late summer. The most common morphospecies occurring at this young phenology were *Prunus, L. tulipifera, C. caroliniana,* and *A. rubrum* (Table 6c). While *Prunus,*

L. tulipifera, *A. rubrum*, and *C. florida* decreased in prevalence over the season, *C. caroliniana* and *Carya* were observed in greater numbers.

Deer Herbivory

Deer browse was generally less pronounced in herbs than in woody species. Most of the common herbs shared the trends of decadal and interannual declines in deer herbivory but a prominent seasonal increase throughout 2012 (Table 10a). The range of average deer browse was highest in 2001, with the browse of many herbs recorded in much greater numbers than in subsequent years. Among the most heavily browsed herbs were *Circaea canadensis, Galium,* and *Sanicula canadensis*, all of which increased noticeably in deer browse throughout the summer of 2012 along with most of the common herbs.

Deer herbivory of shrubs was assessed separately for the small shrub and large shrub strata, with the latter category incorporating data from both the 8 m^2 quadrats and the plotwide sampling. Small shrubs displayed a mean browse of 5.2% in the early summer of 2012 and 21.3% in the late summer, compared with the mean browse of large shrubs being 7.3% in their single early-summer sampling period (Table 10b). Although the invasive *R. multiflora* experienced the most deer browse in the small shrub stratum during both sampling periods, most other invasive shrubs such as *E. umbellata*, *Rubus*, *B. thunbergii*, and *L. japonica* had only minimal browse in 2012. Within the large shrub stratum, native shrubs *V. acerifolium, Smilax,* and *Rubus* were closely followed by *R. multiflora* as the most browsed species (Table 10c). Across the decade, most large shrubs declined in their recorded browse, with the exceptions of perceptible increases in *R. multiflora* and *L. benzoin.*

Tree seedlings experienced an increase in deer browse throughout the summer of 2012 that accompanied their overall decline in number (Table 10d). On average, 1.6% of seedlings

were browsed in the early summer compared with a greater 12.9% in the late summer. There was comparatively high browse in *N. sylvatica, C. caroliniana, Carya,* and *F. grandifolia.* The two most prevalent seedling species, *L. tulipifera* and *Prunus*, exhibited relatively little browse, especially in the early summer, and this pattern was shared by *A. rubrum*.

Discussion

My results offer visible evidence of decadal changes in the MPEA's vegetation, most overwhelmingly exotic species in the herbaceous and shrub strata as well as some discernible changes in the tree stratum. Though the level of change exhibited by mature trees was relatively the lowest, this change was concentrated in a consistent direction and is indicative of the predicted successional trajectories of an eastern deciduous forest. Affirming my predictions, the late-successional tree *Fagus grandifolia* obviously became more dominant, especially amongst the youngest saplings to have entered the mature height class since 2001. Shrubs also had a noticeable change across the decade. However, reflecting the MPEA's vulnerability as a disturbed forest fragment in the suburbs (McDonald et al. 2008; Mattingley & Orrock 2013; Schulz & Gray 2013), shrubs differed from trees in experiencing a reduction in native species richness and a proliferation of invasive species, namely *Elaeagnus umbellata, Rosa multiflora,* and *Berberis thunbergii.* Unlike woody species, the MPEA's herbaceous vegetation varied considerably and in no singular direction, precluding true successional change from being discerned from the high degree of variation that this most dynamic, short-lived growth habit undergoes both seasonally and interannually. Nevertheless, there is indeed evidence that three major invasive species in the herbaceous stratum — *Microstegium vimineum, Alliaria petiolata,* and *Oplismenus undulatifolius* — have been expanding throughout the MPEA since 2001 at a disconcerting rate.

Both beta diversity and proportional effective species turnover tended to be higher for herbaceous species than for either of the woody strata, even when comparing the two shorter timeframes at which exclusively herbs were analyzed alongside woody data spanning the decade. Forest biodiversity is generally higher for herbaceous vegetation (Gilliam 2007; Buraniak et al. 2013), which can display substantial variation seasonally as a result of rapidly-completed life cycles and a greater sensitivity than woody plants to such seasonally fluctuating factors as canopy openness and soil moisture content (Bellemare et al. 2005; Chapman & McEwan 2013). That the highest discrepancy in the proportional effective species turnover of herbs was between the seasonal 2012 datasets and not at the decadal or interannual scales underscores the ephemeral nature of many of the MPEA's herbs. This seasonal variation should inform the MPEA's adaptive management plan, accounting for the statistically significant decline of *Alliaria petiolata*, the proliferation of *Microstegium vimineum* and *Oplismenus undulatifolius*, and the dynamic behaviors of native spring ephemerals such as *Podophyllum peltatum*, of which it would be grossly misleading to compare June abundance in certain microhabitats with that of other areas sampled in September.

In addition to the relatively high herbaceous beta diversity, the lack of a uniform directionality in the NMDS configuration substantiates that a high degree of ongoing variability is obscuring any strong patterns at even this longest decadal timeframe, differing remarkably from the overwhelming directional movements throughout species space that are present in the NMDS results of the shrub and tree strata. In attempting to discern patterns of long-term successional change, it is clear that for this most early-successional growth form, a longer timescale is needed to unambiguously differentiate ecological succession from fleeting, short-term variations. In addition, the fact that herbaceous turnover was correlated neither with

distance to forest edge, which would reflect a gradient of disturbance and variable microclimates, nor with canopy openness or length of time since reforestation, both of which would associate herbaceous variation with successional progress towards a more mature forest, further underscores that herbs do not seem to be consistently responding in the same direction in accordance with the successional stage of the forest. This lack of an overarching trend among herbs corroborates findings of the Buell-Small Successional Study (Bartha et al. 2003; Cadenasso et al. 2009) and other forest understory studies (Bakker et al. 1996; Brunet et al. 2011; Chaideftou et al. 2012; Fridley & Wright 2012) that found high interannual variations among understory herbs. Additionally, interobserver variation can also play some role in interannual vegetation studies conducted by multiple observers and is perhaps a greater factor for herbs than for woody species (Gotfryd & Hansell 1985; Milberg et al. 2008; Moore et al. 2011; Jordan et al. 2013).

Despite the high level of herbaceous noise, there are indeed some observable patterns of change in this non-woody stratum, mainly involving invasive species. *Microstegium vimineum* has served as a major engineer of herbaceous species change at the MPEA, as indicated by its steadily expanding frequency, its colonization of unoccupied plots as was measured by plot turnover, its strong correlations with movement of sample units throughout species space in the NMDS configuration, and its persistently high abundance, even with a pronounced decrease in abundance over the decade. *Microstegium vimineum* may be declining in abundance in areas that are progressing towards a more mature forest while reasserting a stronger presence under newly exposed gaps and along forest edges, as it can be more competitive under the lower light levels of canopy gaps than many other typical grasses (Schramm & Ehrenfeld 2010; Cheplick & Fox 2011; Huebner 2011; Kuebbing et al. 2013). A concurrent study at the MPEA (Duguay &

Farfaras 2011) found this invasive species to be expanding its range into the forest understory in response to deer herbivory of woody seedlings, which has reduced interspecific competition. Other research in suburban forests has corroborated the aptitude of *M. vimineum* at colonizing empty areas decimated by deer browse, which can have the long-term effect of delaying forest succession by severely limiting the number of young trees entering the mature ecosystem (Aronson & Handel 2011; Anderson et al. 2013). Though *M. vimineum* spreads relatively slowly on its own (Rauschert et al. 2010), human contact can greatly accelerate its spread and is thus of particular concern in a fragmented forest with both a high edge-to-area ratio and heavily-utilized hiking trails.

Like *M. vimineum*, other exotic herbs have also displayed discernible patterns of change. *Alliaria petiolata*'s combined increase in frequency at the decadal scale, its highest decadal increase in abundance among common herbs, and its shared correlation with the vertical movement in the NMDS plot illustrate that this early-summer weed has been expanding throughout the MPEA at a fast rate and that is certainly likely to continue to do so (Blossey 1999; Katz et al. 2010; Waller & Maas 2013). Though not a common species, the increased presence of invasive *Oplismenus undulatifolius* warrants efforts to completely eradicate this weed from the MPEA before it achieves the omnipresence of *M. vimineum* and *A. petiolata* (Beauchamp unpubl. data). The incorporation of the general public into the control and continued monitoring of these invasive species at the MPEA may be worthwhile, and the MPEA and nearby Patapsco State Park have already had success in organizing volunteer sessions to pull stands of *A. petiolata.* None of the major exotics were very palatable to deer, which among their herbaceous food options seemed to prefer less frequent native species.

These early-successional herbs have been reestablishing themselves below canopy gaps caused by storm damage, in sparse understories decimated by deer browse, and around hiking trails and pipeline corridors that are regular maintained. Disturbance and weather events can temporarily reverse successional trajectories and may disproportionately reset successional pathways in the herbaceous stratum (Basler & Korner 2012; Fu et al. 2013), such as initiating the reemergence of *M. vimineum* and other graminoids under newly established canopy gaps (Roberts 2004; Copenheaver 2008; Banasiak & Meiners 2009; Bruelheide & Luginbuhi 2009). *Potentilla indica* also thrives in disturbed edge habitats and suffers decreased growth rates under reduced light intensity (Wang et al. 2012). Despite these increases in early-successional herbs, there is indeed some evidence of expected forest succession with the significantly greater abundance over the decade of *Polystichum acrostichoides*, one of the MPEA's most common understory herbs and one that would be expected to increase in conjunction with the progression towards a more mature forest (Singleton et al. 2001; Welch et al. 2007).

At the other extreme of temporal change, the lowest beta diversity and smallest discrepancy in proportional effective species turnover of the tree stratum were anticipated over the relatively small span of woody growth from 2001 to 2012 because of the longer life cycles of this growth form (Li et al. 2012; Chetelat et al. 2013; Evans et al. 2013). Among woody species, tree beta diversity's positive correlation with reforested history and negative correlation with tree density indicate that it was the areas of the MPEA with the most recently cleared legacy that changed the greatest in tree species composition between 2001 and 2012. Though shrubs intuitively fell in between herbs and trees in both of these metrics of change, the fact that proportional effective species turnover in the shrub stratum was so much lower in 2012 than in 2001 is cause for alarm and suggests that an increased colonization by invasive species may be

responsible for having not only reduced all three species of native *Viburnum* but also wiped out some of the less common native shrubs completely. The significant correlations of shrub beta diversity with distance to forest edge and reforested legacy substantiate that it is these most disturbed habitats that are experiencing the greatest change in shrub species composition (Schulte et al. 2011; Henkin et al. 2013; Schulz & Gray 2013) and suggest areas of the MPEA that should be prioritized for restoration efforts, as they may be most susceptible for further colonization.

In contrast with the herbaceous stratum, the two woody strata displayed distinct patterns of change between 2001 and 2012, with the shrub stratum's behaviors raising further concerns over the proliferation of exotic species. The most prevalent shrubs at the MPEA are clearly the native *Lindera benzoin* and the invasives *Elaeagnus umbellata* and *Rosa multiflora.* These three species were consistently the most common and the most abundant, with their abundances in the large shrub stratum exceeding most other species by large margins. However, it was three invasive species — the aforementioned *R. multiflora* and *E. umbellata* along with *Berberis thunbergii* — that displayed the most pronounced increases in shrub abundance and were the main engineers of the long-term successional change observed at the MPEA over the decade. Exotic species may deter secondary succession on abandoned agricultural lands, prolonging an old field's existence and delaying development of a regrowth forest (Tognetti et al. 2010; Tognetti & Chaneton 2012; Kuebbing et al. 2013*b*). The low plot turnover of these three major invasive shrubs suggests that they will continue to maintain a stronghold, rather than exhibit only a fleeting dominance in response to the creations of canopy gaps or edge disturbances.

A number of studies have found *R. multiflora* to be much more strongly associated with edge habitats than comparable invasives such as *B. thunbergii* or *E. umbellata* (Yates et al. 2004;

Banasiak & Meiners 2009; Brym et al. 2011; Matlack & Schaub 2011; Schulz & Gray 2013), and it is conceivable that maintenance of these edges may foster conditions for *R. multiflora* to invade. Though *R. multiflora* can be dispersed by birds like *E. umbellata* and *L. benzoin* (Mooney et al. 2010; Brym et al. 2011), it differs drastically from these other two most common shrubs in that it reproduces more prominently through clonal spread after it has colonized a suitable habitat (Jesse et al. 2010). Clonal reproduction is widely regarded as a major advantage of invasive species colonization (Myster & Pickett 1990).

Like *R. multiflora, E. umbellata* is also more of a sun-demanding shrub (Catling et al. 1997; Brym et al. 2011; Moore et al. 2013). *E. umbellata* has advantages in colonization over the MPEA's other two most prevalent shrubs in its unpalatability to deer (Knapp et al. 2008), its allelopathic effects (Orr et al. 2005), and its broad crowns that severely limit the light that reaches native shrubs and tree seedlings (Brantley & Young 2009; Kern et al. 2012; Evans et al. 2013). In comparison, *L. benzoin* can thrive in shadier habitats (Mooney et al. 2010; Mooney & Niesenbaum 2012), but it is more susceptible than *E. umbellata* to deer herbivory (Schramm & Ehrenfeld 2010; Lind et al. 2012). The MPEA's adaptive management plan may want to consider an incorporation of *E. umbellata* removal, as this invasive may be infringing upon the traditional niche of *L. benzoin* and the early-successional *Viburnum prunifolium*. The increase of *Berberis thunbergii* by over a third was the most of any invasive shrub and should be considered worrisome. *Berberis thunbergii* is also unique among the MPEA's most common invasive shrubs in that is a shade-tolerant species that can be expected to increase along with forest succession, and it has been found to thrive under forests on regenerated agricultural lands and also within forest-edge habitats (DeGasperis & Motzkin 2007; Mosher et al. 2009; Lubell & Brand 2010; Brand et al. 2012; Ward et al. 2013).

Concerning trees, the overwhelming dominance of *Liriodendron tulipifera* supports that the MPEA is by and large still a relatively young forest recovering from a lengthy cleared legacy, as *L. tulipifera* is commonly the first tree to colonize canopy gaps in the decades following agricultural abandonment (Elliott et al. 1998; Hart et al. 2008; Richards & Hart 2011). *Liriodendron tulipifera*'s low palatability to deer has also contributed to its success at the MPEA (Terwei et al. 2013). At the same time, the increasing presence of *Fagus grandifolia* offers evidence that there are indeed portions of the MPEA with a longer-forested history that are steadily progressing towards a later successional stage (Abrams & Hayes 2008; Busby et al. 2008; Copenheaver 2008). It is astounding that over half of the plots in 2012 lacked any trees in the sapling (1–1.5 m) height range at all, and *F. grandifolia*'s overwhelming majority in this height range suggests that it will continue to expand over the following decades and cause the MPEA to more closely resemble a mature forest (Wilder et al. 1999; Morgan 2009; Richards & Hart 2011). *Fagus grandifolia* also benefits from an ability to propagate via root sprouts (Takahashi et al. 2010; Morris et al. 2014) as well as from being one of the least preferred woody food choices of deer (Busby et al. 2008; Krueger et al. 2009), allowing it a substantial advantage at growing into the mature tree stratum.

The fact that most trees declined in abundance and the overall smaller numbers of trees assigned to all but the largest DBH class suggest that dieoff, instigated by such factors as storm damage, is reducing trees at a greater rate than at which intensely browsed juveniles are surpassing a critical height threshold at which they can escape deer herbivory. The most dramatic decline of *Cornus florida* can be attributed to dogwood anthracnose, an aggressive disease spreading through eastern deciduous forests (Holzmueller et al. 2006; Katz et al. 2010; Murphy & McCarthy 2012). Though *Acer rubrum* was indeed prevalent throughout the MPEA and

remained consistently more abundant than *Quercus* and *Carya*, it was much less abundant than either *L. tulipifera* or *C. caroliniana.* The fact that *A. rubrum* decreased in abundance over the decade to a degree that was second only to *C. florida*'s is noteworthy because *A. rubrum* is overwhelmingly expanding in deciduous forests across the United States (Abrams 1998; Flinn & Marks 2007), a result of the halt of natural disturbances that has hindered the regeneration *Quercus* and *Carya* (Albrecht & McCarthy 2006; Goins et al. 2013; Cowden et al. 2014). However, it has been found that forest type is a serious driver of seedling recruitment in deciduous forests and that *A. rubrum* is significantly more common in pine forests than hardwood forests due to its affinity for low organic matter, carbon, and phosphorus (Bughalho et al. 2013); these soil factors may have influenced *A. rubrum*'s more limited abundance at the MPEA.

The MPEA's estimated deer density of 41/km^2 (Duguay & Farfaras 2011) is relatively very high for a suburban community (Bughalho et al. 2013; Urbanek & Nielsen 2013; Williams et al. 2013; Nuttle et al. 2014). Deer herbivory has been seriously threatening the tree seedling stratum and increased steadily throughout the summer of 2012, as evidenced by both the reduction of seedlings by nearly a third and their rise in browse rate of over 10%. Though the seasonal decline of seedlings may be partially explained by some individuals recorded in June having grown taller than 1 m by September and therefore left unrecorded, the greater prevalence of deer browse in the late summer suggests that herbivory is the primary cause of this reduction in seedlings. The overall lack of correlation between the dominant seedling species and the corresponding dominant species in the mature tree stratum further substantiates this conjecture. It follows logically that the two most prolific seedlings, *L. tulipifera* and *Prunus,* were two of the least palatable species to deer (Abrams & Steiner 2013; Terwei et al. 2013).

Management Implications

Repeated monitoring of the MPEA's 99 permanent plots would not only produce valuable data for the management of natural resources at the MPEA but would also contribute more knowledge of secondary succession to the greater scientific community in a similar manner as the classic Buell-Small Successional Study (Pickett et al. 2001; Cadenasso et al. 2006; Meiners et al. 2009). Herbaceous vegetation should be re-sampled every five years in both June and September to account for the observed seasonal variation. Mature trees and shrubs can be re-sampled at ten-year intervals that repeat the 2012 sampling protocols, though seedlings should be monitored more frequently in conjunction with the herbs. Additional woody sampling after a large disturbance such as a hurricane or in response to any changes in deer management would also be valuable for investigating vegetation recovery processes (Boucher & Mallona 1997; Krueger et al. 2009; Zenner et al. 2013). As many of the MPEA's most pronounced changes in both the herbaceous and woody strata involved invasive species and deer herbivory altering the natural trajectories of succession, two factors that tend to be much more pronounced in forest fragments with a high edge ratio, the MPEA should continuously re-evaluate vegetation in these plots in response to any changes in the park's invasive plant control efforts or managed deer hunt.

Chapter Two

The influence of agricultural abandonment and the abiotic environment on the vegetation communities of a suburban deciduous forest

Abstract

Length of time since agricultural abandonment, variations in topography and soil, and forest fragmentation associated with suburban development can influence dominant vegetation and foster exotic species invasion in a secondary successional forest. The Middle Patuxent Environmental Area (MPEA) in Maryland, USA is a regrowth forest adjacent to suburban sprawl that was abandoned from agriculture at staggered rates. I surveyed vegetation throughout the MPEA to investigate how these factors have influenced distribution and abundance and to identify which forest microhabitats are at greatest risk of invasive species colonization. My predictions were that time since abandonment would explain the broader differences in succession but that topography and an interface with suburbia would be the strongest determinants of microhabitat differences and invasive species within an area of similar abandonment history. I performed a hard noise clustering analysis using the R package vegclust to classify the MPEA into herbaceous, shrub, and tree communities each dominated by similar species. Tree communities differed distinctly in accordance with agricultural abandonment, proximity to suburban edges, and soil nutrients, with dominant species reflecting the expected trends of a deciduous forest. Shrub and herbaceous communities also displayed some pattern reflecting time since abandonment, but there was a greater dominance of early-successional invasive species such as *Microstegium vimineum, Elaeagnus umbellata,* and *Rosa multiflora* in these strata. A prevalence of disturbance, as well as invasive species encroachment into the

mature forest understory, underscores the need for invasive species management to be prioritized throughout various successional stages.

Introduction

Vegetation succession describes an ongoing, directional change in the species composition and three-dimensional dynamics of a plant community, with sequential stages in which herbaceous species, shrubs, shade-intolerant trees, and finally shade-tolerant trees replace each other as the dominant vegetation type (Clements 1916; Anderson 2007; Pickett et al. 2009). A disturbance to established vegetation initiates secondary succession by reverting the environment to an earlier successional stage. Time since abandonment can be a major determinant of the present-day successional stage, species composition, and species richness of vegetation (Myster & Pickett 1990; Bain & Brush 2004; Fraterrigo et al. 2006; Brudvig & Damschen 2011). When compared with forests that have matured under succession for a longer time, secondary successional sites with a more recent agricultural legacy typically differ in their abundance of understory vegetation, availability of seed propagules (Van Diggelen & Marrs 2003; Devlaeminck et al. 2005; Beauchamp et al. 2013), herbivore habitat (Miles 1979; Duguay & Farfaras 2011), and soil nutrients (Cousins et al. 2009; Chiang et al. 2010; Catorci et al. 2012; Wright et al. 2012), all of which can persistently influence vegetation recovery for decades or even centuries to come (Price et al. 2010; Sato et al. 2010; Paal et al. 2011; Zenner et al. 2013).

Landscape features including topography, elevation, slope, and light intensity have influenced historical choices in land use (Fraterrigo et al. 2006; Abrams & Hayes 2008; Brush 2009) and continue to have their own ongoing effects on vegetation, irrespective of time since abandonment (Motzkin et al. 1999; Baeten et al. 2010). Forest fragmentation can instigate dual negative effects by not only a reducing a woodland’s overall area but also creating more at-risk

edge habitats with a greater fluctuation in microclimates (Meffe & Carroll 1994; Zhou et al. 2011), susceptibility to liana invasion (Ladwig & Meiners 2010; Brudvrig & Damschen 2011), and physical barriers for seed dispersal (Cadenasso & Pickett 2001). Present-day suburban development constructed on previously rural farmland enhances these edge effects on forest remnants, as the more frequent human disturbances that occur along a high edge-to-area ratio can perpetuate early-successional conditions (Pickett & Cadenasso 2008; Barbati et al. 2013; Copenheaver et al. 2013; Lohmus & Liira 2013). Especially when adjacent to human disruptions, early-successional habitats are at a higher risk of colonization by invasive plants such as the aggressive annual grass *Microstegium vimineum* and the annual herb *Alliaria petiolata* (Kuhman et al. 2011; Tognetti et al. 2010; Morris et al. 2011; Anderson et al. 2013).

