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Factors influencing the current and historical invasion trends in the Connecticut College Arboretum

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Factors influencing the current and historical invasion trends in the Connecticut

College Arboretum

A thesis submitted in partial fulfillment of the requirements for Honors Study in the Botany
major

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Abstract

Invasive species present a growing risk to native ecosystems. It would be impossible to eliminate them, but by learning where they are more likely to occur it may be possible to concentrate resources on removal and management in the most at risk areas. A number of site characteristics may influence invasive species presence and invasion trends. In order to determine what factors affect species presence and historical invasion trends, I utilized data from decennial surveys conducted in the Bolleswood Natural Area of the Connecticut College Arboretum in New London, Connecticut. In 1952, 4 transects were established across the area, composed of contiguous 3.05 by 3.05 meter plots. Every ten years, presence, height, DBH, and cover of all species in each plot were recorded. Other environmental variables in the plots were recorded as well. I used logistic regression models to determine the factors that explained the distribution of invasive species in 2012. I also determined if the factors that influenced invasion changed over time. Models were formulated to analyze how overall presence of invasives in 2012 and new occurrences in each sample year related to site history in regard to disturbance, soil characteristics, topography, light availability, dispersal, and species richness. For presence data in 2012, plots on historically agricultural land with moister and less well-drained soils and higher soil pH were more likely to host invasive species. For historical invasion trends, plots on historically agricultural land with greater total richness and proximately to the fence during initial invasion and later proximity to adult plants were the best indicators. However, age class appears to play a role beyond absolute forest age, as invasion was consistently found in the youngest, historically agricultural, plots even after 60 years of forest development. These conclusions suggest that there are factors that can be utilized to

predict invasion, and confirm the benefit of long term studies within a large area, such as the one at hand.

Introduction

Invasive plant species present an imminent threat to native plant communities and ecosystems. It is impossible to eliminate all known invasives given their pervasiveness. However, by identifying where they are more likely to occur it may be possible to concentrate resources on management of these areas and thus reduce the risk faced by native ecosystems. Many factors may influence invasion, but the ones that are easiest to target and identify are site characteristics that increase the susceptibility of native landscapes (Johnson et al., 2006). Though life history traits may affect invasion trends also (Martin et al, 2009), it is not possible to control these. Thus, by identifying site characteristics that affect invasion and hence identifying the areas at risk, it may be possible to limit future invasions by monitoring for and removing invasives. Site characteristics that affect invasion trends, particularly of woody species, can be placed in six categories: site disturbance history, soil characteristics, topography, light abundance, dispersal, and species richness.

Invasive species have been able to dominate landscapes partly due to their nature as early successional species, which allows them to thrive in disturbed sites (Rejmanek and Richardson, 1996). Their invasion is attributed to their long distance dispersal, high fecundity, small seed size, short generation time, and long fruiting periods (Martin et al., 2009), lending to broad dispersal and quick establishment. This raises concern particularly in landscapes subjected to historical and current disturbance regimes (Mosher et al., 2009). The nature of invasives as early successional species is further supported by their general

decline as the landscape ages (Mosher et al., 2009), though the documented role some play as forest invaders is somewhat contradictory to this trend and raises questions about invasion occurrences as a forest ages (Martin et al., 2009).

A number of examples of disturbance leading to invasion are prevalent throughout New England. The unique history of agricultural abandonment over the past 300 years along with current land use patterns that show ongoing disturbance has led to a patchwork of landscapes of different ages that have prompted study on how land use patterns affect invasion trends (Mosher et al., 2009). Increased invasion on historically agricultural land has been documented in a number of studies, even decades after disturbance (Johnson et al., 2006; Mosher et al., 2009; Von Holle and Motzkin, 2007).

Current land use trends, particularly those associated with development, often lead to disturbance in a modern context (Mosher et al., 2009). Invasive species have been found to occur more frequently along roads and developed areas than along trails or intact forest segments (Lundgren et al., 2004), and roads located near mature forest may allow invasive establishment that will eventually lead to forest infiltration (Flory and Clay, 2009). Fences can also be indicative of human disturbance, as they are often located in close proximity to roads and housing developments, which have been found in previous studies to be associated with abundance of invasive plants (Lundgren et al., 2004). Such sites represent edge habitat, which are often subjected to ongoing disturbance regimes (Mosher et al., 2009), and thus may be subject to increased invasion.

Soil characteristics, though not as widely studied as disturbance regimes, have also been found to affect where invasive species are present. Moisture and nutrients have particularly been studied. Invasives have been demonstrated to tolerate a larger range of

soil moisture than their native competitors, though they have been observed in generally moister soil in New England (Leicht-Young et al., 2007; McNab and Loftis, 2002; Silander and Klepeis, 1999). Invasives have also been found more commonly in finer textured soils with more clay, where water-holding capacity is higher, than in sandier, coarse soils (Johnson et al., 2006). Another factor related to soil moisture that may affect invasion is drainage capacity, a topographically determined variable (Lundgren et al., 2004).

In a number of invasive species, a positive association has been found between presence and pH (Gilbert and Lechowicz, 2005; Johnson et al., 2006) and a negative one between presence and organic matter (Compton and Boone, 2000). Nitrate and calcium are also significantly higher where invasive species thrive, and are good indicators for both abundance and relative cover (Dreiss and Volin, 2013). Phosphorous has also been shown to be higher where invasive species are present (Suding et al., 2004). These increased nutrient levels may be more common in historically agricultural areas, where the addition of fertilizers has a long-term impact on the soil (Compton and Boone, 2000). In addition, former agricultural sites often have high pH and low organic content because of over farming (Compton and Boone, 2000). Higher nutrient levels may also be prevalent along roads, which can serve as sources of runoff (Mosher et al., 2009).

Presence of invasive species has shown some association with topographic position, particularly in relation to elevation and slope. An association with elevation is well demonstrated in *Celastrus orbiculatus*, though only on a large scale (McNab and Loftis, 2002). Additionally, a study of patterns among invasive species overall has shown the significance of decreased slope (Van Holle and Motzkin, 2007), possibly implying moister

soils, as these tend to occur in flatter areas. However, there has been relatively little study on invasive presence based on elevation and slope, and particularly aspect.

Many invasive species thrive at intermediate and high light levels, but are able to persist at lower ones (Ellsworth et al., 2004; Silander and Klepeis, 1999, Martin et al., 2009). Invasive species presence has been shown to have a positive relationship to light level in a number of studies, particularly in