The eastern Piedmont physiographic province was originally the most productive agricultural region of the United States prior to the settlement of more fertile soils in the Midwest, after which many Piedmont farms were left to revert to forest (Curtin et al. 2001; Bowen et al. 2007; Napton et al. 2010). In a comprehensive chronosequence of secondary successional forests throughout the Piedmont Plateau, Matlack (2009) found soil organic matter and sulfur to increase along with forest succession, approaching uncleared forests within 100 years, while other nutrients such as calcium and phosphorus decline sharply in the decades following agricultural abandonment. These differences in soil chemistry can promote the dominance of different plant species.

In this study, my objectives were to investigate how time since agricultural abandonment, variations in landscape and soil features, and a juxtaposition against modern suburbia have jointly affected the present-day distribution and abundance of vegetation throughout a secondary successional forest. Additional goals were to identify the forest microhabitats at greatest risk of

invasive species spread, so that restoration efforts may be prioritized, and to better understand the circumstances in which successful vegetation recovery can occur passively in conjunction with forest succession. I surveyed herbaceous and woody plants throughout a secondary successional forest on the Piedmont Plateau that had previously been utilized in agriculture to differing degrees before abandonment, in addition to displaying variation in topographic features such as elevation and proximity to forest-edge and riparian habitats. I predicted that a gradient of time since abandonment would explain the more broadly observed differences in forest successional stages but that within an area of similar abandonment history, the strongest determinants of microhabitat differences and colonization by invasive species would be topography and an interface with suburbia along forest edges and hiking trails (Morris et al. 2011; Catorci et al. 2012).

Materials and Methods

Study Area

The Middle Patuxent Environmental Area (MPEA) is located on the Piedmont Plateau in Howard County, Maryland, near the suburban communities of Columbia and Clarksville (lat 39°12’35’’N, long 76°54’27’’W). It encompasses 413 ha of secondary successional forest, as well as a few managed meadows and riparian habitats along the park’s bisecting Middle Patuxent River. The reserve is bounded by housing developments on three sides and a major roadway on the fourth. The MPEA’s topography includes minor hills and valleys along with soils dominated by Manor and Gladstone types, which are relatively well drained (Kraft 2008). Collaboratively managed by the Howard County Department of Recreation and Parks and the non-profit Middle Patuxent Environmental Foundation, the MPEA’s mission is centered on natural resource conservation, environmental education, research, and passive recreation.

Most of the MPEA was previously cleared and utilized in agriculture beginning in the eighteenth century before being abandoned at different intervals and forming a secondary successional forest (Fig. 5a). The most northern 296 ha represent part of a historical land tract known as Doughoregan Manor, which was first settled by the family of Charles Carroll in 1711 and utilized in various farming operations for roughly two centuries (Dorsey 1968; Curtin et al. 2001). A hand-drawn map produced in 1834 (Dawson 1834) indicates that most of Doughoregan Manor at that time contained farmland but that there were two sizeable patches of forest, though it is unknown whether those woodlands remained continually forested while a regrowth forest was established throughout most of the Doughoregan Manor tract prior to the earliest known aerial photograph taken in 1943. In contrast, the MPEA's southern 117 ha are situated in a separate historical land tract known as The Discovery, which housed a grist and textile mill from the mid 1700s through the 1920s (Dorsey 1968). In the 1960s, developer James Rouse incrementally purchased tracts of formerly rural farmland to build the planned suburban community of Columbia and chose to set aside the MPEA for conservation, though a few small farms and a game preserve continued to operate until the property was formally bestowed to the Howard County Department of Recreation and Parks in 1996 to be overseen by the Middle Patuxent Environmental Foundation (Schwierjohann & Farfaras 2000; Stebenne & Mitchell 2007).

Vegetation Sampling

To analyze the spatial distributions of vegetation at the MPEA and relate these patterns to different environmental gradients and time since reforestation, I sampled the vegetation throughout 99 20 x 20 m (0.04 ha) permanent plots in 2012 that had previously been established as part of a long-term vegetation monitoring study. I accounted for seasonal variation in

herbaceous phenology by collecting two complete datasets, first in the early summer from June 4, 2012 to July 6, 2012 and again during the late summer from August 21, 2012 to September 23, 2012. The percent coverage of all herbaceous and woody species less than 1 m in height, as well as the number of woody seedlings in this height category, was recorded in eight 1 x 1 m quadrats. Large shrubs taller than 1 m had both their percent coverage recorded in four larger, 2 x 4 m quadrats and their total numbers of individuals tallied throughout the entire plot (Brockerhoff et al. 2008*a*; Wiser et al. 2011). Also throughout the plot, the number of trees and large shrubs with vines or lianas and the identity of each twining species present on each tree or large shrub were recorded. Mature tree data collected in 2009 (Koontz 2011) were analyzed alongside the herbaceous, shrub, and tree seedling data collected in 2012 because mature trees were not expected to have changed substantially since the 2009 dataset was collected.

Environmental Data

Within each plot's eight 1 x 1 m quadrats in which understory vegetation was sampled, environmental variables including the percent coverage of total understory vegetation, bare soil, leaf litter, woody debris, rocks, and water were also recorded during both sampling periods in 2012. Leaf litter depth was measured at three diagonal points starting at the quadrat's bottom left corner. These environmental data were subsequently averaged for each plot. To assess canopy cover and transmitted light, a single set of four photographs was taken between the two sampling periods in July to August 2012 using a DSLR camera equipped with a hemispherical lens. The camera was positioned along each transect at 7 m, attached to a level tripod at 1.4 m high. Canopy photographs were taken on overcast days to prevent bright sun from distorting the measure of light intensity. Average values of canopy openness and transmitted light were subsequently derived using the software programs SideLook and Gap Light Analyzer.

During previous sampling efforts in 2009, soil samples were gathered from each corner of the four 1 x 1 m quadrats positioned at 4–5 m along each transect, using a tulip bulb planter extended to a depth of 12–15 cm (Koontz 2011; Beauchamp et al. 2013). Each plot's samples were then consolidated and sent to Brookside Labs in Knoxville, OH, where they underwent soil chemistry analyses to determine the soil pH (McLean 1982); the percentage of organic matter (Schulte & Hopkins 1986); the concentrations of nutrients including nitrate, nitrogen release, phosphorus, calcium, and sulfur; and the percentages of sand, silt, and clay.

Time Since Reforestation

Spatial data and historical records were acquired from the Howard County Department of Recreation and Parks, the Columbia Archives, and the Maryland State Archives. Aerial photographs, which are commonly utilized in land-use studies to create a historical timeline of land-use changes (Ruiz & Domon 2009; Zhou et al. 2011; Brachetti et al. 2012; Martin et al. 2013), were acquired from the Howard County GIS Division and/or purchased from Air Photographics, Inc. The earliest known aerial photograph covering the MPEA, captured in 1943, was compared with subsequent images taken in 1952, 1966, 1970, 1977, 1988, 1997, 2002, and 2011 (Hogan & Walbridge 2009; Chetelat et al. 2013). The aerial photographs were georectified in ArcGIS 10 using spatial layers of Howard County's major roads and waterways (Bishop & McBratney 2001; Zhou et al. 2011), and the total forested area and cleared area of each time slice were calculated.

Digital Data

Digital data pertaining to soil and landscape features were also related to the MPEA using ArcGIS 10. Elevation values were obtained from National Elevation Dataset (NED) 30 m Digital Elevation Model (DEM) data generated by the U.S. Geological Survey (Gesch et al. 2002; Gesch

2007; Bain & Brush 2008). The elevation of each long-term monitoring plot was extracted from the DEM using the Spatial Analyst extension in ArcMap. Soil series and soil drainage data were acquired from the SSURGO soil database (Natural Resource Conservation Service 2013). Soil drainage data consisted of three descriptive categories: well-drained, moderately well-drained, or poorly drained. Lastly, the distances of each plot to the nearest forest edge and a river or stream were also calculated in ArcMap to assess any correlations with these major landscape features, with a forest edge defined as either the MPEA's boundary, the nearest hiking trail, or the nearest of two managed meadows, whichever was closer.

Data Analyses

Multivariate analysis is a widespread approach for classifying vegetation into similar communities and studying the relationships between species composition and land management (Chytry et al. 2002; Cooper et al. 2006; Oliver et al. 2013; Peters et al. 2013). I performed a hard noise clustering analysis using the R statistical package vegclust (R Development Core Team 2013) to classify the MPEA into five herbaceous communities, four shrub communities, and five mature tree communities each dominated by similar species, plus a reasonably sized noise class of outliers for each stratum (De Caceres et al. 2010; De Caceres & Wiser 2012; Wiser & De Caceres 2013). This analysis was conducted using coverage values for the herbs and importance values for the shrubs and trees that incorporated both relative frequency and relative abundance. For the noise clustering and indicator species analyses, the seasonal herbaceous datasets that I collected in June and September of 2012 were consolidated into a single dataset listing the maximum coverage of each species. The parameter delta (δ), a pre-specified distance that determines the cutoff for defining outliers for the noise class, was set at 1.0. The number of communities per stratum was determined by plotting graphs of the number of groups versus

changes in the noise class, cluster variance, and proportion of all objects and identifying the value at which the number of groups leveled off. After defining the groups, I used PC-ORD version 5.10 (McCune & Mefford 2013) to perform an indicator species analysis to identify the species most associated with each group (Dufrene & Legendre 1997; McCune & Grace 2002).

To determine if the resulting communities differed significantly with respect to continuous spatial and environmental gradients, I performed a permutation procedure in R in which the result of an ANOVA was compared with a reference distribution derived from my own data. Post-hoc assessments between individual communities were made by comparing the overlap of their 95% confidence intervals. Whether the categorical variables of soil type and soil drainage differed among communities was analyzed through a chi-square analysis in SPSS. In addition, a Spearman's correlation analysis was conducted in SPSS to determine whether abundance of the major invasive species differed significantly in terms of these underlying environmental factors. For the shrub stratum, invasive species were grouped first by stratum and then by shade-tolerance for this latter analysis. The correlation analysis was not performed on trees because there were very few invasive trees.

I also conducted non-metric multidimensional scaling (NMDS), one of the most robust ordination techniques applied to vegetation studies (Clarke 1993; McCune & Grace 2002; Austin 2013; Salako et al. 2013), in PC-ORD to visualize relationships among the monitoring plots as determined by their species composition and to examine the major relationships between species and the environmental gradients of canopy openness, transmitted light, distance to forest edge, distance to river/stream, elevation, slope, latitude, reforested date (since 1943), exchange capacity, pH, percent organic matter, nitrogen release, sulfur, phosphorus, phosphates, calcium, magnesium, potassium, sodium, other bases, hydrogen, beryllium, iron, magnesium, copper,

zinc, aluminum, nitrate, ammonia, sand, silt, and clay. The NMDS settings in each analysis included a Sorensen distance measure, the slow-and-thorough autopilot mode, 250 runs with real data, a maximum of 500 iterations, and a random starting configuration. In the herbaceous stratum, species present in fewer than 5 plots were excluded from the ordination to reduce noise. To control for the large discrepancies in scale of the environmental gradients, all of the environmental data were relativized by maximum for the NMDS (McCune & Grace 2002). Ordination results were assessed using the criteria of McCune and Grace (2002) that included a target mean final stress of less than 20, ideally between 10 and 15. The squared values of the Pearson's (r) correlation coefficients identify the proportion of variation on an ordination axis that is explained by each variable, and the most notable environmental gradients with r^2 values exceeding 0.2 were rendered on the NMDS plots.

Results

While most of the MPEA's northernmost Doughoregan Manor tract had already become reforested before the first aerial photograph was taken in 1943, considerable central and southwestern portions across both major tracts remained cleared until agriculture had ceased completely during the following decades (Fig. 5b). Corresponding with this regional variation in reforestation, the MPEA also differed regionally in several of its major landscape and soil properties. Elevation was highest in the park's long-forested, northwestern quadrant and lowest throughout the riparian basin that supports more early-successional, herbaceous vegetation (Fig. 6a). Consequently, though a majority of the MPEA's soils was well-drained, soils classified as moderately or poorly drained coincided with the early-successional, low elevation regions surrounding the river and its tributary streams (Fig. 6b). When grouped by soil series, Gladstone loam predominated in the MPEA's most late-successional regions west and northeast of the

river, Manor loam defined the western riparian habitats and the eastern forested region almost entirely, and Codorus loam comprised the riverbed itself (Fig. 6c). Likewise, soil exchange capacity, nitrate, calcium, and to a lesser extent phosphorus were generally lower in the MPEA's late-successional forests and higher closer to the riparian region defined by more early-successional vegetation; both sulfur and nitrogen release displayed an opposite pattern (Fig. 7a–f).

Herbaceous Species

The hard noise clustering analysis organized the herbaceous stratum into five communities with the major indicator species of *Microstegium vimineum, Potentilla indica/ Fragaria vesca, Polystichum acrostichoides, Desmodium nudiflorum,* and *Thelypteris noveboracensis* (Fig. 8a). *Microstegium vimineum* is a noxious invasive species in the Mid-Atlantic region that prolifically establishes dense monocultures in early-successional habitats, though the weed can also exhibit some shade-tolerance in disturbed environments. *Potentilla indica* and *F. vesca,* respectively exotic mock strawberry and native woodland strawberry, were combined as a single morphospecies to control for interobserver variation, and their community represents a second more recently reforested group. The final three *Desmodium, Polystichum,* and *Thelypteris* groups are late-successional communities defined by shade-tolerant herbs. The early-successional *Microstegium* and late-successional *Desmodium* communities each comprised just under a third of the overall plots, followed in number by the late-successional *Polystichum* community and finally, with much smaller membership, by the *Thelypteris* and *Potentilla/Fragaria* communities.

In the NMDS configuration (Fig. 9a), which had a mean final stress of 16.52 that explained 70.7% of the variance, the horizontal distribution of plots was correlated with the late-

successional fern *P. acrostichoides* ($r_{x\text{-axis}} = 0.66$) and the vertical arrangement was associated with the early-successional herbs *M. vimineum* ($r_{y\text{-axis}} = 0.67$), *Persicaria* ($r_{y\text{-axis}} = 0.45$), *P. indica/ F. vesca* ($r_{y\text{-axis}} = 0.44$), and *Alliaria petiolata* ($r_{y\text{-axis}} = 0.43$). Herbaceous communities differed in their average dates of reforestation ($p < 0.01$), with the *Microstegium* and *Potentilla/Fragaria* communities not becoming reforested until the 1960s on average and the average known year of reforestation for each of the other three assemblages falling very close to the earliest known date of 1943 (Table 11a). Low elevation ($r_{x\text{-axis}} = –0.42$) was the most important topographical feature separating the *Microstegium* community from the other groups. This early-successional community also had a high nitrate level ($r_{y\text{-axis}} = 0.62$; $p < 0.01$), which was identified as the most important environmental gradient by the NMDS. Soil organic matter ($p = 0.02$) differentiated the late-successional *Desmodium* and *Polystichum* communities, whereas nitrogen release ($p = –0.01$) differed between the *Polystichum* and *Thelypteris* communities. Edge effects, as indicated by distance and transmitted light, were not apparent in the herbaceous stratum, nor did these communities differ in soil series ($\chi^2 = 34.93$, $p = 0.09$) or drainage class ($\chi^2 = 10.53$, $p = 0.40$).

Like *M. vimineum*, the other major exotic herbs also tended to be more common in early-successional habitats. Two such exotics, *Persicaria perfoliata* and *Alliaria petiolata*, were more secondary indicators of the *Microstegium* community. The newly invasive perennial *Oplismenus undulatifolius*, which was recorded throughout the MPEA for management purposes wherever it happened to be observed, was most congregated in the park's central quadrant (Fig. 10) and overlapped most strongly with the *Potentilla/Fragaria* community. Irrespective of community assignments, the Spearman's correlation analysis found abundance of exotic herbs to be the most correlated with the early-successional characteristics of high nitrate levels, a recent date of

reforestation, low elevation, high phosphorus content, and proximity to the riparian region (Table 12a), the latter of which was also reflected by the greater abundance of exotics on poorly drained soils and Codorus loam. The three forest-understory communities possessed less understory vegetation, less exotic species coverage and lower exotic species richness than the *Microstegium* community.

Shrubs

The four shrub communities categorized by the noise clustering analysis had the indicator species of *Rosa multiflora*, *Elaeagnus umbellata*, *Lindera benzoin*, and the mixed native shrubs *Smilax*, *Viburnum prunifolium*, and *Viburnum acerifolium* (Fig. 8b). Two of these main indicators, *R. multiflora* and *E. umbellata*, are invasive species of great concern in the Mid-Atlantic region, in contrast to the native *Lindera* and *Smilax–Viburnum* communities better reflecting a natural and healthy understory of an eastern deciduous forest.

The NMDS for the shrub stratum had a mean final stress of 14.86 that explained a high 84.9% of the variance (Fig. 9b). The most major species correlatations included *L. benzoin* ($r_{\text{x-axis}} = -0.75$), *Vaccinium* ($r_{\text{x-axis}} = 0.52$), and *R. multiflora* ($r_{\text{x-axis}} = -0.46$) with the horizontal axis and the major exotic shrubs *E. umbellata* ($r_{\text{y-axis}} = 0.61$), *R. multiflora* ($r_{\text{y-axis}} = 0.56$), and *B. thunbergii* ($r_{\text{y-axis}} = -0.51$) with the vertical axis. There was both a rightward and downward progression from early-successional to late-successional habitats, and this variation was best explained by a vertical correlation with reforested history ($r_{\text{y-axis}} = 0.53$). The *Lindera* and *Smilax–Viburnum* communities were correlated with an earlier reforested date, the *Elaeagnus* community was most strongly associated with a recent date of reforestation, and the *Rosa* community predominantly comprised more recently reforested plots but also contained some more scattered, earlier forested plots.

The distribution of shrub communities did not reflect elevation or edge effects. Neither soil series ($\chi^2 = 14.68$, $p = 0.48$) nor drainage class ($\chi^2 = 3.32$, $p = 0.77$) differed among shrub communities, and there were few significant differences in soil properties other than singling out the smallest *Smilax–Viburnum* community differing from the other three groups in its low exchange capacity ($p = 0.04$), high organic matter ($p = 0.04$), high nitrogen ($p = 0.05$), low phosphorus ($p < 0.01$), and low calcium ($p = 0.05$) (Table 11b). It was lower calcium ($r_{\text{x-axis}} = -0.49$) and copper ($r_{\text{x-axis}} = -0.49$) content that best separated this mixed native community from the similarly long-forested *Lindera* community in the NMDS configuration. This mixed faction of native shrubs also had less abundant understory vegetation ($p < 0.01$) and exotic herbs ($p < 0.01$) than the other three groups.

Exotic shrubs were naturally more common in the two communities defined by invasive shrubs than in the two native communities ($p < 0.01$). Exotic shrubs had fewer significant correlations with the abiotic environment than exotic herbs, though their most notable correlation was with the more recently reforested sites (Table 12b). This correlation was even higher amongst the majority of exotic shrubs that are shade-intolerant, early-successional species. Both *Celastrus orbiculatus* and *Lonicera japonica* were classified as shade-intolerant despite exhibiting some degree of success under the forest canopy, as these species are generally more common in early-successional habitats and along forest edges (Robertson et al. 1994). Exotic shade-tolerant shrubs, a category limited to *Berberis thunbergii* and the infrequently observed *Euonymus alatus*, were correlated with a longer forested history and a more enclosed forest canopy. The *Elaeagnus* community had less coverage of exotic shade-tolerant shrubs than the *Lindera* and *Rosa* communities ($p < 0.01$).

Trees

The five mature tree communities that were classified by the noise clustering analysis included a riparian community defined by *Acer negundo* and *Juglans nigra*; an early-successional community associated with *Prunus, Robinina pseudoacacia,* and *Acer rubrum*; another early/mid-successional *Liriodendron tulipifera* community; and late-successional *Carpinus caroliniana* and *Fagus grandifolia* communities (Fig. 8c). The smallest *Acer negundo–Juglans* community was restricted to riparian and edge habitats with ongoing disturbances, spanning regions with different dates of abandonment and causing the community's average reforested date to fall near the middle of the overall range. While the two early-successional communities were distributed throughout the MPEA, distribution of the two late-successional groups was much more segregated, with the *Fagus* community restricted to the most northern quadrant and the *Carpinus* community found almost exclusively east of the Middle Patuxent River. Every plot assigned to either the *Fagus* or *Carpinus* communities had remained forested since at least the first aerial photograph was taken in 1943. The concentration of tree seedlings in each of the five communities increased in relation to the community's stage in forest succession, with the *Fagus* community having the most seedlings per area (Fig. 11).

The NMDS for the trees resulted in a three-dimensional solution with a mean final stress of 16.02 that explained 81.4% of the variance (Fig. 9c). Species that were most correlated with the horizontal axis included *F. grandifolia* ($r_{\text{x-axis}} = 0.69$), *L. tulipifera* ($r_{\text{x-axis}} = 0.42$), *A. rubrum* ($r_{\text{x-axis}} = –0.48$), and *R. pseudoacacia* ($r_{\text{x-axis}} = –0.44$), whereas *C. caroliniana* ($r_{\text{y}} = 0.69$) and *Prunus* ($r_{\text{y}} = –0.64$) were correlated with the vertical axis, producing both an upward and rightward direction of succession. Similar to the shrub stratum, this variation in NMDS space was best explained by date of reforestation ($r_{\text{y-axis}} = –0.68$), which clearly separated the early-

reforested *Fagus* and *Carpinus* communities from the more recently reforested *Liriodendron* and *Prunus–Robinia–Acer rubrum* communities. Topographically, the *Fagus* community was furthest from a forest edge than any of the other tree communities ($p = 0.02$).

The tree communities of different successional stages generally differed much more in their environmental gradients than the communities of either of the two shorter-lived strata (Table 11c). The tree stratum was also the only stratum in which the communities differed in soil series ($\chi^2 = 59.49$, $p < 0.01$), with Gladstone loam more common in the *Fagus* and *Liriodendron* groups, Manor loam in the *Carpinus* and *Prunus–Robinia–Acer rubrum* groups, and Codorus loam in the *Acer negundo–Juglans* group. Though soil drainage class did not differ significantly ($\chi^2 = 17.44$, $p = 0.07$), there was a trend in which the *Acer negundo–Juglans* community was mainly limited to moderately and poorly drained soils. The greater nitrate level ($r^2_{\text{y-axis}} = 0.28$) and soil exchange capacity ($r^2_{\text{y-axis}} = 0.24$) of the early-successional groups trailed reforestation as explainers of the NMDS variation. The early-successional *Prunus–Robinia–Acer rubrum* and *Liriodendron* communities had higher levels of both nitrate ($p = 0.03$) and calcium ($p < 0.01$) as well as lower organic matter ($p = 0.03$), nitrogen ($p = 0.05$), and sulfur ($p < 0.01$) than the late-successional *Carpinus* and *Fagus* groups.

Coverage of understory vegetation ($p = 0.01$) was highest in the early-successional *Microstegium* and *Potentilla/Fragaria* communities, and the disturbance-maintained tree community of *Acer negundo–Juglans* community had the most abundant understory vegetation. The *Prunus–Robinia–Acer rubrum* and *Liriodendron* communities were distributed throughout recently reforested habitats, mostly in the central and southern portions of the MPEA. Invasive species were more common in the two least mature tree communities; the *Acer negundo–Juglans* group had the highest concentrations of *M. vimineum, A. petiolata,* and *P. perfoliata* and the

Prunus–Robinia–Acer rubrum community ranked highest in abundance of *E. umbellata* and *R. multiflora,* with plentiful *M. vimineum* and *P. perfoliata* as well. The *Fagus* community had the sparsest understory vegetation ($p < 0.01$) and fewest exotic herbs ($p < 0.01$).

Lianas

Lianas were attached to a total of 672 mature trees or large shrubs throughout 75 of the plots. The vast majority of affected trees and shrubs — 558 individuals — had only one twining species attached. The native genus *Vitis* was observed in the most plots, followed by the invasive lianas *Celastrus orbiculatus* and *Lonicera japonica*. *Celastrus orbiculatus* was attached to the most trees. Trees assigned to the early-successional *Prunus–Robinia–Acer rubrum* community had the most lianas, both proportionally and with their total of 248 individuals. Liana frequency was correlated with proximity to the riparian region (Table 12c) but not with distance to a forest edge.

Discussion

The MPEA's vegetation is broadly distributed in a manner indicative of differing times of agricultural abandonment, landscape features, and soil chemistry. Most conspicuously among trees, sections of the MPEA where agriculture ceased more recently differed remarkably from more isolated, lengthier forested areas in their community assignments, and the dominant species reflected predictable successional patterns of a temperate deciduous forest. Suburban edge effects were most apparent in the tree stratum as well, with the late-successional *Fagus grandifolia* community being concentrated furthest from forest edges. Both the shrub and herbaceous communities displayed some pattern corresponding to time since abandonment, but there was more noise and a greater importance of early-successional invasive species in these two strata. Soil properties were strong determinants of vegetation distributions in especially the

herbaceous and tree strata, most notably with the higher nitrate levels of early-successional communities.

In the herbaceous understory, the skewed assignment of the *Microstegium vimineum* community to plots on the MPEA's more recently cleared central and southern regions aligns with the expectations of an early-successional habitat that has yet to support a mature forest. The second major pattern of the *Desmodium nudiflorum* community dominating the understory of forests at the most mature successional stage corroborated the expected trajectories of understory vegetation resembling an intact forest within 60 to 80 years after reforestation (Abrams & Hayes 2008; Brunet et al. 2011). The Doughoregan Manor tract's known history of having two heavily forested sections as far back as 1834 further suggests that the *Desmodium* and *Thelypteris* communities may occupy areas that have been forested for much longer than the start of the time series in 1943. This conjecture is further supported by the *Desmodium* community's strong overlap with the tree stratum's late-successional *Fagus grandifolia* community, in contrast to the *Polystichum* community sharing a higher proportion of overlap with the more recently reforested *Prunus–Robinia–Acer rubrum* or *Liriodendron* communities.

Shrub communities were assigned with a clear relation to reforested date as illustrated in the NMDS configuration, and the fact that the *Smilax–Viburnum* community differed the most in its environmental gradients is likely explained by its most regionally uniform distribution in the MPEA's northern quadrant. Nevertheless, the behavior of invasive *Elaeagnus umbellata* mirrors that of *M. vimineum* in its dominance on the more recently forested Discovery tract and expansion into disturbed plots in the MPEA's more established Doughoregan forest. The *Elaeagnus* community's correlation with less understory vegetation reflects the power of this invasive shrub's allelopathic effects (Orr et al. 2005), its formation of dense and impenetrable

stands (Lemke et al. 2013), and the heightened ability of its broad crowns to decelerate succession by severely limiting the light that reaches vegetation growing upon the forest floor (Brantley & Young 2009; Kern et al. 2012; Evans et al. 2013). The native *Lindera* community was consistently assigned to areas with a more stable forested history where the shade-intolerant *E. umbellata* has yet to attain dominance. The early-successional *Rosa multiflora* community's unexpectedly skewed distribution in northern, longer-abandoned plots is best explained by *R. multiflora* being an inferior competitor to *E. umbellata* in more recently cleared sites but being able to thrive where there is a much sparser shrub layer (Meiners 2007; Kuhman et al. 2010).

Trees were the vegetation stratum most strongly assigned their community membership in accordance with time since agricultural abandonment. There is an expected successional trajectory at the MPEA in which old fields first come to be dominated by shade intolerant subcanopy trees such as *Prunus serotina*, *Acer rubrum*, or — in more riparian or disturbed habitats — *Acer negundo*, after which the shade-intolerant canopy dominant *Liriodendron tulipifera* is the first tree to colonize gaps and build an enclosed forest canopy (Hart et al. 2008; Richards & Hart 2011; Evans et al. 2013). This function of *L. tulipifera* was substantiated at the MPEA by its community's least number of trees. Placement of the early-successional *Prunus–Robinia–Acer rubrum* community and to a lesser extent the *Liriodendron* community was also mainly influenced by agricultural legacy, as evidenced by the congregation of these plots in the MPEA's central and southwestern quadrants that were most recently cleared.

Shade-tolerant trees, most prominently *Fagus grandifolia* and *Carpinus caroliniana*, subsequently develop under a shady *L. tulipifera* canopy and become dominant in the decades to follow (Brisson & Bouchard 2003; Bobiec et al. 2011; Terwei et al. 2013). The mature *Fagus* community differs the most from the other four groups and clearly represents a less disturbed,

late-successional forest. Compared to many of the more fleeting understory herbs, the broadleaf growth form of ferns and their affinity for growing in dense patches (Karst et al. 2005; Sabatini et al. 2013) can result in less understory habitat for tree seedlings (Engelman & Nylund 2006), thus contributing to the *Fagus* community's highest concentration of tree seedlings coinciding with an understory defined largely by the *Desmodium* community rather than either of the fern communities.

Generally corresponding with date of agricultural abandonment were the MPEA's local soil properties, which largely reflect the expected successional pathways of an eastern deciduous forest. In the decades following agricultural abandonment, an eastern regrowth forest can be expected to increase in soil organic matter, moisture content, and sulfur and decrease in pH, nitrate, calcium, and phosphorus until it resembles an uncleared forest within a century (Motzkin et al. 1999; Groffman et al. 2006; Flinn & Marks 2007; Matlack 2009). The MPEA exhibited some of these patterns in its great discrepancies in sulfur, calcium, and nitrate concentrations between the early-successional riparian basin and the longest-forested, northwestern quadrant. In fact, these soil properties appear to be an effective predictor of time since abandonment and can complement the incomplete information obtained from the aerial photographs.

Early-successional herbs such as *Microstegium vimineum* can accelerate nitrogen mineralization rates in nitrate-rich habitats (Ehrenfeld et al. 2001; Kuebbing et al. 2013). For a monoculture of *M. vimineum* to thrive, it requires specific edaphic conditions that include high transmitted light (Schramm & Ehrenfeld 2010; Cheplick & Fox 2011; Anderson et al. 2013), soil moisture (Barden 1987; Ho & Richardson 2013), and soil exchange of cations such as calcium (Hogan & Walbridge 2009; Kuhman et al. 2011). Forest-understory herbs such as *D. nudiflorum* can tolerate more elevated, well-drained soils with less clay content (Elliott et al. 1998; Welch et

al. 2007). The significant difference in soil organic matter and related differences in elevation, soil type, and distance to waterway between the *Desmodium* and *Polystichum* communities align with *Polystichum acrostichoides'*s role as an indicator of high soil moisture (Choi et al. 2012) and its affinity for organic matter (Bellemare et al. 2005), which is typically higher in more intensely farmed habitats (Wiser 1998; Clemens et al. 2010; Dyer 2010).

Because every plot in both the *Fagus* and *Carpinus* communities was already forested when the first aerial photograph was taken in 1943, it appears that a finer scale of soil series and particularly soil nitrate content are the best distinguishing gradients between these two long-established communities. Tree communities differed more strongly in their environmental gradients than communities of the other two strata, and the *Fagus* community's highest levels of nitrogen and organic matter along with its lowest nitrate and calcium levels reflect the aforementioned expectations of the longest-forested, most elevated, and least disturbed portions of a deciduous forest. The shrubs were unique in lacking major correlations with soil chemistry, aside from the native *Smilax*-*Viburnum* displaying such significant traits as low calcium and phosphorus that would be anticipated for a group restricted to the longest forested, least disturbed sites.

Specific to the MPEA's pocket within suburbia and distinguishing the reserve from a more intact deciduous forest is the ongoing disturbance associated with a high proportion of forest edges, heavily utilized hiking trails, and location that function as local determinants of vegetation across all three strata (Bruelheide & Luginbuhi 2009; Bernhardt-Romermann et al. 2011). That neither the herbaceous nor shrub communities differed significantly with respect to distance to forest edge may be explained by typical edge effects being so pervasive throughout

such a small and frequently-hiked forest remnant, except perhaps in the northwestern quadrant that is most isolated from human contact.

Though *M. vimineum* is most commonly established as early-successional monocultures, this invasive grass does have some level of shade tolerance (Fraterrigo et al. 2011; Tekiela & Barney 2013) and can exhibit a source-sink behavior in which early-successional monocultures can easily disperse seed into the adjacent forest, where the weed is often the best competitor at colonizing newly disturbed microhabitats below canopy gaps and along forest edges (Huebner et al. 2011; Warren et al. 2011; Schramm & Ehrenfeld 2012). While a relationship with edges is not apparent in the MPEA's more recently reforested, south-central portion, the minority of plots on the Doughoregan tract assigned to the *Microstegium* community generally border the edges of either suburban development, hiking trails, or the mowed pipeline corridor that runs parallel to the Middle Patuxent River. Graminoid encroachment into the forest is often transitory, easily giving way to more robust, shade-tolerant herbs as the forest canopy encloses. A related factor to the spread of *M. vimineum* is that the selective deer herbivory of woody seedlings can facilitate the spread of *M. vimineum* into the forest understory, and Duguay and Farfaras's (2011) previous study at the MPEA concluded that deer will continue to have a positive feedback on this invasive grass unless deer density is reduced, further delaying forest succession (Flory & Clay 2010).

Not all of the MPEA's major invasive species are early-successional. For the *Rosa multiflora* community, *R. multiflora*'s adaptive capability in response to disturbances involving canopy gaps and forest edges (Yates et al. 2004; Jones 2012) was an important factor in controlling its dominance, as evidenced by the group's assorted distribution and average year of reforestation that fell near the middle of the overall range (Brym et al. 2011; Moore et al. 2013). This feedback with disturbance was likely the most important factor explaining the different

distribution patterns of the two invasive, early-successional assemblages in the shrub stratum. Unlike the shade-intolerant *E. umbellata*, *R. multiflora* can easily colonize established forests (Matlack & Schaub 2011) and exhibits a more frequent turnover within a forest in response to shifting microclimates (Banasiak & Meiners 2009). Much more significant in this shade-tolerant characteristic is *Berberis thunbergii*, the only major invasive species at the MPEA that is expected to continue increasing along with forest succession (Mosher et al. 2009; Lubell & Brand 2010; Brand et al. 2012). Though *B. thunbergii* may originate as an escaped ornamental, it was strongly correlated with an enclosed forest canopy can prosper in late-successional, nitrogen-rich soils (Ehrenfeld et al. 2011) such as those in the MPEA's most northwestern quadrant, the area that is otherwise sparsest in the understory and bolsters the fewest invasive species.

In the tree stratum, membership of the smallest *Acer negundo–Juglans nigra* community was directly tied to ongoing disturbances, either at suburban boundaries or along the bisecting river. At the opposite end of the tree spectrum, the *Fagus* community's most significant correlation with the forest interior was evident in its lacking of negative edge effects such as liana invasion. The skewed prevalence of most major lianas in early-successional habitats, especially within the riparian corridor, is related to an affinity for edge habitats, and lianas have been observed in Piedmont forests to rebound quickly after disturbances (Ladwig & Meiners 2010; Leight-Young et al. 2010).

An understanding of how time since agricultural abandonment, soil and topographic variation, and differential suburban effects have affected vegetation at the MPEA can offer great value towards the prioritization of invasive plant management efforts. The herbaceous and shrub strata featured both more variation and a greater dominance of early-successional invasive

species, though the shade tolerance of *B. thunbergii* and the ability of such species as *M. vimineum, Rosa multiflora,* and increasingly *E. umbellata* to expand beyond forest edges under the enclosed canopy warrant concern for ongoing invasive species management long after the establishment of a regrowth forest. Very few exotic trees were identified at the MPEA, aside from a few scattered *Ailanthus altissima* and a forest-edge stand of *Paulownia tomentosa* that has been removed.

The MPEA's other most prominent invasive species in the herbaceous strata each overlap with the microhabitats favored by *M. vimineum* to some degree. The annual vine *Persicaria perfoliata* requires a similar niche as *M. vimineum* and can form intense monocultures in these early-successional habitats, but unlike the latter weed it is often restricted to forest edges and lacks the adaptability to expand into the forest understory (Kumar & DiTomasso 2005; Hough-Goldstein et al. 2012; Lake et al. 2013). *Alliaria petiolata* shares *M. vimineum*'s advantage of limited shade tolerance while forming monocultures mainly in the sunniest riparian habitats (Lankau 2013). However, unlike *M. vimineum, A. petiolata* is palatable to deer and can protect rarer forest-understory herbs from herbivory, which also reduces interspecific competition and enhances native species richness (Dornbush & Hahn 2013; Waller & Maas 2013). Lastly, though *Oplismenus undulatifolius* had a more limited dispersal, it is of pressing concern because it is the invasive species with the most realistic chance of being eradicated from the MPEA if effective control efforts are soon undertaken. *Oplismenus undulatifolius* is a more formidable opponent because it is a perennial and produces gelatinous seeds that are easily dispersed via animal and human contact (Beauchamp unpubl. data). The incorporation of the general public into the control and continued monitoring of these invasive species at the MPEA may be worthwhile, and

the MPEA and nearby Patapsco State Park have already had success in organizing volunteer sessions to pull stands of *A. petiolata.*

Today, the MPEA supports a fragmented landscape at different stages along the spectrum from old field to mature forest. Portions of the reserve that have reverted to forest over a longer timeframe are naturally dominated by vegetation that is more typical of an undisturbed eastern deciduous forest, such as the trees *F. grandifolia* and *C. caroliniana,* the shrub *L. benzoin,* and a sparse understory with scattered forbs, graminoids, and woody seedlings; however, the shade-tolerant, invasive shrub *B. thunbergii* and *R. multiflora* are encroaching upon this more pristine habitat. In contrast, sections of the MPEA that were more recently utilized in agriculture are dominated by early-successional plants along the lines of the tree *L. tulipifera,* the invasive shrub *E. umbellata,* and abundant understory vegetation led in magnitude by the invasive grass *M. vimineum.* At a finer scale, the MPEA's unique attribute as a forest fragment that is regularly disturbed by suburban dwellers throughout both its disproportionate boundary and interior hiking trails has further modified the reserve by promoting dominance of early-successional trees such as *Acer negundo,* fostering invasion by twining *P. perfoliata* and lianas, and maintaining riparian pipeline corridors with source populations for *M. vimineum* invasions. This prevalence of edge-like disturbance underscores the need for invasive species management in a suburban forest remnant to be comprehensively focused across multiple successional stages.

Tables

Table 1. Number of vascular plant taxa recorded in each sampling period. (Note that *Microstegium vimineum* was the only graminoid identified to the species level in 2001 and that mature trees >1.5 m tall were not sampled in 2012.)

Growth Habit	June–Sept. 2001	June 2009	June–Sept. 2012
Herbs (excluding graminoids)	74	119	94
Graminoids	1	29	33
Shrubs	20	31	22
Trees	36	44	23
Vines/Lianas	9	13	13
Totals	140	236	185

Table 2. Measures of mean (±SE) beta diversity and mean (±SE) proportional effective species turnover for herbaceous vegetation, shrubs, and trees.

Stratum	Beta diversity	Proportional effective species turnover	
		first	second
Herbs			
2001–2012	0.60 (±0.02)[a]	0.42 (±0.01)[a]	0.48 (±0.01)[a,b]
2009–2012	0.54 (±0.02)[b]	0.39 (±0.01)[a]	0.42 (±0.01)[a]
June–Sept. 2012	0.45 (±0.02)[c]	0.42 (±0.01)[a]	0.50 (±0.01)[b]
Shrubs			
2001–2012	0.48 (±0.02)	0.33 (±0.01)	0.10 (±0.01)
Trees			
2001–2012	0.21 (±0.01)	0.08 (±0.01)	0.17 (±0.01)

Table 3. Significant correlations between beta diversity of a) herbaceous species, b) shrubs, and c) trees and major environmental characteristics.
* Significance of ≤ 0.05.
** Significance of ≤ 0.01.

a)

Variable	Herbaceous Beta Diversity		
	2001–2012	2009–2012	June–Sept. 2012
Total species coverage	–0.39**	–0.42**	–0.43**
Native species coverage	–0.35**	–0.38**	–0.22**
Exotic species coverage	–0.21*	–0.31**	–0.38**
Total species richness	–0.22*	–0.42**	–0.26**
Native species richness	–0.17	–0.30**	–0.17
Exotic species richness	–0.16	–0.35**	–0.23*
Time since reforestation	–0.12	–0.08	–0.17
Elevation	0.10	0.39**	0.28**
Distance to forest edge	–0.08	0.09	0.05
Distance to river/stream	0.03	0.26**	0.25*
Canopy openness	0.07	0.11	–0.03
Leaf litter depth	0.26**	0.35**	0.26**
Leaf litter coverage	0.30**	0.35**	0.24*
Bare ground	–0.27**	–0.32**	–0.14
Tree density	0.20*	0.23*	0.06
Soil organic matter	0.15	0.35**	0.27**
Nitrogen	0.16	0.36**	0.27**
Sulfur	0.18	0.28**	0.25*
Ammonia	0.13	0.26**	0.24*
Alliaria petiolata	0.01	–0.13	–0.23*
Arisaema triphyllum	–0.03	–0.22*	0.20*
Circaea canadensis	–0.16	–0.10	0.07
Desmodium nudiflorum	–0.09	0.08	–0.06
Galium	–0.28**	–0.18	–0.19
Graminoids	–0.05	–0.08	–0.20*
Microstegium vimineum	–0.35**	–0.32**	–0.32**
Parthenocissus quinquefolia	–0.13	0.20	0.05
Persicaria	–0.15	–0.23*	–0.28**
Polystichum acrostichoides	–0.17	–0.40**	–0.20*
Potentilla/Fragaria	–0.11	–0.19	–0.04
Viola	–0.19	–0.28**	–0.21*

b)

Variable	Shrub Beta Diversity 2001–2012
Native species importance	–0.10
Exotic species importance	–0.06
Species richness	0.28**
Native species richness	0.34**
Exotic species richness	0
Time since reforestation	–0.35**
Elevation	0.04
Distance to forest edge	0.20*
Distance to river/stream	–0.03
Canopy openness	0.13
Leaf litter depth	0.21*
Leaf litter coverage	0.10
Bare ground	–0.14
Berberis thunbergii	0.29**
Celastrus orbiculatus	< –0.01
Elaeagnus umbellata	–0.18
Lindera benzoin	–0.24*
Lonicera japonica	0.06
Rosa multiflora	–0.02
Rubus	0.29**
Smilax	0.08
Viburnum prunifolium	–0.08
Vitis	0.12

c)

Variable	Tree Beta Diversity 2001–2012
Time since reforestation	0.28**
Elevation	0.07
Canopy openness	0.04
Distance to forest edge	–0.07
Distance to river/stream	–0.05
Species richness	0.25*
Leaf litter depth	–0.04
Leaf litter coverage	0.02
Bare ground	0.01
Tree density	–0.21*
Acer negundo	–0.02
Acer rubrum	–0.01
Carpinus caroliniana	–0.06
Carya	–0.04
Fagus grandifolia	–0.13
Fraxinus	0.12
Liriodendron tulipifera	0.01
Prunus	–0.09
Quercus	0.01

Table 4. Number of plots containing the most common: a) herbaceous species and the change in frequency at the decadal (2001–2012), interannual (2009–2012), and semiannual (June–September 2012) timeframes; b) shrub species and the change in frequency at the decadal (2001–2012) timeframe; and c) tree species and the change in frequency at the decadal (2001–2012) timeframe. Common species were defined as those present in ≥30 in at least one dataset.

a)

	Frequency					Change in Frequency		
Common Herbaceous Species	June–Sept. 2001	June 2009	June 2012	Sept. 2012	June–Sept. 2012	2001–2012	2009–2012	June–Sept. 2012
Alliaria petiolata	31	52	48	45	47	16	–4	–3
Arisaema triphyllum	56	64	66	43	51	–5	2	–23
Circaea canadensis	58	74	66	54	55	–3	–8	–12
Desmodium nudiflorum	50	42	21	25	19	–31	–21	4
Galium	68	72	78	73	76	8	6	–5
Geum	46	23	22	42	28	–18	–1	20
Graminoids	82	75	82	77	80	–2	7	–5
Microstegium vimineum	77	73	81	85	84	7	8	4
Osmorhiza claytonii	22	32	27	20	21	–1	–5	–7
Oxalis	33	30	37	24	26	–7	7	–13
Parthenocissus quinquefolia	92	88	89	69	75	–17	1	–20
Persicaria	55	59	67	66	63	8	8	–1
Persicaria perfoliata	30	29	29	15	16	–14	0	–14
Persicaria virginianum	50	27	35	36	31	–19	8	1
Pilea pumila	7	4	20	31	28	21	16	11
Podophyllum peltatum	32	49	36	4	23	–9	–13	–32
Polystichum acrostichoides	32	40	46	42	46	14	6	–4
Potentilla/ Fragaria	58	57	71	69	70	12	14	–2
Ruellia strepens	0	42	1	0	1	1	–41	–1
Sanicula canadensis	52	54	58	44	44	–8	4	–14
Solidago	38	23	17	18	16	–22	–6	1
Stellaria pubera	0	0	30	8	9	9	30	–22
Viola	72	87	77	57	69	–3	–10	–20

b)

Common Shrub Species	2001	2012	Change in Frequency
Berberis thunbergii	33	68	35
Celastrus orbiculatus	72	93	21
Elaeagnus umbellata	58	77	19
Lindera benzoin	89	90	1
Lonicera japonica	91	94	3
Rosa multiflora	75	90	15
Rubus	67	79	12
Smilax	51	74	23
Toxicodendron radicans	76	48	28
Viburnum acerifolium	31	43	12
Viburnum dentatum	43	38	–5
Viburnum prunifolium	57	71	14
Vitis	67	62	–5

c)

Common Tree Species	2001	2009–2012	Change in Frequency
Acer rubrum	83	72	–11
Carpinus caroliniana	47	49	2
Carya	61	62	1
Cornus florida	80	66	–14
Fagus grandifolia	29	35	6
Liriodendron tulipifera	85	85	0
Nyssa sylvatica	63	56	–7
Prunus	45	30	–15
Quercus	63	53	–10

Table 5. Mean temperature and precipitation in Howard County, Maryland during January, June, and September of the three survey years.

	Temperature (^{o}C)			Precipitation (cm)		
	2001	2009	2012	2001	2009	2012
January	0.6	5.0	12.2	0.2	6.9	6.5
June	23.3	25.6	28.9	0.3	14.0	6.8
September	18.3	19.4	26.1	0.1	8.8	5.6

Table 6. Change in abundance of the most common understory vegetation, as represented by: a) mean coverage of herbaceous species and their change in coverage at the decadal (2001–2012), interannual (2009–2012), and semiannual (June–September 2012) timeframes; b) mean coverage of shrub species (≤1 m tall) and their change in coverage at the decadal (2001–2012) timeframe; and c) frequency of tree seedlings (≤1 m tall) and their change in frequency at the semiannual (June–September 2012) timeframe. Common species were defined as those present in ≥30 plots in at least one dataset.

a)

Common Herbaceous Species	Mean coverage				Change in coverage			
	June–Sept. 2001	June 2009	June 2012	Sept. 2012	June–Sept. 2012	2001–2012	2009–2012	June–Sept. 2012
Alliaria petiolata	0.9	3.0	2.4	1.3	1.7	0.8	–0.5	–1.1
Arisaema triphyllum	1.2	1.6	0.7	0.2	0.3	–0.9	–1.0	–0.4
Circaea canadensis	0.9	2.3	0.9	0.4	0.6	–0.3	–1.4	–0.6
Desmodium nudiflorum	0.8	1.8	0.1	0.1	0.1	–0.7	–1.7	0
Galium	0.9	0.7	0.9	0.6	0.7	–0.2	0.1	–0.2
Geum	0.5	0.2	0.1	0.2	0.1	–0.4	–0.1	0.2
Graminoids	4.5	1.8	3.0	2.7	2.9	–1.6	1.2	–0.3
Microstegium vimineum	12.5	5.5	5.2	6.8	5.7	–6.8	–0.3	1.6
Osmorhiza claytonii	0.2	0.4	0.2	0.1	0.1	–0.1	–0.2	–0.1
Oxalis	0.3	0.1	0.1	0.1	0.1	–0.2	0	0
Parthenocissus quinquefolia	1.3	2.2	0.7	0.5	0.6	–0.7	–1.4	–0.3
Persicaria	1.3	1.4	1.0	1.4	1.1	–0.1	–0.4	0.4
Persicaria perfoliata	0.8	0.9	0.6	0.3	0.4	–0.4	–0.3	–0.3
Persicaria virginianum	1.1	0.7	0.4	0.3	0.3	–0.8	–0.3	–0.1
Pilea pumila	0.1	0	0.5	0.4	0.4	0.2	0.5	–0.1
Podophyllum peltatum	0.3	0.6	0.1	0	0.1	–0.2	–0.5	–0.1
Polystichum acrostichoides	1.9	3.3	1.6	1.6	1.7	–0.2	–1.6	0
Potentilla/ Fragaria	1.8	1.8	1.7	1.9	1.8	0	–0.2	0.3
Ruellia strepens	0	0.5	0	0	0.0	0	–0.5	0
Sanicula canadensis	0.5	0.3	0.2	0.1	0.1	–0.3	–0.1	–0.1
Solidago	0.2	0.2	0.2	0.2	0.1	–0.1	0	0
Stellaria pubera	0	0	0.1	0	0.0	0	0.1	–0.1
Viola	1.2	1.6	0.8	0.3	0.4	–0.8	–0.8	–0.5

b)

Common Shrub Species	2001	2012	Change
Berberis thunbergii	0.6	2.1	1.5
Celastrus orbiculatus	1.6	1.7	0.1
Elaeagnus umbellata	2.0	1.5	–0.5
Lindera benzoin	6.5	4.3	–2.2
Lonicera japonica	4.5	2.9	–1.6
Rosa multiflora	3.6	4.2	0.6
Rubus	0.9	1.4	0.5
Smilax	0.6	0.3	–0.3
Toxicodendron radicans	1.2	0.3	–0.9
Viburnum acerifolium	0.7	0.2	–0.5
Viburnum dentatum	0.5	0.2	–0.3
Viburnum prunifolium	1.0	0.3	–0.7
Vitis	0.6	0.2	–0.4

c)

Common Tree Species	June 2012	Sept. 2012	Change
Acer rubrum	418	165	–253
Carpinus caroliniana	320	288	–32
Carya	128	147	19
Cornus florida	134	35	–99
Fagus grandifolia	22	15	–7
Liriodendron tulipifera	650	336	–314
Nyssa sylvatica	21	37	16
Prunus	654	462	–192
Quercus	131	106	–25

Table 7. Number of common a) herbaceous morphospecies (n=23), b) shrubs (n=13), and c) trees (n=9) as grouped by plot turnover. Noted are whether a species exhibited a net increase, decrease, or constancy in its plot frequency during each of the three timeframes and whether such change involved a shift in distribution among individual plots.

a)

Herbaceous Species	2001–2012	2009–2012	June–Sept. 2012
Net decrease	14	9	17
Shifted to new plots	13	9	16
Not present in new plots	1	0	1
Net increase	9	14	6
Shifted to new plots	7	13	6
All in new plots	2	1	0

b)

Shrubs	2001–2012
Net decrease	2
Shifted to new plots	2
Not present in new plots	0
Net increase	11
Shifted to new plots	10
All in new plots	1

c)

Trees	2001–2012
Net decrease	5
Shifted to new plots	5
Not present in new plots	0
Net increase	3
Shifted to new plots	3
All in new plots	0
No change	1
Shifted to new plots	1
Not present in new plots	0

Table 8. Number of a) common large shrubs (≥1 m tall) and b) mature trees (≥1 m tall) observed in 2001 and 2012 and their change in number. (* includes both generic *Rosa*, recorded only in 2001, and *Rosa multiflora*.)

a)

Common Shrub Species	2001	2012	Change
Berberis thunbergii	17	277	260
Celastrus orbiculatus	1	0	–1
Elaeagnus umbellata	989	2316	1327
Lindera benzoin	1334	1797	463
Lonicera japonica	0	1	1
*Rosa**	640	1125	485
Rubus	28	355	327
Smilax	0	7	7
Viburnum acerifolium	89	4	–85
Viburnum dentatum	59	4	–55
Viburnum prunifolium	705	174	–531
Vitis	0	1	1

b)

Common Tree Species	2001	2009–2012	Change
Acer rubrum	572	380	–192
Carpinus caroliniana	919	814	–105
Carya	308	259	–49
Cornus florida	538	270	–268
Fagus grandifolia	401	592	191
Liriodendron tulipifera	751	633	–118
Nyssa sylvatica	429	299	–130
Prunus	199	112	–87
Quercus	222	142	–80

Table 9. Change in number of common mature trees (>1 m tall) in each DBH class between 2001 and 2009–2012.

Common Tree Species	DBH Class (cm)					
	0–13.2	13.3–27.6	27.7–42	42.1–56.4	>56.5	Total
Acer rubrum	–178	–9	–7	1	1	–192
Carpinus caroliniana	–86	–18	–1	0	0	–105
Carya	–30	–24	6	3	–4	–49
Cornus florida	–258	–10	0	0	0	–268
Fagus grandifolia	192	–2	2	0	–1	191
Liriodendron tulipifera	–114	–34	4	3	23	–118
Nyssa sylvatica	–120	–4	–4	0	–2	–130
Prunus	–66	–22	2	0	–1	–87
Quercus	–31	–7	–24	–14	–4	–80
Total	–691	–130	–22	–7	12	–838

Table 10. Average deer browse of the most common: a) herbaceous species; b) small shrubs (<1 m); c) large shrubs (>1 m); and d) tree seedlings (<1 m) in 2001, 2009, and 2012. Common species were defined as those present in ≥30 in at least one dataset.

a)

Common Herbaceous Species	June–Sept. 2001	June 2009	June 2012	Sept. 2012
Alliaria petiolata	0	6.1	0.5	0.2
Arisaema triphyllum	0	5.4	0.2	4.7
Circaea canadensis	23.5	5.5	3.1	5.4
Desmodium nudiflorum	7.3	4.9	1.1	1.7
Galium	6.5	4.1	0.6	3.8
Geum	19.8	4.7	2.6	5.5
Graminoids	0.03	4.4	0.1	0
Microstegium vimineum	0.02	4.3	0.01	0.2
Osmorhiza claytonii	19.7	3.8	0.04	0
Oxalis	3.2	3.3	0	0
Parthenocissus quinquefolia	9.6	4.2	0.01	7.0
Persicaria	2.6	4.7	0.4	0.2
Persicaria perfoliata	0	3.5	0	0
Persicaria virginianum	3.9	3.9	3.6	6.3
Pilea pumila	8.3	3.6	0.4	5.4
Podophyllum peltatum	3.5	6.9	0.3	0
Polystichum acrostichoides	0.6	6.0	1.2	1.3
Potentilla/ Fragaria	6.0	5.3	0.6	0.2
Ruellia strepens	–	8.3	–	–
Sanicula canadensis	18.5	4.7	0.8	2.2
Solidago	49.3	4.6	4.3	10.3
Stellaria pubera	–	–	1.2	12.9
Viola	6.5	4.8	0.4	0

b)

Common Shrub Species	June 2012	Sept. 2012
Berberis thunbergii	0.3	7.8
Celastrus orbiculatus	5.1	25
Elaeagnus umbellata	2.9	9.3
Lindera benzoin	12.6	19.8
Lonicera japonica	0.4	0.6
Rosa multiflora	26.9	62.1
Rubus	4.4	15.3
Smilax	7.5	19.4
Toxicodendron radicans	0.4	5.5
Viburnum acerifolium	0	19.4
Viburnum dentatum	0.7	17.5
Viburnum prunifolium	20	40.4
Vitis	0.1	1.6

c)

Common Shrub Species	2001	2012
Berberis thunbergii	9.2	2.5
Celastrus orbiculatus	0	0
Elaeagnus umbellata	10.8	3.1
Lindera benzoin	9.8	14.0
Lonicera	11.5	40.5
Rosa multiflora	6.8	17.0
Rubus	21.9	3.3
Smilax	–	22.5
Toxicodendron radicans	–	0
Viburnum acerifolium	19.3	30.4
Viburnum dentatum	6.8	0.8
Viburnum prunifolium	10.9	3.1
Vitis	–	–

d)

Common Tree Species	June 2012	Sept. 2012
Acer rubrum	0.9	1.6
Carpinus caroliniana	3.2	19.9
Carya	2.3	19.2
Cornus florida	0.2	14.1
Fagus grandifolia	5.1	17.4
Liriodendron tulipifera	0	1.0
Nyssa sylvatica	3.4	39.8
Prunus	1.1	15.1
Quercus	0.6	14.7

Table 11. Average environmental factors and environmental conditions of: a) herbaceous communities; b) shrub communities; and c) tree communities. Letters denote significant differences among groups, according to an ANOVA permutation procedure and post-hoc comparison of 95% confidence intervals.

a)

	Microstegium vimineum	*Potentilla/ Fragaria*	*Desmodium nudiflorum*	*Polystichum acrostichoides*	*Thelypteris noveboracensis*
N	31	7	32	15	9
Environmental Factors					
Transmitted Light (%)	16.8	15.1	14.4	13.2	14.6
Distance to nearest edge (m)	69.1	82.4	97.5	75.0	102.5
Distance to river/stream (m)	99.1	136.2	129.9	107.2	191.7
Elevation (m)	104.1	109.3	110.5	100.5	112.3
Slope (^{o})	15.3	16.3	14.0	18.1	15.3
Aspect (most common direction)	NW	NE/SW	SW	SW	SE/SW
Soil exchange capacity (meq^{+}/100g)	8.4	8.6	7.4	7.2	6.6
Soil organic matter (%)	5.7 ^{a,b}	5.8 ^{a,b}	6.3 ^{a}	5.4 ^{b}	6.6 ^{a}
Nitrogen Release (mg/kg)	102.2 ^{a,b}	103.4 ^{a,b}	106.4 ^{a,b}	101.0 ^{a}	107.9 ^{b}
Nitrate (mg/kg)	7.5 ^{a}	4.6 ^{b}	3.1 ^{b}	4.9 ^{b}	3.1 ^{b}
Sulfur (mg/kg)	13.7	13.9	14.9	12.9	17.0
Phosphorus (mg/kg)	16.9	12.9	11.2	13.1	10.4
Calcium (mg/kg)	710.1	810.3	641.2	633.8	487.8
Average reforested date (since 1943)	1969 ^{a}	1962 ^{a,b}	1947 ^{b,c}	1946 ^{b,c}	1943 ^{c}
Vegetation Conditions					
Understory vegetation (%)	46.3 ^{a}	37.9 ^{a,b}	25.9 ^{c}	30.0 ^{b,c}	29.3 ^{b,c}
Exotic herbaceous coverage (%)	60.2 ^{a}	22.0 ^{b}	16.7 ^{b}	19.8 ^{b}	13.5 ^{b}
Exotic herbaceous richness (%)	4.2 ^{a}	4.0 ^{a}	2.5 ^{b}	3.6 ^{a,b}	2.8 ^{a,b}
Leaf litter (%)	74.6	59.4	76.1	72.1	74.9
Bare ground (%)	8.5	16.5	8.5	12.4	9.5

b)

	Rosa multiflora	*Elaeagnus umbellata*	*Lindera benzoin*	*Smilax–Viburnum*
N	26	33	31	9
Environmental Factors				
Transmitted Light (%)	16.2	16.1	13.6	14.7
Distance to nearest edge (m)	100.1	69.9	88.2	72.0
Distance to river/stream (m)	159.1	106.2	114.8	105.9
Elevation (m)	108.1	105.7	105.9	112.1
Slope (^{o})	13.2	16.7	14.5	17.3
Aspect (most common direction)	SE	SW	SW	SW
Soil exchange capacity (meq^{+}/100g)	8.1 [a]	7.5 [a,b]	8.0 [a]	6.3 [b]
Soil organic matter (%)	5.9 [a]	6.0 [a]	5.8 [a]	7.3 [b]
Nitrogen Release (mg/kg)	103.6 [a]	104.4 [a]	103.7 [a]	111.2 [b]
Nitrate (mg/kg)	4.3	3.1	4.1	0.9
Sulfur (mg/kg)	15.1	13.2	13.2	19.7
Phosphorus (mg/kg)	17.7 [a]	11.9 [a]	14.0 [a]	7.4 [b]
Calcium (mg/kg)	678.2 [a,b]	640.7 [a,b]	753.0 [a]	431.2 [b]
Average reforested date (since 1943)	1957	1964	1946	1949
Vegetation Conditions				
Understory vegetation (%)	38.6 [a]	33.7 [a]	38.1 [a]	13.3 [b]
Exotic herbaceous coverage (%)	29.3 [a,b]	36.0 [a]	33.5 [a]	8.6 [b]
Exotic shrub coverage (%)	62.3 [a]	75.1 [a]	39.8 [b]	30.8 [b]
Exotic shade-intolerant shrubs (%)	50.8	71.7	31.7	26.1
Exotic shade-tolerant shrubs (%)	11.5 [a]	3.4 [b]	8.1 [a]	4.6 [a,b]
Leaf litter (%)	70.9[a]	76.1 [a,b]	71.0 [a]	82.2 [b]
Bare ground (%)	10.4 [a]	8.8 [a]	11.6 [a]	4.8 [b]

c)

	Acer negundo–Juglans nigra	*Prunus–Robinia–Acer rubrum*	*Liriodendron tulipifera*	*Carpinus caroliniana*	*Fagus grandifolia*
N	6	22	22	29	19
Environmental Factors					
Transmitted light (%)	18.7	15.7	14.9	14.5	15.2
Distance to nearest edge (m)	89.9 [a]	59.7 [a]	79.5 [a,b]	59.1 [a]	155.2 [b]
Distance to nearest river/stream (m)	33.0	127.3	178.2	94.2	121.4
Elevation (m)	95.6	105.6	109.7	103.1	113.9
Slope (^{o})	11.3	16.3	14.5	15.4	15.8
Aspect (most common direction)	NW	SW	SW	NE	SW
Soil exchange capacity (meq^{+}/100g)	8.9	9.2	8.0	6.6	6.9
Soil organic matter (%)	5.9 [a,b,c]	5.6 [a,b]	5.4 [a]	6.4 [b,c]	6.8 [c]
Nitrogen Release (mg/kg)	103.7 [a,b,c]	101.5 [a,b]	101.2 [a]	107.0 [b,c]	108.7 [c]
Nitrate (mg/kg)	8.4 [a]	7.7 [a]	5.5 [a,b]	3.5 [b]	1.7 [c]
Sulfur (mg/kg)	10.7 [a]	14.8 [b]	13.0 [b]	13.8 [b]	16.9 [b]
Phosphorus (mg/kg)	24.8	16.6	11.3	13.6	10.3
Calcium (mg/kg)	1023.5 [a]	711.8 [a,b,c]	762.6 [a,b]	575.6 [b,c]	538.0 [c]
Average reforested date (since 1943)	1952	1970	1965	1943	1943
Vegetation Conditions					
Understory vegetation (%)	68.3 [a]	38.8 [b]	38.7 [b]	30.1 [b,c]	20.1 [c]
Exotic herbaceous coverage (%)	78.5 [a]	46.9 [b]	32.3 [b,c]	19.9 [c,d]	11.2 [d]
Exotic shrub coverage (%)	47.7	70.6	55.8	57.7	43.2
Exotic shade-intolerant shrubs (%)	45.5	67.5	52.1	45.6	33.4
Exotic shade-tolerant shrubs (%)	2.1	3.1	3.7	12.2	9.7
Leaf litter (%)	78.9	75.4	63.2	79.0	73.7
Bare ground (%)	5.9	8.9	15.0	8.1	8.6

Table 12. Spearman's correlations of the major environmental gradients with: a) abundance of herbaceous invasive species (all classified as shade-intolerant); b) abundance of major invasive shrubs (classified by shade tolerance); and c) frequency of lianas.
* Correlation is significant at the 0.05 level (2-tailed).
** Correlation is significant at the 0.01 level (2-tailed).

a)

Environmental Gradient	Coverage of Invasive Herbs
Canopy Openness	0.20*
Distance to forest edge	–0.08
Distance to river/stream	–0.27**
Elevation	–0.32**
Reforested Date	0.46**
Soil Exchange Capacity	0.27**
Soil Organic Matter	–0.28**
Nitrogen	–0.29**
Nitrate	0.63**
Sulfur	–0.22*
Phosphorus	0.45**
Calcium	0.26**
Latitude	0.13

b)

Environmental Gradient	Invasive Shrubs		
	All	Shade-Intolerant	Shade-Tolerant
Canopy Openness	0.14	0.24*	–0.30**
Distance to forest edge	–0.25*	–0.27**	0.18
Distance to river/stream	0.03	0.07	–0.02
Elevation	–0.19	–0.15	0.03
Reforested Date	0.42**	0.53**	–0.39**
Soil Exchange Capacity	0.16	0.22*	–0.16
Soil Organic Matter	–0.19	–0.19	0.15
Nitrogen	–0.19	–0.20*	0.16
Nitrate	0.14	0.19	–0.17
Sulfur	–0.24*	–0.24*	0.04
Phosphorus	0.06	0.06	–0.06
Calcium	0.12	0.13	–0.05
Latitude	0.23*	0.17	0.03

c)

Environmental Gradient	Liana Frequency
Canopy Openness	0.11
Distance to forest edge	–0.02
Distance to river/stream	–0.22*
Elevation	0.02
Reforested Date	0.07
Soil Exchange Capacity	0.02
Soil Organic Matter	0.13
Nitrogen	0.13
Nitrate	–0.07
Sulfur	–0.10
Phosphorus	–0.10
Calcium	0.06
Latitude	0.14

Figures

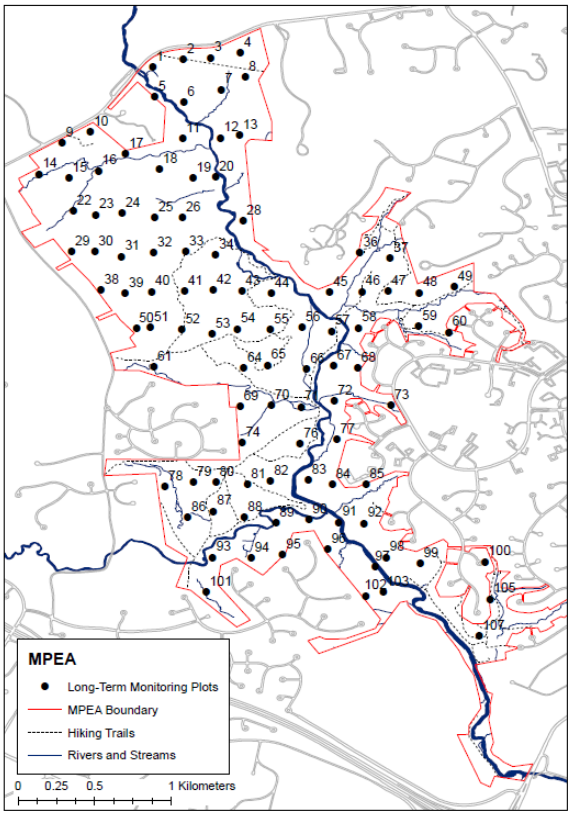


Figure 1. Layout of the current 99 long-term monitoring plots at the Middle Patuxent Environmental Area.

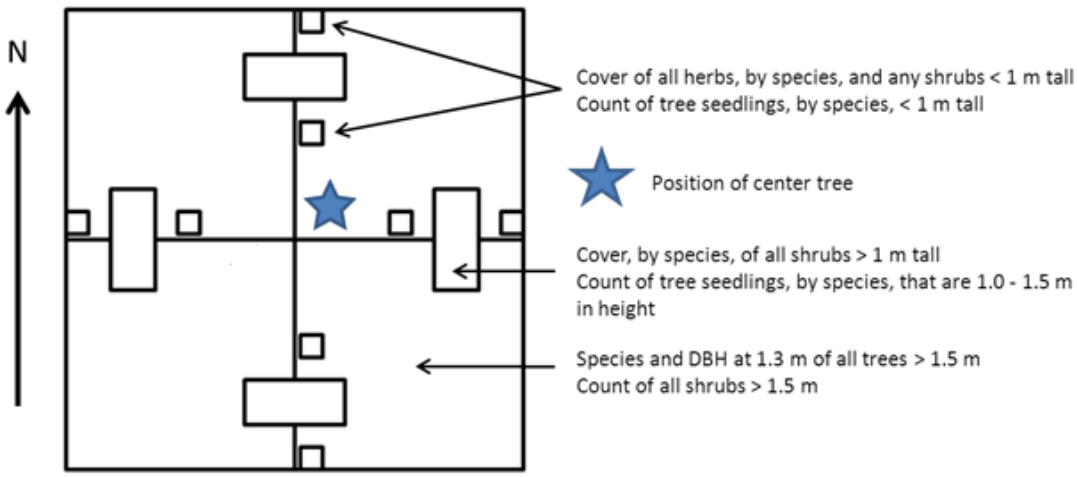


Figure 2. Sampling design of each 20 x 20 m plot, including eight 1 x 1 m subplots for understory vegetation sampling and four 2 x 4 m subplots for shrub sampling.

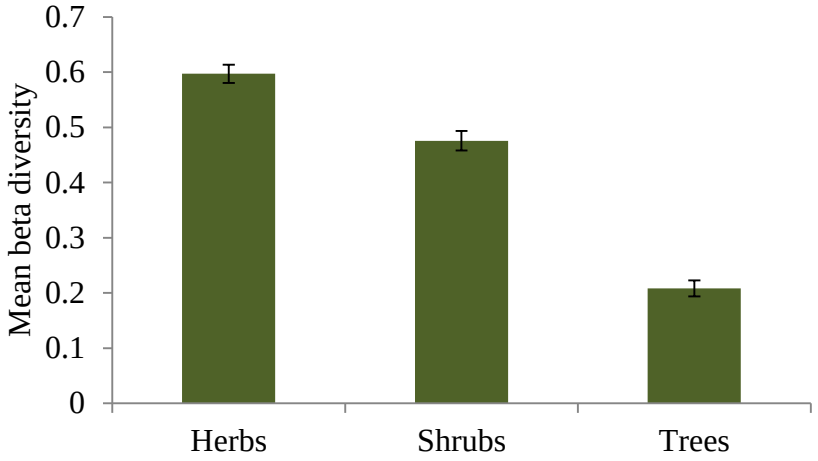
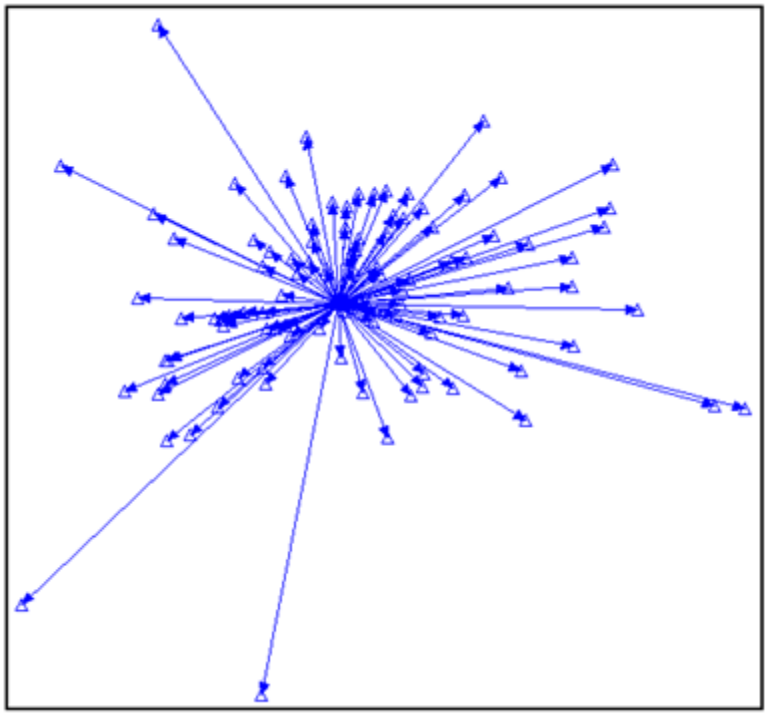
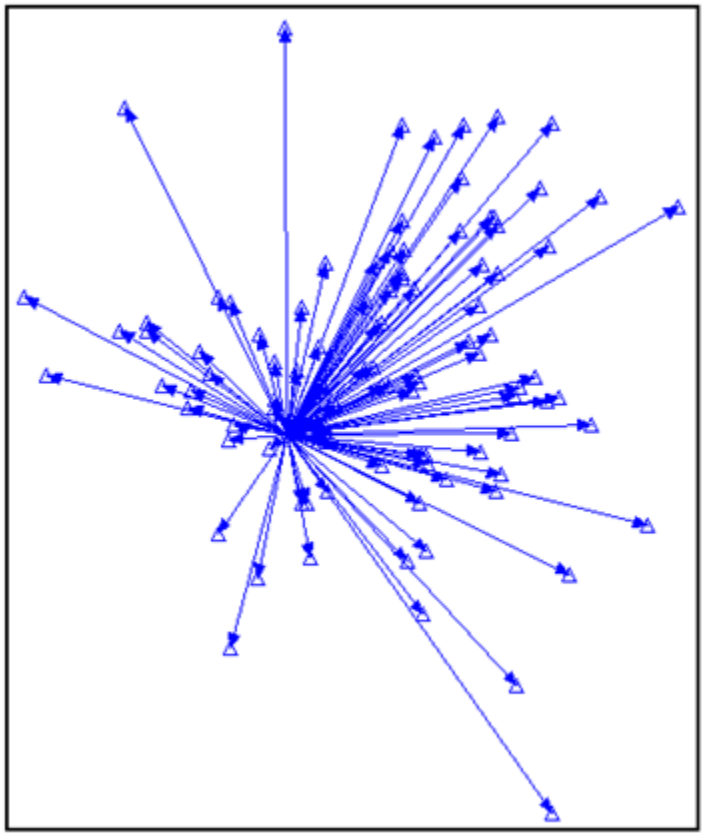


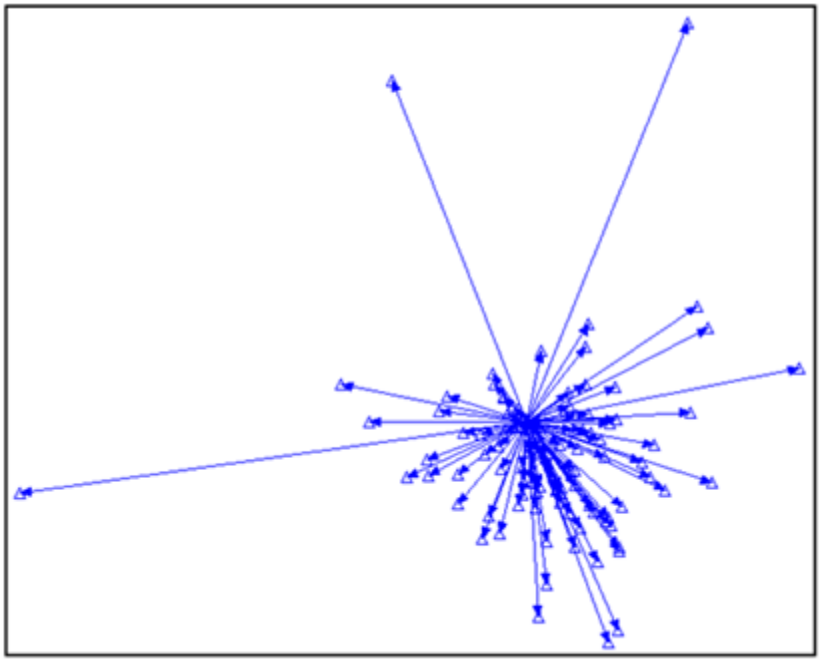
Figure 3. Mean (±SE) beta diversity of herbs, shrubs, and trees at the decadal (2001–2012) time scale.



a)

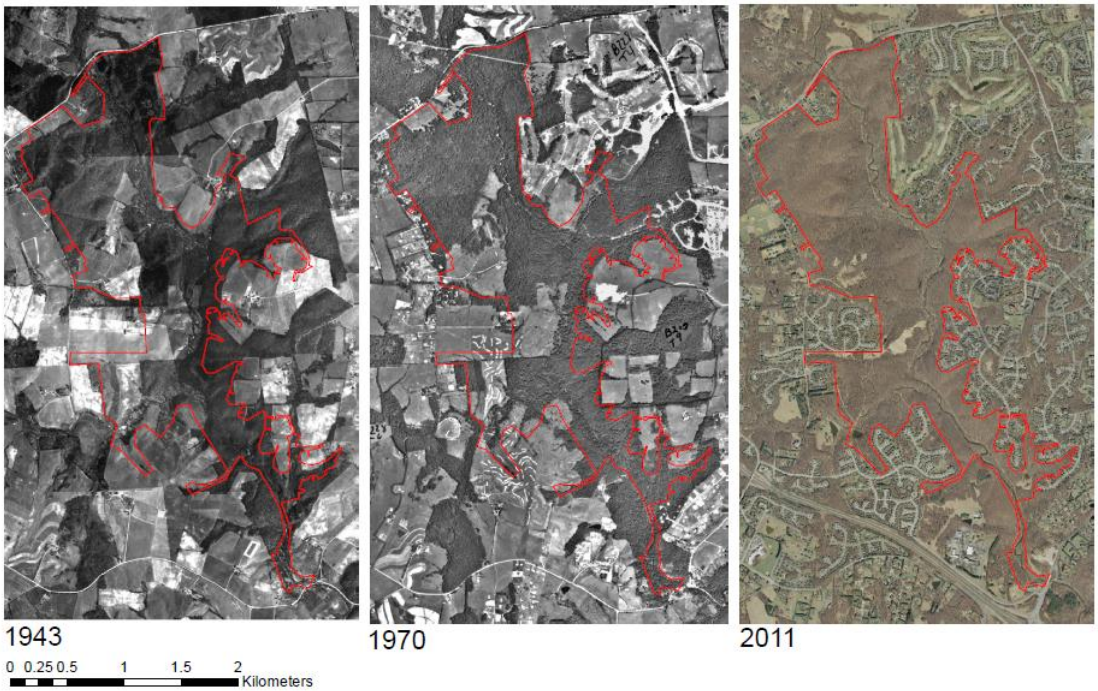


b)

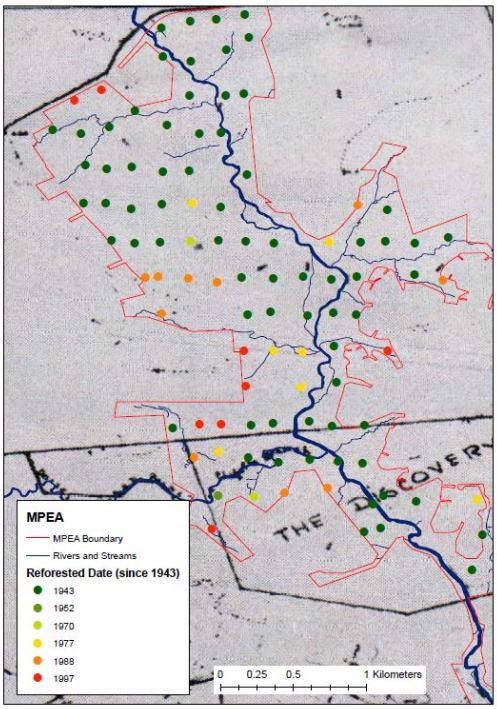


c)

Figure 4. NMDS results of a) herbaceous vegetation, b) shrubs, and c) trees, each at the decadal (2001–2012) timeframe. Major species correlations included: for herbaceous vegetation, the x-xis with *M. vimineum* (r = –0.74) and the y-axis with *P. indica/F. vesca* (r = 0.51), *Persicaria* (r = 0.38), and graminoids (r = 0.36); for shrubs, the x-axis with *L. benzoin* (r = –0.42) and *E. umbellata* (r = 0.88) and the y-axis with *L. benzoin* (r = 0.69), *R. multiflora* (r = 0.47), *V. acerifolium* (r = –0.54), and *Vaccinium* (r = –0.52); and for trees, the x-axis with *Prunus* (r = 0.50), *L. tulipifera* (r = 0.45), and *C. caroliniana* (r = –0.79) and the y-axis with *R. pseudoacacia* (r = 0.60), *Prunus* (r = 0.47), *L. tulipifera* (r = –0.56), and *F. grandifolia* (r = –0.51).

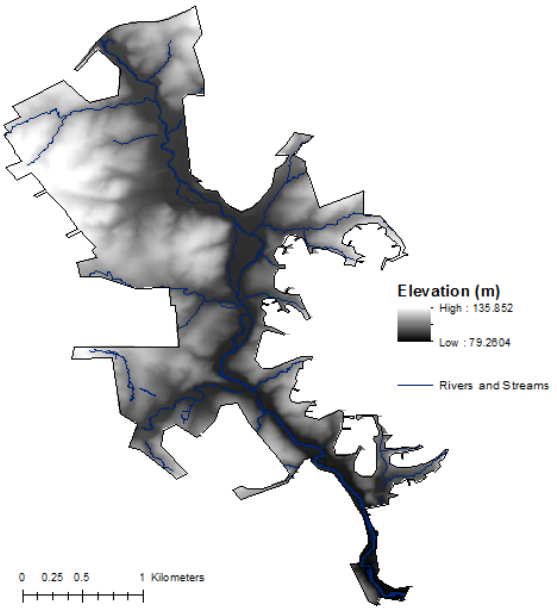


a)

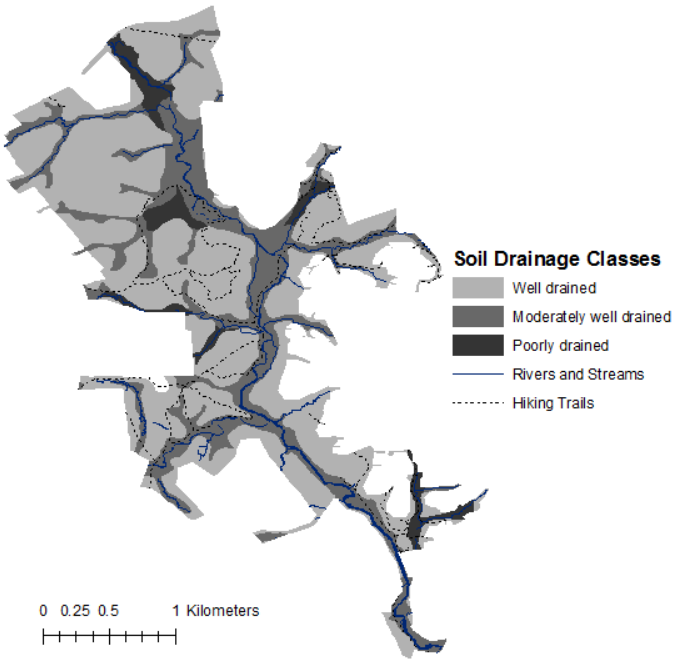


b)

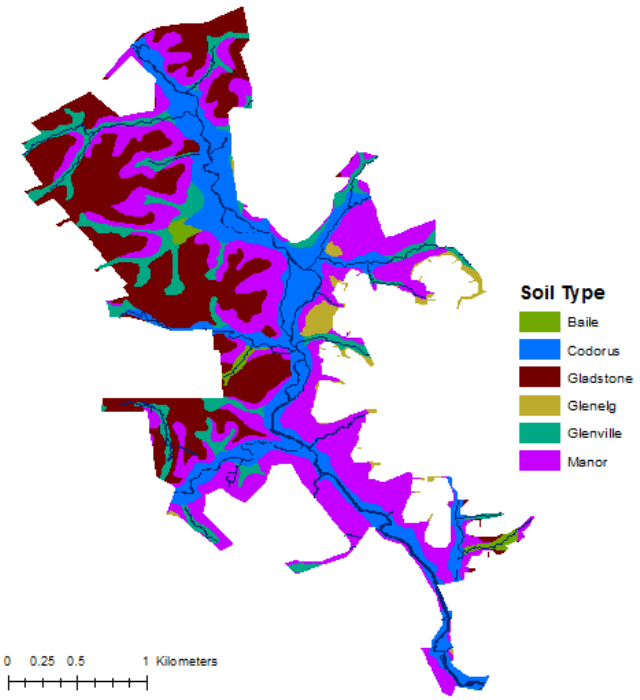
Figure 5. a) Forest cover and surrounding landscape at the MPEA in 1943, 1970, and 2011, with the MPEA's present-day boundary outlined in red, and b) each long-term monitoring plot's first known date of reforestation since 1943, also noting the boundary between the historical Doughoregan Manor and Discovery tracts.


Elevation (m)
High : 135.852
Low : 79.2604
Rivers and Streams
0 0.25 0.5 1 Kilometers

a)


Soil Drainage Classes
Well drained
Moderately well drained
Poorly drained
Rivers and Streams
Hiking Trails
0 0.25 0.5 1 Kilometers

b)



c)

Figure 6. Major landscape features of the MPEA, including: a) elevation, b) soil drainage classes, and c) soil types.

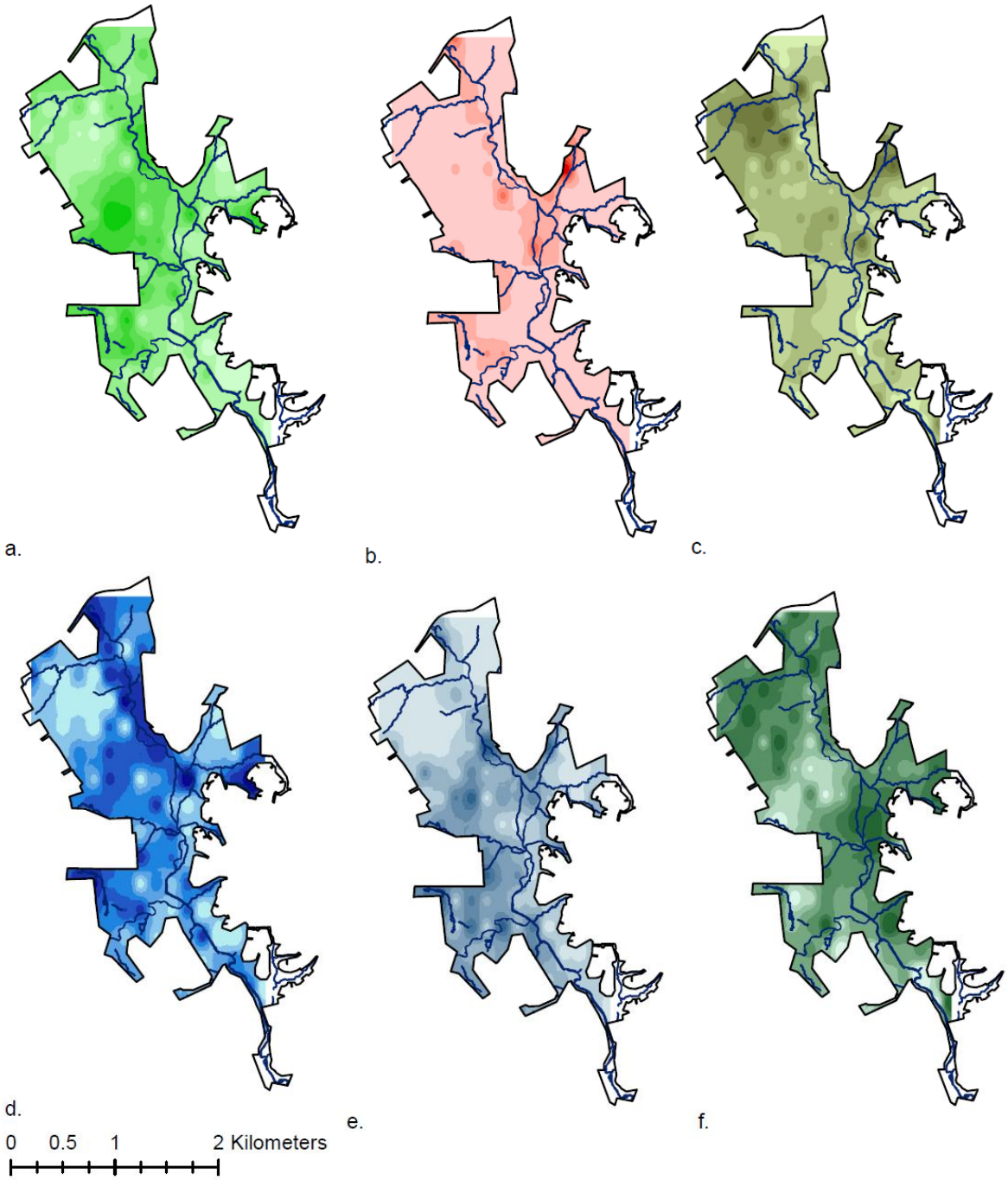
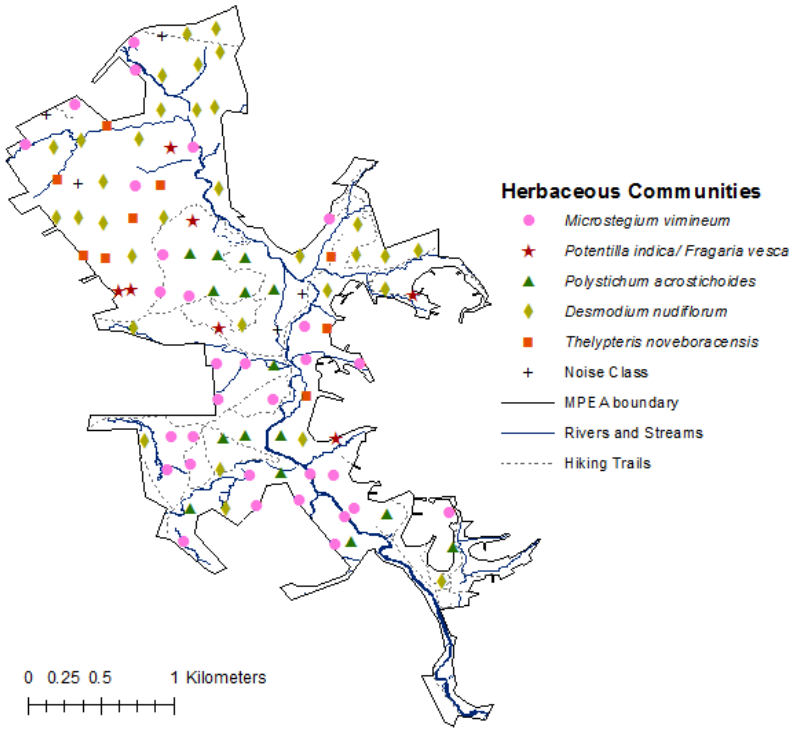
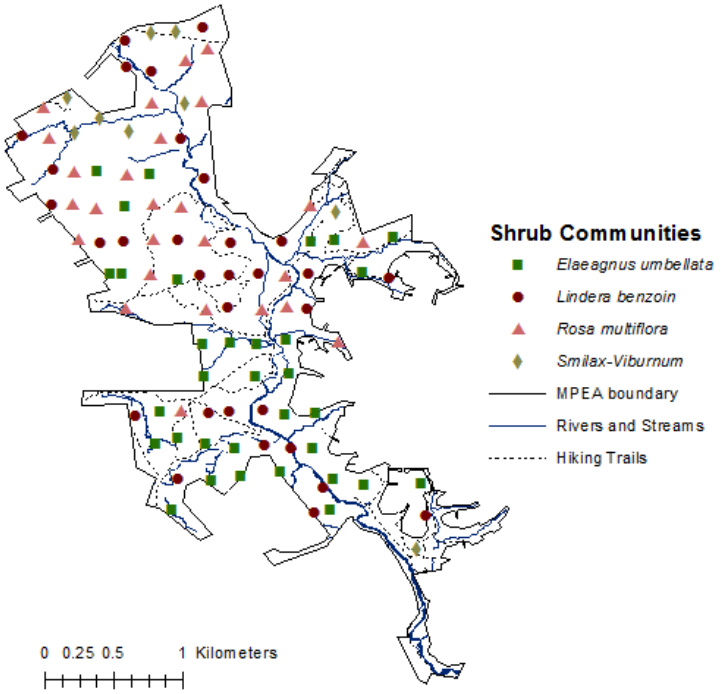


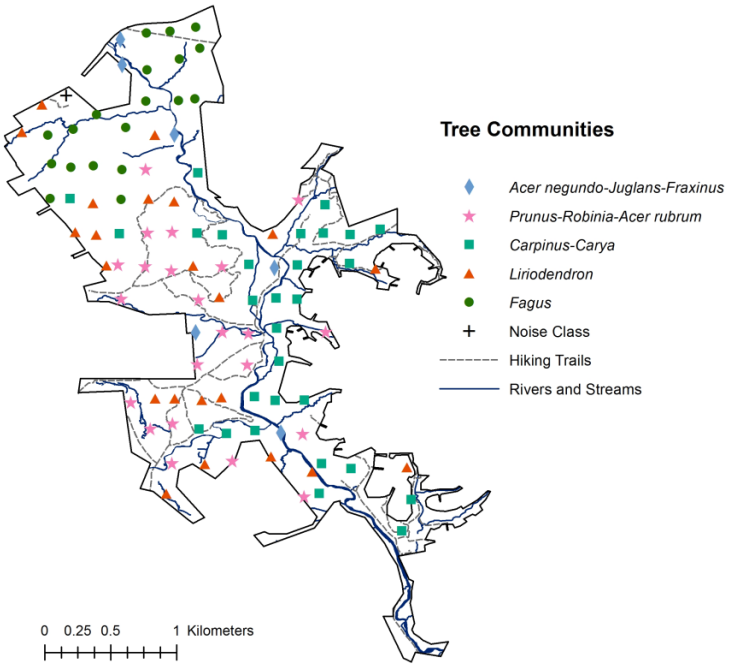
Figure 7. Variation in a) soil exchange capacity, b) phosphorus, c) sulfur, d) calcium, e) nitrate, and f) nitrogen throughout the MPEA's soils.


Herbaceous Communities
Microstegium vimineum
Potentilla indica/ Fragaria vesca
Polystichum acrostichoides
Desmodium nudiflorum
Thelypteris noveboracensis
Noise Class
MPEA boundary
Rivers and Streams
Hiking Trails
0 0.25 0.5 1 Kilometers

a)

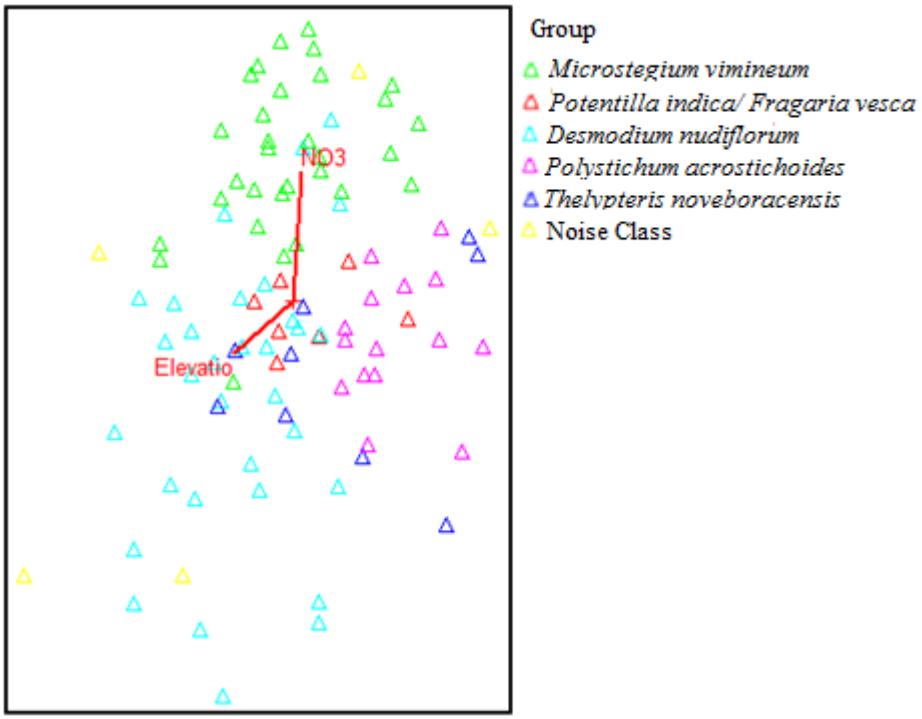

Shrub Communities
Elaeagnus umbellata
Lindera benzoin
Rosa multiflora
Smilax-Viburnum
MPEA boundary
Rivers and Streams
Hiking Trails
0 0.25 0.5 1 Kilometers

b)

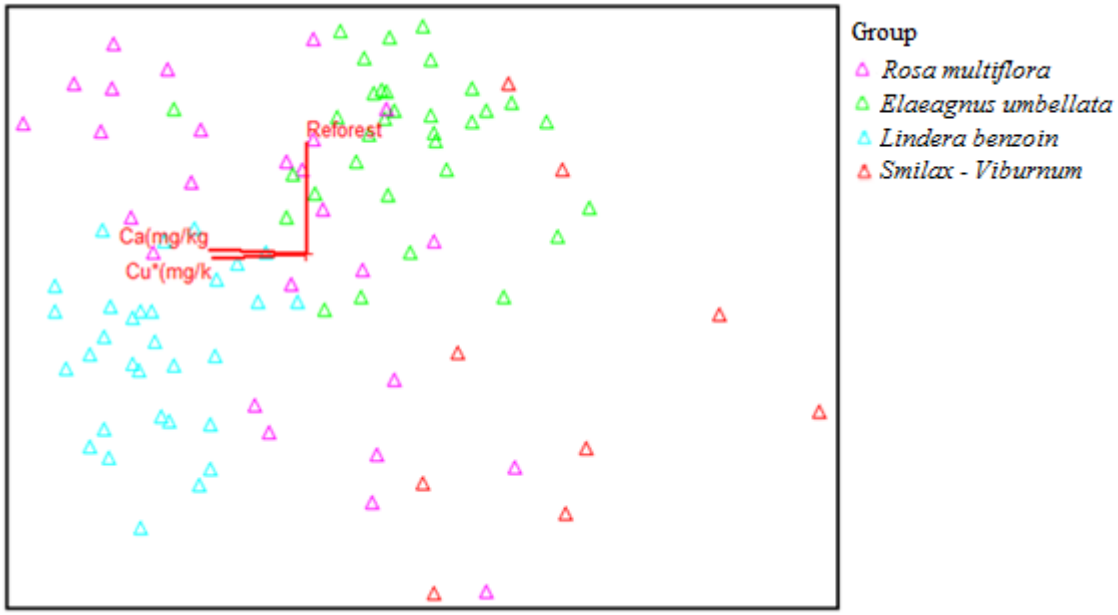


c)

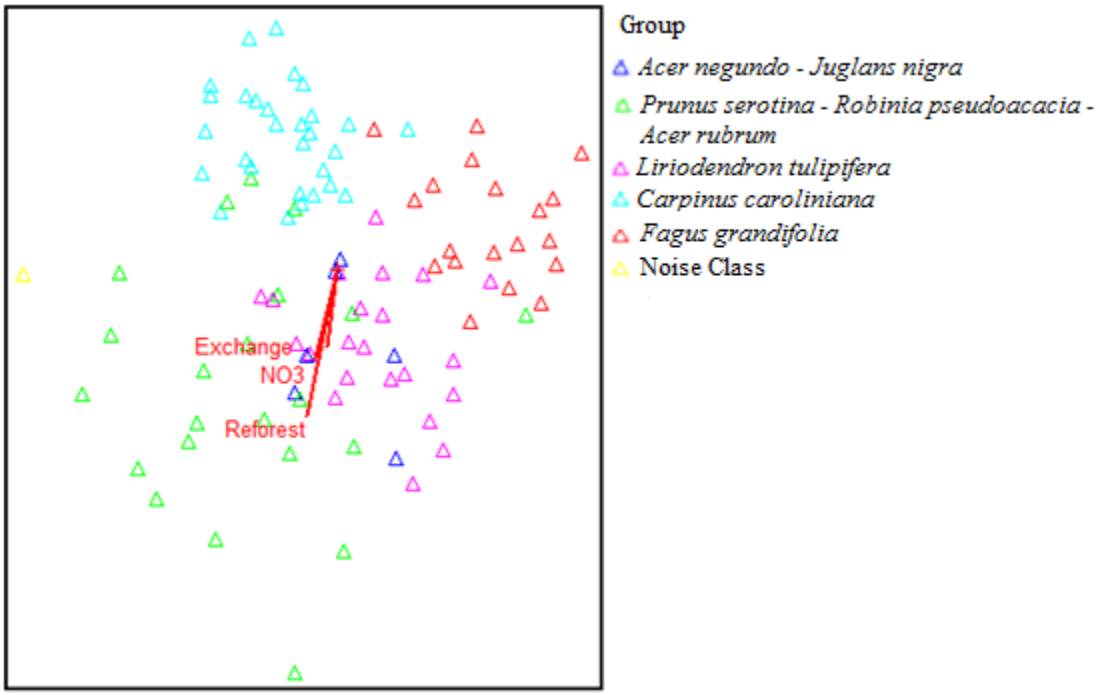
Figure 8. Spatial distributions throughout the MPEA in 2012 of the: a) herbaceous communities; b) shrub communities; and c) mature tree communities.


NO3
Elevatio
Group
Microstegium vimineum
Potentilla indica/ Fragaria vesca
Desmodium nudiflorum
Polystichum acrostichoides
Thelypteris noveboracensis
Noise Class

a)


Reforest
Ca(mg/kg
Cu*(mg/k
Group
Rosa multiflora
Elaeagnus umbellata
Lindera benzoin
Smilax - Viburnum

b)



c)

Figure 9. NMDS results displaying the distributions of long-term monitoring plots throughout species space and correlations with major environmental variables: a) herbaceous species, b) shrubs, and c) trees.

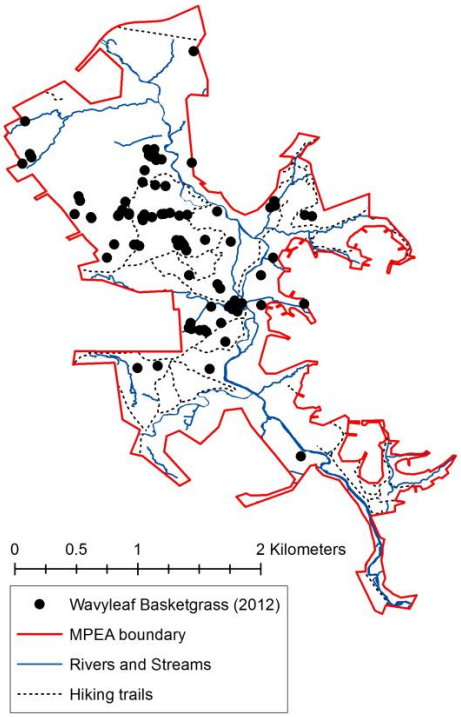


Figure 10. Distribution of the newly invasive *Oplismenus undulatifolius* (wavyleaf basketgrass) at the MPEA in 2012.

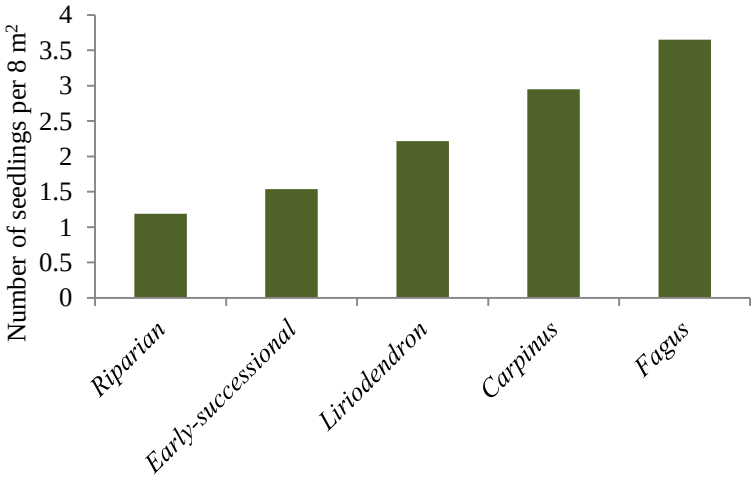


Figure 11. Number of seedlings per 8 m^2 sampled in each mature tree community.

Literature Cited

Abrams, M.D. 1998. The red maple paradox. BioScience 48: 355-364.

Abrams, M. D. and C. A. Copenheaver. 1999. Temporal variation in species recruitment and dendroecology of an old-growth white oak forest in the Virginia Piedmont, USA. Forest Ecology and Management 124: 275-284.

Abrams, M. D. and V. L. W. Hayes. 2008. Impacts of contrasting land-use history on composition, soils, and development of mixed-oak, coastal plain forests on Shelter Island, New York. Journal of the Torrey Botanical Society 135: 37-52.

Abrams, M. D. and K. C. Steiner. 2013. Long-term seedling height growth and compositional changes following logging and wildfire in a Central Pennsylvania Oak Forest. Castanea 78: 256-265.

Albrecht, M. A. and B. C. McCarthy. 2006. Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. Forest Ecology and Management 226: 88-103.

Anderson, K.J. 2007. Temporal patterns in rates of community change during succession. American Naturalist 169: 780-793.

Anderson, D. P., M.G. Turner, S.M. Pearson, T.P. Albright, R.K. Peet, and A. Wieben. 2013. Predicting *Microstegium vimineum* invasion in natural plant communities of the southern Blue Ridge Mountains, USA. Biological Invasions 15: 1217-1230.

Aronson, M. F. J. and S. N. Handel. 2011. Deer and invasive plant species suppress forest herbaceous communities and canopy tree regeneration. Natural Areas Journal 31: 400-407.

Austin, M.P. 2013. Inconsistencies between theory and methodology: A recurrent problem in ordination studies. Journal of Vegetation Science 24: 251-268.

Baeten, L., D. Velghe, M. Vanhellemont, P. De Frenne, M. Hermy, and K. Verheyen. 2010. Early trajectories of spontaneous vegetation recovery after intensive agricultural land use. Restoration Ecology 18: 379-386.

Bain, D. J. and G. S. Brush. 2004. Placing the pieces: Reconstructing the original property mosaic in a warrant and patent watershed. Landscape Ecology 19:843-856.

Bain, D. J. and G. S. Brush. 2008. Gradients, property templates, and land use change. The Professional Geographer 60:224-237.

Bakker, J. P., H. Olff, J.H. Willems, and M. Zobel. 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? Journal of Vegetation Science 7: 147-156.

Banasiak, S. E. and S. J. Meiners. 2009. Long term dynamics of *Rosa multiflora* in a successional system. Biological Invasions 11: 215-224.

Basler, D. and C. Körner. 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree species. Agricultural and Forest Meteorology 165: 73-81.

Barbati, A., P. Corona, L. Salvati, and L. Gasparella. 2013. Natural forest expansion into suburban countryside: Gained ground for a green infrastructure? Urban Forestry and Urban Greening 12: 36-43.

Barden, L.S. 1987. Invasion of *Microstegium vimineum* (Poaceae), an exotic, annual, shade-tolerant, C4 grass, into a North Carolina floodplain. American Midland Naturalist 118:40-45.

Bartha, S., S.J. Meiners, S.T.A. Pickett, and M.L. Cadenasso. 2003. Plant colonization windows in a mesic old field succession. Applied Vegetation Science 6: 205-212.

Beauchamp, V. B., N. Ghuznavi, S.M. Koontz, and R.P. Roberts. 2013. Edges, exotics and deer: The seed bank of a suburban secondary successional temperate deciduous forest. Applied Vegetation Science. In press.

Bellemare, J., G. Motzkin, and D.R. Foster. 2005. Rich Mesic Forests: Edaphic and physiographic drivers of community variation in Western Massachusetts. Rhodora 107: 239-283.

Bernhardt-Römermann, M., A. Gray, A.J. Vanbergen, L. Berges, A. Bohner, R.W. Brooker, L. De Bruyn, B. De Cinti, T. Dirnbock, U, Grandin, A.J. Hester, R. Kanka, S. Klotz, G. Loucougaray, L. Lundin, G. Matteucci, I. Mesazaros, V. Olah, E. Preda, B. Prevosto, J. Pykala, W. Schmidt, M.E. Taylor, A. Vadineanu, T. Waldmann, and J. Stadler. 2011. Functional traits and local environment predict vegetation responses to disturbance: A pan-European multi-site experiment. Journal of Ecology 99: 777-787.

Bishop, T. F. A. and A. B. McBratney. 2001. A comparison of prediction methods for the creation of field-extent soil property maps. Geoderma 103: 149-160.

Blossey, B. 1999. Before, during and after: The need for long-term monitoring in invasive plant species management. Biological Invasions 1: 301-311.

Bobiec, A., D.P.J. Kuijper, M. Niklasson, A. Romankiewicz, and K. Solecka. 2011. Oak (*Quercus robur* L.) regeneration in early successional woodlands grazed by wild ungulates in the absence of livestock. Forest Ecology and Management 262: 780-790.

Bolton, N. W. and A. W. D'Amato. 2011. Regeneration responses to gap size and coarse woody debris within natural disturbance-based silvicultural systems in northeastern Minnesota, USA. Forest Ecology and Management 262: 1215-1222.

Boucher, D. H. and M. A. Mallona. 1997. Recovery of the rain forest tree *Vochysia ferruginea* over 5 years following Hurricane Joan in Nicaragua: A preliminary population projection matrix. Forest Ecology and Management 91: 195-204.

Bowen, M. E., C.A. McAlpine, A.P.N. House, and G.C. Smith. 2007. Regrowth forests on abandoned agricultural land: A review of their habitat values for recovering forest fauna. Biological Conservation 140: 273-296.

Bracchetti, L., L. Carotenuto, and A. Catorci. 2012. Land-cover changes in a remote area of central Apennines (Italy) and management directions. Landscape and Urban Planning 104: 157-170.

Brand, M. H., J.M. Lehrer, and J.D. Lubell. 2012. Fecundity of Japanese barberry (*Berberis thunbergii*) cultivars and their ability to invade a deciduous woodland. Invasive Plant Science and Management 5: 464-476.

Brantley, S. T. and D. R. Young. 2009. Linking light attenuation, sunflecks, and canopy architecture in mesic shrub thickets. Plant Ecology 206: 225-236.

Bressette, J. W., H. Beck, and V.B. Beauchamp. 2012. Beyond the browse line: Complex cascade effects mediated by white-tailed deer. Oikos 121: 1749-1760.

Brisson, J. and A. Bouchard. 2003. In the past two centuries, human activities have caused major changes in the tree species composition of southern Quebec, Canada. Ecoscience 10: 236-246.

Brockerhoff, E. G., H. Jactel, J.A. Parotta, C.P. Quine, and J. Sayer. 2008*a*. Plantation forests and biodiversity: Oxymoron or opportunity? Biodiversity and Conservation 17: 925-951.

Brockerhoff, E. G., W. B. Shaw, B. Hock, M. Kimberley, T. Paul, J. Quinn, and S. Pawson. 2008*b*. Re-examination of recent loss of indigenous cover in New Zealand and the

relative contributions of different land uses. New Zealand Journal of Ecology 32: 115-126.

Brown, M.L. and R.G. Brown. 1972. Woody Plants of Maryland. Baltimore: Port City Press, Inc.

Brown, M.L. and R.G. Brown. 1984. Herbaceous Plants of Maryland. Baltimore: Port City Press, Inc.

Brudvig, L.A., and E.I. Damschen. 2011. Land-use history, historical connectivity, and land management interact to determine long-leaf pine woodland understory richness and composition. Ecography 34: 257-266.

Bruelheide, H. and U. Luginbühi. 2009. Peeking at ecosystem stability: Making use of a natural disturbance experiment to analyze resistance and resilience. Ecology 90: 1314-1325.

Brunet, J., K. Valtinat, M.L. Mayr, A. Felton, M. Lindbladh, and H.H. Bruun. 2011. Understory succession in post-agricultural oak forests: Habitat fragmentation affects forest specialists and generalists differently. Forest Ecology and Management 262: 1863-1871.

Brush, G. S. 2009. Historical land use, nitrogen, and coastal eutrophication: A paleoecological perspective. Estuaries and Coasts 32: 18-28.

Brym, Z. T., J.K. Lake, D. Allen, and A. Ostling. 2011. Plant functional traits suggest novel ecological strategy for an invasive shrub in an understorey woody plant community. Journal of Applied Ecology 48: 1098-1106.

Bugalho, M. N., I. Ibanez, and J.S. Clark. 2013. The effects of deer herbivory and forest type on tree recruitment vary with plant growth stage. Forest Ecology and Management 308: 90-100.

Buriánek, V., R. Novotny, K. Hellebrandova, and V. Sramek. 2013. Ground vegetation as an important factor in the biodiversity of forest ecosystems and its evaluation in regard to nitrogen deposition. Journal of Forest Science 59: 238-252.

Busby, P. E., G. Motzkin, and D.R. Foster. 2008. Multiple and interacting disturbances lead to *Fagus grandifolia* dominance in coastal New England. Journal of the Torrey Botanical Society 135: 346-359.

Busby, P. E. and G. Motzkin. 2009. Dwarf beech forests in coastal New England: Topographic and edaphic controls on variation in forest structure. The American Midland Naturalist 162: 180-194.

Cadenasso, M. L. and S. T. A. Pickett. 2001. Effect of edge structure on the flux of species into forest interiors. Conservation Biology 15: 91-97.

Cadenasso, M. L., S.T.A. Pickett, and J.M. Grove. 2006. Dimensions of ecosystem complexity: Heterogeneity, connectivity, and history. Ecological Complexity 3: 1-12.

Cadenasso, M. L., S.J. Meiners, and S.T.A. Pickett. 2009. The success of succession: A symposium commemorating the 50th anniversary of the Buell-Small succession study. Applied Vegetation Science 12:3-8.

Carlson, P., E. Connor, J. Heaps, S. MacConnell, M. Jones, G. Plucer, S. Hockhauser, D. Buckwald, M. Pavillard, and R. Nichols. 1971. Report on the Inventory of the Middle Patuxent River Valley. Antioch College, Prepared for the Howard Research and Development Corporation and Columbia Association.

Catling, P. M., M.J. Oldham, D.A. Sutherland, V.R. Brownell, and B.M.H. Larson. 1997. The recent spread of autumn-olive, *Elaeagnus umbellata*, into southern Ontario and its current status. Canadian Field-Naturalist 111: 376-380.

Catorci, A., F.M. Tardella, S. Cesaretti, M. Bertellotti, and R. Santolini. 2012. The interplay among grazing history, plant-plant spatial interactions and species traits affects vegetation recovery processes in Patagonian steppe. Community Ecology 13: 253-263.

Čepelová, B. and Z. Münzbergová. 2012. Factors determining the plant species diversity and species composition in a suburban landscape. Landscape and Urban Planning 106: 336-346.

Chaideftou, E., A. Kallimanis, E. Bergmeier, and P. Dimopoulos. 2012. How does plant species composition change from year to year? A case study from the herbaceous layer of a submediterranean oak woodland. Community Ecology 13: 88-96.

Chapman, J. I. and R. W. McEwan. 2013. Spatiotemporal dynamics of α- and β-diversity across topographic gradients in the herbaceous layer of an old-growth deciduous forest. Oikos 122: 1679-1686.

Cheplick, G. P. and J. Fox. 2011. Density-dependent growth and reproduction of *Microstegium vimineum* in contrasting light environments. Journal of the Torrey Botanical Society 138: 62-72.

Chetelat, J., M. Kalbermatten, K.S.M. Lannas, T. Spiegelberger, J. Wettstein, F. Gillet, A. Peringer, and A. Buttler. 2013. A contextual analysis of land-use and vegetation changes in two wooded pastures in the Swiss Jura Mountains. Ecology and Society 18: 39-54.

Chiang, L., I. Chaubey, M.W. Gitau, and J.G. Arnold. 2010. Differentiating impacts of land use changes from pasture management in a CEAP watershed using the SWAT model. Transactions of the Asabe 53:1569-1584.

Choi, B., J.C. Dewey, J.A. Hatten, A.W. Ezell, and Z. Fan. 2012. Changes in vegetative communities and water table dynamics following timber harvesting in small headwater streams. Forest Ecology and Management 281: 1-11.

Chytry, M., L. Tichy, J. Holt, and Z. Botta-Dukat. 2002. Determination of diagnostic species with statistical fidelity measures. Journal of Vegetation Science 13: 79-90.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117-143.

Clemens, G., S. Fiedler, D.C. Nguyen, V.D. Nyuyen, U. Schuler, and K. Stahr. 2010. Soil fertility affected by land use history, relief position, and parent material under a tropical climate in NW-Vietnam. Catena 81: 87-96.

Clements, F.E. 1916. Plant Succession: An Analysis of the Development of Vegetation. Carnegie Institute, Washington, D.C.

Clements, F.E. 1949. Dynamics of Vegetation: Selections from the Writings of Frederic E. Clements, PhD. The H.W. Wilson Company, New York.

Connor, E. F., D. Buchwald, P. Wagner, A. Geis, and C. S. Robbins. 1971. Upland tulip-tree-maple-oak. American Birds 25:971.

Cooper, A., T. McCann, and R.G.H. Bunce. 2006. The influence of sampling intensity on vegetation classification and the implications for environmental management. Environmental Conservation 33: 118-127.

Copenheaver, C. A. 2008. Old-field Succession in Western New York: The progression of forbs and woody species from abandonment to mature forest. Rhodora 110: 157-170.

Copenheaver, C. A., J.R. Seiler, J.A. Peterson, A.M. Evans, J.L. McVay, and J.H. White. 2013. Stadium Woods: A dendroecological analysis of an old-growth forest fragment on a university campus. Dendrochronologia. In press.

Côté, S. D., T.P. Rooney, J.P. Tremblay, C. Dussault, and D.M. Waller. 2004. Ecological impacts of deer overabundance. 35: 113-147.

Cousins, S. A. O., R. Lindborg, and S. Mattsson. 2009. Land use history and site location are more important for grassland species richness than local soil properties. Nordic Journal of Botany 27: 483-489.

Cowden, M. M., J.L. Hart, and M.L. Buchanan. 2014. Canopy accession strategies and climate responses for three *Carya* species common in the eastern deciduous forest. Trees - Structure and Function 28: 223-235.

Cowles, H. C. 1919. Plant succession. Botanical Gazette 68: 477-478.

Curtin, P. D., G. S. Brush, and G. W. Fisher. 2001. Discovering the Chesapeake: The History of an Ecosystem. Baltimore: Johns Hopkins University Press.

Cypher, B., R.H. Yahner, and E.A. Cypher. 1988. Seasonal food use by white-tailed deer at Valley Forge National Historical Park, Pennsylvania, USA. Environmental Management 12: 237-242.

Dahlstrom, A., H. Rydin, and S.O. Borgegard. 2010. Remnant habitats for grassland species in an abandoned Swedish agricultural landscape. Applied Vegetation Science 13: 305-314.

Daubenmire, R. 1959. A canopy-coverage method of vegetation analysis. Northwest Science 33: 43-64.

Dawson, W.M., Jr., 1834. Map of Doughoregan Manor Enlarged: The Property of Charles Carroll, Esq. [map]. 1 inch : 40 perches.

De Cáceres, M., X. Font, and F. Oliva. 2010. The management of vegetation classifications with fuzzy clustering. Journal of Vegetation Science 21: 1138-1151.

De Cáceres, M. and S. K. Wiser. 2012. Towards consistency in vegetation classification. Journal of Vegetation Science 23: 387-393.

DeGasperis, B.G., and G. Motzkin. 2007. Windows of opportunity: Historical and ecological controls of *Berberis thunbergii* invasions. Ecology 88: 3115-3125.

Del Tredici, P. 2010. Wild Urban Plants of the Northeast. Ithaca, New York: Cornell University Press.

Devlaeminck, R., B. Bossuyt, and M. Hermy. 2005. Inflow of seeds through the forest edge: Evidence from seed bank and vegetation patterns. Plant Ecology 176: 1-17.

D'Orangeville, L., A. Bouchard, and A. Cagliasto. 2011. Unexpected seedling growth in the understory of post-agricultural forests from Eastern Canada. Annals of Forest Science 68: 759-769.

Dornbush, M.E. and P.G. Hahn. 2013. Consumer and establishment limitation contribute more than competitive interactions in sustaining dominance of the exotic herb garlic mustard in a Wisconsin, USA forest. Biological Invasions 15: 2691-2705.

Dorsey, C. 1968. Original Land Grants of Howard County, Maryland [map]. 1 inch : 2340 feet.

Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs 67: 345-366.

Duguay, J. P. and C. Farfaras. 2011. Overabundant suburban deer, invertebrates, and the spread of an invasive exotic plant. Wildlife Society Bulletin 35: 243-251.

Duguay, S., F. Eigenbrod, and L. Fahrig. 2007. Effects of surrounding urbanization on non-native flora in small forest patches. Landscape Ecology 22: 589-599.

Dyer, J. M. 2010. Land-use legacies in a central Appalachian forest: Differential response of trees and herbs to historic agricultural practices. Applied Vegetation Science 13: 195-206.

Ehrenfeld, J. G., P. Kourtev, and W. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. Ecological Applications 11: 1287-1300.

Elliott, K. J., L.R. Boring, and W.T. Swank. 1998. Changes in vegetation structure and diversity after grass-to-forest succession in a southern Appalachian watershed. American Midland Naturalist 140: 219-232.

Engelman, H. M. and R. D. Nyland. 2006. Interference to hardwood regeneration in northeastern North America: Assessing and countering ferns in northern hardwood forests. Northern Journal of Applied Forestry 23: 166-175.

Evans, D. M., C.E. Zipper, J.A. Burger, B.D. Strahm, and A.M. Villamagna. 2013. Reforestation practice for enhancement of ecosystem services on a compacted surface mine: Path toward ecosystem recovery. Ecological Engineering 51: 16-23.

Finegan, B. 1984. Forest succession. Nature 312: 109-114.

Flinn, K. M. and P. L. Marks. 2007. Agricultural legacies in forest environments: Tree communities, soil properties, and light availability. Ecological Applications 17: 452-463.

Flory, S. L. and K. Clay. 2010. Non-native grass invasion suppresses forest succession. Oecologia 164: 1029-1038.

Fraterrigo, J. M., M. G. Turner, and S.M. Pearson. 2006. Interactions between past land use, life-history traits and understory spatial heterogeneity. Landscape Ecology 21: 777-790.

Fridley, J. D. and J. P. Wright. 2012. Drivers of secondary succession rates across temperate latitudes of the Eastern USA: Climate, soils, and species pools. Oecologia 168: 1069-1077.

Fu, Y. H., M. Campioli, G. Deckmyn, and I.A. Janssens. 2013. Sensitivity of leaf unfolding to experimental warming in three temperate tree species. Agricultural and Forest Meteorology 181: 125-132.

Gavier-Pizarro, G. I., V.C. Radeloff, S.I. Stewart, C.D. Huebner, and N.S. Keuler. 2010. Rural housing is related to plant invasions in forests of southern Wisconsin, USA. Landscape Ecology 25: 1505-1518.

Gesch, D.B., 2007. The National Elevation Dataset. *In* D. Maune, Ed., Digital Elevation Model Technologies and Applications: The DEM Users Manual, pp. 99-118. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland.

Gesch, D., M. Oimoen, S. Greenlee, C. Nelson, M. Steuck, and D. Tyler. 2002. The National Elevation Dataset. Photogrammetric Engineering and Remote Sensing 68: 5-11.

Gilliam, F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 57: 845-858.

Goins, S. M., J.I. Chapman, and R.W. McEwan. 2013. Composition shifts, disturbance, and canopy-accession strategy in an oldgrowth forest of Southwestern Ohio, USA. Natural Areas Journal 33: 384-394.

Gotfryd, A. and R. I. C. Hansell. 1985. The impact of observer bias on multivariate analyses of vegetation structure. Oikos 45: 223-234.

Groffman, P. M., R.V. Pouyat, M.L. Cadenasso, W.C. Zipperer, K. Szlavecz, I.D. Yesilonis, L.E. Band, and G.S. Brush. 2006. Land use context and natural soil controls on plant

community composition and soil nitrogen and carbon dynamics in urban and rural forests. Forest Ecology and Management 236: 177-192.

Hall, B., G. Motzkin, D.R. Foster, M. Syfert, and J. Burk. 2002. Three hundred years of forest and land-use change in Massachusetts, USA. Journal of Biogeography 29: 1319-1335.

Hamlin, B. T., W.T. Kittredge, D.P. Lubin, and E.B. Wright. 2012. Changes in the vascular flora of the Middlesex Fells reservation, Middlesex County, Massachusetts, from 1895 to 2011. Rhodora 114: 229-308.

Hanberry, B. B. 2013. Changing eastern broadleaf, southern mixed, and northern mixed forest ecosystems of the eastern United States. Forest Ecology and Management 306: 171-178.

Hart, J. L., S.L. Van De Gevel, and H.D. Grissino-Mayer. 2008. Forest dynamics in a natural area of the southern Ridge and Valley, Tennessee. Natural Areas Journal 28: 275-289.

Heiri, C., A. Wolf, L. Rohrer, P. Brang, and H. Bugmann. 2012. Successional pathways in Swiss mountain forest reserves. European Journal of Forest Research 131: 503-518.

Henkin, M. A., K.E. Medley, R.J. Abbitt, and J.M. Patton. 2013. Invasion dynamics of nonnative Amur honeysuckle over 18 Years in a southwestern Ohio forest. American Midland Naturalist 170: 335-347.

Hitchcock, A.S. 1971. Manual of the Grasses of the United States. New York: Dover Publications, Inc.

Ho, M. and C. J. Richardson. 2013. A five year study of floristic succession in a restored urban wetland. Ecological Engineering 61: 511-518.

Hobbs, R.J., L.M. Hallett, P.R. Ehrlich, and H.A. Mooney. 2011. Intervention ecology: Applying ecological science in the twenty-first century. BioScience 61: 442-450.

Hogan, D. M. and M. R. Walbridge. 2009. Recent land cover history and nutrient retention in riparian wetlands. Environmental Management 44: 62-72.

Holzmueller, E., S. Jose, M. Jenkins, A. Camp, and A. Long. 2006. Dogwood anthracnose in eastern hardwood forests: What is known and what can be done? Journal of Forestry 104: 21-26.

Hough-Goldstein, J., and S. LaCoss. 2012. Interactive effects of light environment and herbivory on growth and productivity of an invasive annual vine, Persicaria perfoliata. Arthropod-Plant Interactions 6:103-112.

Huebner, C. D. 2011. Seed mass, viability, and germination of Japanese stiltgrass (*Microstegium vimineum*) under variable light and moisture conditions. Invasive Plant Science and Management 4: 274-283.

Jesse, L. C., J.D. Nason, J.J. Obrycki, and K.A. Moloney. 2010. Quantifying the levels of sexual reproduction and clonal spread in the invasive plant, *Rosa multiflora*. Biological Invasions 12: 1847-1854.

Johnson, S. E. and M. D. Abrams. 2009. Age class, longevity and growth rate relationships: Protracted growth increases in old trees in the eastern United States. Tree Physiology 29: 1317-1328.

Jones, C. C. 2012. Challenges in predicting the future distributions of invasive plant species. Forest Ecology and Management 284: 69-77.

Jordan, R. C., W.R. Brooks, D.V. Howe, and J.G. Ehrenfeld. 2012. Evaluating the performance of volunteers in mapping invasive plants in public conservation lands. Environmental Management 49: 425-434.

Jurasinski, G., V. Retzer, and C. Beierkuhnlein. 2009. Inventory, differentiation, and proportional diversity: A consistent terminology for quantifying species diversity. Oecologia 159: 15-26.

Karst, J., B. Gilbert, and M.J. Lechowicz. 2005. Fern community assembly: The roles of chance and the environment at local and intermediate scales. Ecology 86: 2473-2486.

Katz, D. S. W., G.M. Lovett, C.D. Canham, and C.M. O'Reilly. 2010. Legacies of land use history diminish over 22 years in a forest in southeastern New York. Journal of the Torrey Botanical Society 137: 236-251.

Kern, C. C., P.B. Reich, R.A. Montgomery, and T.F. Strong. 2012. Do deer and shrubs override canopy gap size effects on growth and survival of yellow birch, northern red oak, eastern white pine, and eastern hemlock seedlings? Forest Ecology and Management 267: 134-143.

Knapp, L. B., J.H. Fownes, and R.A. Harrington. 2008. Variable effects of large mammal herbivory on three non-native versus three native woody plants. Forest Ecology and Management 255: 92-98.

Komuro, T. and F. Koike. 2005. Colonization by woody plants in fragmented habitats of a suburban landscape. Ecological Applications 15: 662-673.

Koncz, G., P. Torok, M. Papp, G. Matus, and B. Tothmeresz. 2011. Penetration of weeds into the herbaceous understory and soil seed bank of a Turkey oak-sessile oak forest in Hungary. Community Ecology 12: 227-233.

Koontz, S.M. 2011. Community structure and exotic species dynamics of an eastern deciduous forest and implications for management at the Middle Patuxent Environmental Area. Unpubl. M.S. Thesis, Towson Univ., Towson, Maryland.

Kraft, J. 2008. Soil Survey of Howard County, Maryland. Natural Resources Conservation Service and Department of Agriculture, Maryland Agricultural Experiment Station., Washington, D.C.

Krueger, L. M., C.J. Peterson, A. Royo, and W.P. Carson. 2009. Evaluating relationships among tree growth rate, shade tolerance, and browse tolerance following disturbance in an eastern deciduous forest. Canadian Journal of Forest Research 39: 2460-2469.

Kuebbing, S., M.A. Rodriguez-Cabal, D. Fowler, L. Breza, J.A. Schweitzer, and J.K. Bailey. 2013*a*. Resource availability and plant diversity explain patterns of invasion of an exotic grass. Journal of Plant Ecology 6: 141-149.

Kuebbing, S. E., L. Souza, and N.J. Sanders. 2013*b*. Effects of co-occurring non-native invasive plant species on old-field succession. Forest Ecology and Management. In press.

Kuhman, T.R., S.M. Pearson, and M.G. Turner. 2010. Effects of land-use history and the contemporary landscape on non-native plant invasion at local and regional scales in the forest-dominated southern Appalachians. Landscape Ecology 25: 1433-1445.

Kuhman, T. R., S.M. Pearson, and M.G. Turner. 2011. Agricultural land-use history increases non-native plant invasion in a southern Appalachian forest a century after abandonment. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 41: 920-929.

Kumar, V. and A. DiTommaso. 2005. Mile-a-minute (*Polygonum perfoliatum*): An increasingly problematic invasive species. Weed Technology 19: 1071-1077.

Ladwig, L. M. and S. J. Meiners. 2010. Spatiotemporal dynamics of lianas during 50 years of succession to temperate forest. Ecology 91: 671-680.

Lake, E.C., J. Hough-Goldstein, and V. D'Amico. 2013. Integrating management techniques to restore sites invaded by mile-a-minute weed, *Persicaria perfoliata*. Restoration Ecology. In press.

Lankau, R. A. 2013. Species invasion alters local adaptation to soil communities in a native plant. Ecology 94: 32-40.

Lebrija-Trejos, E., J.A. Meave, L. Poorter, E.A. Perez-Garcia, and F. Bongers. 2010. Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession. Perspectives in Plant Ecology, Evolution and Systematics 12: 267-275.

Leicht-Young, S. A., N.B. Pavlovic, K.J. Frohnapple, and R. Grundel. 2010. Liana habitat and host preferences in northern temperate forests. Forest Ecology and Management 260: 1467-1477.

Lemke, D., C.J. Schweitzer, W. Tadesse, Y. Wang, and J.A. Brown. 2013. Geospatial assessment of invasive plants on reclaimed mines in Alabama. Invasive Plant Science and Management 6: 401-410.

Li, M., Z. Du, H. Pan, C. Yan, W. Xiao, and J. Lei. 2012. Effects of neighboring woody plants on target trees with emphasis on effects of understorey shrubs on overstorey physiology in forest communities: A mini-review. Community Ecology 13: 117-128.

Lind, E. M., E.P. Myron, J. Giaccai, and J.D. Parker. 2012. White-tailed deer alter specialist and generalist insect herbivory through plant traits. Environmental Entomology 41: 1409-1416.

Lõhmus, K. and J. Liira. 2013. Old rural parks support higher biodiversity than forest remnants. Basic and Applied Ecology 14: 165-173.

Lubell, J. D. and M. H. Brand. 2010. Germination, growth and survival of *Berberis thunbergii* DC. (Berberidaceae) and *Berberis thunbergii* var. *atropurpurea* in five natural environments. Biological Invasions 13: 135-141.

Martin, G. I., J. Hepinstall-Cymerman, and L.K. Kirkman. 2013. Six decades (1948-2007) of landscape change in the Dougherty Plain of Southwest Georgia, USA. Southeastern Geographer 53: 28-49.

Matlack, G. R. and J. R. Schaub. 2011. Long-term persistence and spatial assortment of nonnative plant species in second-growth forests. Ecography 34: 649-658.

Mattingly, W. B. and J. L. Orrock. 2013. Historic land use influences contemporary establishment of invasive plant species. Oecologia 172: 1147-1157.

McCarthy, B. C., C.J. Small, and D.L. Rubino. 2001. Composition, structure and dynamics of Dysart Woods, an old-growth mixed mesophytic forest of southeastern Ohio. Forest Ecology and Management 140: 193-213.

McCune, B. and J.B. Grace. 2002. Analysis of Ecological Communities. Gleneden Beach, Oregon: MjM Software Design.

McCune, B. and M.J. Mefford. 2011. PC-ORD. Multivariate Analysis of Ecological Data, Version 5.10 [computer software]. Gleneden Beach, Oregon: MjM Software.

McDonald, R. I., G. Motzkin, and D.R. Foster. 2008. Assessing the influence of historical factors, contemporary processes, and environmental conditions on the distribution of invasive species. Journal of the Torrey Botanical Society 135: 260-271.

McKinney, M. L. 2004. Citizens as propagules for exotic plants: Measurement and management implications. Weed Technology 18: 1480-1483.

McLean, E. O. 1982. Chemical equilibrations with soil buffer systems as bases for future soil testing programs. Communications in Soil Science and Plant Analysis 13: 411-433.

Meffe, G.K., and C.R. Carroll. 1994. Habitat fragmentation. *In* G.K. Meffe and C.R. Carroll, Principles of Conservation Biology, pp. 237-264. Sunderland: Sinauer Associates, Inc.

Meiners, S. J. 2007. Apparent competition: an impact of exotic shrub invasion on tree regeneration. Biological Invasions 9: 849-855.

Meiners, S. J., S. T. A. Pickett, and M.L. Cadenasso. 2002. Exotic plant invasions over 40 years of old field successions: Community patterns and associations. Ecography 25: 215-223.

Meiners, S. J., T.A. Rye, and J.R. Klass. 2009. On a level field: The utility of studying native and non-native species in successional systems. Applied Vegetation Science 12: 45-53.

Milberg, P., J. Bergstedt, J. Fridman, G. Odell, and L. Westerberg. 2008. Observer bias and random variation in vegetation monitoring data. Journal of Vegetation Science 19: 633-644.

Miles, J. 1979. Vegetation Dynamics. Chapman and Hall Ltd., London.

Mooney, E., M. Edwards, and R. Niesenbaum. 2010. Genetic differentiation between sun and shade habitats in populations of *Lindera benzoin* L. Population Ecology 52: 417-425.

Mooney, E. H. and R. A. Niesenbaum. 2012. Population-specific responses to light influence herbivory in the understory shrub *Lindera benzoin*. Ecology 93: 2683-2692.

Moore, J. L., C.E. Hauser, J.L. Bear, N.S.G. Williams, and M.A. McCarthy. 2011. Estimating detection-effort curves for plants using search experiments. Ecological Applications 21: 601-607.

Moore, M. R., D.S. Buckley, W.E. Klingerman, and A.M. Saxton. 2013. Distribution and growth of autumn olive in a managed forest landscape. Forest Ecology and Management 310: 589-599.

Moreno, C. E. and P. Rodríguez. 2010. A consistent terminology for quantifying species diversity? Oecologia 163: 279-282.

Morgan, E. C. 2009. The vegetation and vascular flora of the Bartlett Arboretum Forest. Journal of the Torrey Botanical Society 136: 532-540.

Morris, L. R., T.R. Monaco, and R.L. Sheley. 2011. Land-use legacies and vegetation recovery 90 years after cultivation in Great Basin sagebrush ecosystems. Rangeland Ecology and Management 64: 488-497.

Morris, A.B., N.K. Millsaps, K.Q. Mason, J.S. Howell, and J.H. Speer. 2014. Ature beech trees (*Fagus grandifolia*; Fagaceae) are persistently clonal in coves and beech gaps in the Great Smoky Mountains. American Journal of Botany 101: 381-388.

Mosher, E. S., J.A. Silander, and A.M. Latimer. 2009. The role of land-use history in major invasions by woody plant species in the northeastern North American landscape. Biological Invasions 11: 2317-2328.

Motzkin, G., P. Wilson, D.R. Foster, and A. Allen. 1999. Vegetation patterns in heterogeneous landscapes: The importance of history and environment. Journal of Vegetation Science 10: 903-920.

Murphy, S. J. and B. C. McCarthy. 2012. Evidence for topographic control of tree spatial patterning in an old-growth, mixed mesophytic forest in Southeastern Ohio, USA. Journal of the Torrey Botanical Society 139: 181-193.

Myster, R. W. and S. T. A. Pickett. 1990. Initial conditions, history and successional pathways in ten contrasting old fields. American Midland Naturalist 124: 231-238.

Napton, D. E., R.F. Auch, R. Headley, and J.L. Taylor. 2010. Land changes and their driving forces in the Southeastern United States. Regional Environmental Change 10: 37-53.

Natural Resources Conservation Service, United States Department of Agriculture. 2013. Soil Survey Geographic (SSURGO) Database for Howard County, Maryland. Available online at http://soildatamart.nrcs.usda.gov.

Newcomb, L. 1977. Newcomb's Wildflower Guide. New York: Little, Brown and Co.

Nuttle, T., T.E. Ristau, and A.A. Royo. 2014. Long-term biological legacies of herbivore density in a landscape-scale experiment: Forest understoreys reflect past deer density treatments for at least 20 years. Journal of Ecology 102: 221-228.

Oikonomakis, N. and P. Ganatsas. 2012. Land cover changes and forest succession trends in a site of Natura 2000 network (Elatia forest) in northern Greece. Forest Ecology and Management 285: 153-163.

Oliver, I., E.A. Broese, M.L. Dillon, D. Sivertsen, and M.J. McNellie. 2013. Semi-automated assignment of vegetation survey plots within an *a priori* classification of vegetation types. Methods in Ecology and Evolution 4: 73-81.

Orr, S. P., J.A. Rudgers, and K. Clay. 2005. Invasive plants can inhibit native tree seedlings: Testing potential allelopathic mechanisms. Plant Ecology 181: 153-165.

Paal, J., M. Turb, T. Koster, E. Rajandu, and J. Liira. 2011. Forest land-use history affects the species composition and soil properties of old-aged hillock forests in Estonia. Journal of Forest Research 16: 244-252.

Peters, G., F. Crespo, P. Lingras, and R. Weber. 2013. Soft clustering – Fuzzy and rough approaches and their extensions and derivatives. International Journal of Approximate Reasoning 54: 307-322.

Pickett, S. T. A. and M. L. Cadenasso. 2008. Linking ecological and built components of urban mosaics: an open cycle of ecological design. Journal of Ecology 96: 8-12.

Pickett, S.T.A., M.L. Cadenasso, and S. Bartha. 2001. Implications from the Buell-Small succession study for vegetation restoration. Applied Vegetation Science 4: 41-52.

Pickett, S.T.A., M.L. Cadenasso, and S.J. Meiners. 2009. Ever since Clements: From succession to vegetation dynamics and understanding to intervention. Applied Vegetation Science 12: 9-21.

Phillips, E.A. 1959. Methods of Vegetation Study. New York: Henry Holt and Company, Inc.

Price, J. N., N.K. Wong, and J.W. Morgan. 2010. Recovery of understorey vegetation after release from a long history of sheep grazing in a herb-rich woodland. Austral Ecology 35: 505-514.

Raciti, S. M., P.M. Groffman, J.C. Jenkins, R.V. Pouyat, T.J. Fahey, S.T.A. Pickett, and M.L. Cadenasso. 2011. Accumulation of carbon and nitrogen in residential soils with different land-use histories. Ecosystems 14: 287-297.

Rauschert, E. S. J., D.A. Mortensen, O.N. Bjornstad, A.N. Nord, and N. Peskin. 2010. Slow spread of the aggressive invader, *Microstegium vimineum* (Japanese stiltgrass). Biological Invasions 12: 563-579.

Reichard, S. H. and P. White. 2001. Horticulture as a pathway of invasive plant introductions in the United States. Bioscience 51: 103-113.

Richards, J. D. and J. L. Hart. 2011. Canopy gap dynamics and development patterns in secondary *Quercus* stands on the Cumberland Plateau, Alabama, USA. Forest Ecology and Management 262: 2229-2239.

Roberts, M. R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. Canadian Journal of Botany 82: 1273-1283.

Ruiz, J. and G. Domon. 2009. Analysis of landscape pattern change trajectories within areas of intensive agricultural use: Case study in a watershed of southern Quebec, Canada. Landscape Ecology 24: 419-432.

R Development Core Team. 2013. R: A Language and Environment for Statistical Computing [computer software]. Vienna, Austria: R Foundation for Statistical Computing. Available from http://www.r-project.org/

Rauschert, E. S. J., D.A. Mortensen, O.N. Bjornstad, A.N. Nord, and N. Peskin. 2010. Slow spread of the aggressive invader, *Microstegium vimineum* (Japanese stiltgrass). Biological Invasions 12: 563-579.

Richards, J. D. and J. L. Hart. 2011. Canopy gap dynamics and development patterns in secondary *Quercus* stands on the Cumberland Plateau, Alabama, USA. Forest Ecology and Management 262: 2229-2239.

Ruiz, J. and G. Domon. 2009. Analysis of landscape pattern change trajectories within areas of intensive agricultural use: Case study in a watershed of southern Quebec, Canada. Landscape Ecology 24: 419-432.

Sabatini, F. M., J.I. Burton, R.M. Scheller, K.L. Amatangelo, and D.J. Mladenoff. 2013. Functional diversity of ground-layer plant communities in old-growth and managed northern hardwood forests. Applied Vegetation Science. In press.

Salako, V.K., A. Adebanji, and R. Glele Kakai. 2013. On the empirical performance of non-metric multidimensional scaling in vegetation studies. International Journal of Applied Mathematics and Statistics 36: 54-67.

Sato, T., S. Ito, Y. Mitsuda, and N. Soen. 2010. Impacts of land-use history on the diversity of a riparian forest landscape in warm-temperate Kyushu, southern Japan. Landscape and Ecological Engineering 6: 89-98.

Schramm, J. W. and J. G. Ehrenfeld. 2010. Leaf litter and understory canopy shade limit the establishment, growth and reproduction of *Microstegium vimineum*. Biological Invasions 12: 3195-3204.

Schramm, J. W. and J. G. Ehrenfeld. 2012. Patterns of patch colonization and expansion in the non-native annual grass *Microstegium vimineum* (Poaceae). Rhodora 114: 1-20.

Schulte, E. E. and B. G. Hopkins. 1996. Estimation of organic matter by weight loss-on-ignition. 21–31. *In*: Magdoff, F. R., M. A. Tabatabai, and E. A. Hanlon. Soil organic matter: analysis and interpretation. Soil Science Society of America. Madison, Wisconsin.

Schulte, L. A., E.C. Mottl, and B.L. Palik. 2011. The association of two invasive shrubs, common buckthorn (*Rhamnus cathartica*) and Tartarian honeysuckle (*Lonicera tatarica*), with oak communities in the midwestern United States. Canadian Journal of Forest Research 41: 1981-1992.

Schulz, B. K. and A. N. Gray. 2013. The new flora of northeastern USA: Quantifying introduced plant species occupancy in forest ecosystems. Environmental Monitoring and Assessment 185: 3931-3957.

Schwierjohann, J. H. and C. Farfaras. 2000. Middle Patuxent Comprehensive Management Plan. Maryland Department of Recreation and Parks, Howard County, Maryland.

Semeniuk, V. and I. D. Cresswell. 2013. A proposed revision of diversity measures. Diversity 5: 613-626.

Singleton, R., S. Gardescu, P.L. Marks, and M.A. Geber. 2001. Forest herb colonization of post-agricultural forests in central New York State, USA. Journal of Ecology 89: 325-338.

Smith, J. R., R.A. Sweitzer, and W.F. Jensen. 2007. Diets, movements, and consequences of providing wildlife food plots for white-tailed deer in central North Dakota. Journal of Wildlife Management 71: 2719-2726.

Stebenne, D. and J. R. Mitchell. 2007. New City Upon a Hill: A History of Columbia, Maryland. Charleston, South Carolina: History Press.

Takahashi, K., K. Arii, and M.J. Lechowicz. 2010. Codominance of *Acer saccharum* and *Fagus grandifolia*: The role of *Fagus* root sprouts along a slope gradient in an old-growth forest. Journal of Plant Research 123: 665-674.

Tekiela, D. R. and J. N. Barney. 2013. Quantifying *Microstegium vimineum* seed movement by non-riparian water dispersal using an ultraviolet-marking based recapture method." PLoS ONE 8(9).

Terwei, A., S. Zerbe, A. Zeileis, P. Annighofer, H. Kawaletz, I. Molder, and C. Ammer. 2013. Which are the factors controlling tree seedling establishment in North Italian floodplain forests invaded by non-native tree species? Forest Ecology and Management 304: 192-203.

Thompson, J. R., D.N. Carpenter, C.V. Cogbill, and D.R. Foster. 2013. Four centuries of change in northeastern United States forests. PLoS ONE 8(9).

Tognetti, P.M., E.J. Chaneton, M. Omacini, H.J. Trebino, and R.J.C. Leon. 2010. Exotic vs. native plant dominance over 20 years of old-field succession on set-aside farmland in Argentina. Biological Conservation 143: 2494-2503.

Tognetti, P. M. and E. J. Chaneton. 2012. Invasive exotic grasses and seed arrival limit native species establishment in an old-field grassland succession. Biological Invasions 14: 2531-2544.

Tuomisto, H. 2010*a*. A consistent terminology for quantifying species diversity? Yes, it does exist. Oecologia 164: 853-860.

Tuomisto, H. 2010*b*. A diversity of beta diversities: Straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography 33(1): 2-22.

Tuomisto, H. 2010*c*. A diversity of beta diversities: Straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. Ecography 33: 23-45.

Tuomisto, H. 2011. Commentary: Do we have a consistent terminology for species diversity? Yes, if we choose to use it. Oecologia 167: 903-911.

Urbanek, R. E. and C. K. Nielsen. 2013. Influence of landscape factors on density of suburban white-tailed deer. Landscape and Urban Planning 114: 28-36.

Uva, R.H., J.C. Neal, and J.M. DiTomaso. 1997. Weeds of the Northeast. Ithaca, New York: Cornell University Press.

Van Breugel, M., F. Bongers, and M. Martinez-Ramos. 2007. Species dynamics during early secondary forest succession: Recruitment, mortality and species turnover. Biotropica 39: 610-619.

Van Diggelen, R. and R.H. Morris. 2003. Restoring plant communities- introduction. Applied Vegetation Science 6: 106-110.

Vepakomma, U., D. Kneeshaw, and M.J. Fortin. 2012. Spatial contiguity and continuity of canopy gaps in mixed wood boreal forests: Persistence, expansion, shrinkage and displacement. Journal of Ecology 100: 1257-1268.

Waller, D. M. and L. I. Maas. 2013. Do white-tailed deer and the exotic plant garlic mustard interact to affect the growth and persistence of native forest plants? Forest Ecology and Management 304: 296-302.

Wang, P., J.P. Lei, M.H. Li, and F.H. Yu. 2012. Spatial heterogeneity in light supply affects intraspecific competition of a stoloniferous clonal plant. PLoS ONE 7(6).

Wang, S., X. Wang, H. Guo, W. Fan, H. Lv, and R. Duan. 2013. Distinguishing the importance between habitat specialization and dispersal limitation on species turnover. Ecology and Evolution 3: 3545-3553.

Ward, J. S., S.C. Williams, and T.E. Worthley. 2013. Comparing effectiveness and impacts of Japanese barberry (*Berberis thunbergii*) control treatments and herbivory on plant communities. Invasive Plant Science and Management 6: 459-469.

Warren, R. J.,II, J.P. Wright, and M.A. Bradford. 2011. The putative niche requirements and landscape dynamics of *Microstegium vimineum*: An invasive Asian grass. Biological Invasions 13: 471-483.

Welch, N. T., J.M. Belmont, and J.C. Randolph. 2007. Summer ground layer biomass and nutrient contribution to above-ground litter in an Indiana temperate deciduous forest. American Midland Naturalist 157: 11-26.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30: 279-338.

Wilder, C. M., F.W. Holtzclaw, Jr., and E.E.C. Clebsch. 1999. Succession, sapling density and growth in canopy gaps along a topographic gradient in a second growth East Tennessee forest. American Midland Naturalist 142: 201-212.

Williams, S. C. and J. S. Ward. 2006. Exotic seed dispersal by white-tailed deer in Southern Connecticut. Natural Areas Journal 26: 383-390.

Williams, S. C., A.J. De Nicola, T. Almendinger, and J. Maddock. 2013. Evaluation of organized hunting as a management technique for overabundant white-tailed deer in suburban landscapes. Wildlife Society Bulletin 37: 137-145.

Wilson, J.B., P.S. White, J.P. Bakker, and S. Diaz. 2004. Restoration, succession, and climatic change. Applied Vegetation Science 7: 151-152.

Wiser, S. K. 1998. Comparison of southern Appalachian high-elevation outcrop plant communities with their northern Appalachian counterparts. Journal of Biogeography 25: 501-513.

Wiser, S. K. and M. De Cáceres. 2013. Updating vegetation classifications: An example with New Zealand's woody vegetation. Journal of Vegetation Science 24: 80-93.

Wiser, S.K., J.M. Hurst, E.F. Wright, and R.B. Allen. 2011. New Zealand’s forest and shrubland communities: a quantitative classification based on a nationally representative plot network. Applied Vegetation Science 14: 506-523.

Wright, D. M., A.J. Tanentzap, O. Flores, S.W. Husheer, R.P. Duncan, S.K. Wiser, and D.A. Coomes. 2012. Impacts of culling and exclusion of browsers on vegetation recovery across New Zealand forests. Biological Conservation 153: 64-71.

Yates, E. D., D.F. Levia, Jr., and C.L. Williams. 2004. Recruitment of three non-native invasive plants into a fragmented forest in southern Illinois. Forest Ecology and Management 190: 119-130.

Young, T.P., D.A. Petersen, and J.J. Clary. 2005. The ecology of restoration: Historical links, emerging issues, and unexplored realms. Ecology Letters 8: 662-673.

Zenner, E. K., Y.L. Dickinson, and J.E. Peck. 2013. Recovery of forest structure and composition to harvesting in different strata of mixed even-aged central Appalachian hardwoods. Annals of Forest Science 70: 151-159.

Zhou, W. Q., G. L. Huang, S.T.A. Pickett, and M.L. Cadenasso. 2011. Ninety years of forest cover change in an urbanizing watershed: Spatial and temporal dynamics. Landscape Ecology 26: 645-659.

CURRICULUM VITA (page 1 of 2)

DANIEL B. BREEN III

[redacted]

EDUCATION:

2011–2014	M.S., Biological Sciences, Towson University, Towson, MD
2002–2006	B.A., Biology, Colby College, Waterville, ME
2005	Semester abroad, School for Field Studies, Cairns, Australia

PROFESSIONAL EXPERIENCE:

2011–2014	Graduate Research Assistant, Department of Biological Sciences, Towson University, Towson, MD
2011–2014	Graduate Teaching Assistant, Department of Biological Sciences, Towson University, Towson, MD
2010–2012	Biological Science Technician, National Park Service, Berlin, MD
2010	Field Technician, University of Georgia, Darien, GA
2009	Biological Science Technician, U.S. Fish and Wildlife Service, Cambridge, MD
2008–2009	Waterbird Conservation/Water Quality Intern, Manomet Center for Conservation Sciences, Plymouth, MA
2008	Biological Science Technician, U.S. Fish and Wildlife Service, Newburyport, MA
2007–2008	Riparian Invasive Species Control and Restoration Assistant, Audubon California, Trabuco Canyon, CA
2005–2006	Undergraduate Teaching Assistant, Department of Biology, Colby College, Waterville, ME
2004–2005	Undergraduate Research Assistant, Department of Biology, Colby College, Waterville, ME

PROFESSIONAL PUBLICATIONS:

Breen, D.B., S.D. Bailey, and H.A. Violi. 2014. Managing remnant and reemerging common reed (*Phragmites australis*) infestations to improve treatment efficacy and mitigate damage to native plants. Invasive Plant Science and Management. In press.

PROFESSIONAL PRESENTATIONS:

2014	The influence of historical land use on the woody communities of an eastern deciduous forest. Mid-Atlantic Chapter of the Ecological Society of America's conference, College Park, MD (talk)
2013	Successional changes in the vegetation communities of an eastern deciduous forest and implications for restoration. Society for Ecological Restoration's world conference, Madison, WI (talk)

CURRICULUM VITA (page 2 of 2)

AWARDS:

2013–2014	Omicron Delta Kappa Membership, Towson University
2013	Graduate Student Association Travel Award, $500, Towson University
2012	Graduate Student Association Research Award, $480, Towson University
2012	Graduate Student Association Research Award, $300, Towson University
2011–2013	Teaching/Research Assistantship, $12,000/year, Towson University
2011	Special Thanks for Achieving Results (STAR) Award, $700, U.S. Department of the Interior

PROFESSIONAL MEMBERSHIPS:

Association of Southeastern Biologists
Ecological Society of America
International Association for Vegetation Science
Society for Conservation Biology
Society for Ecological Restoration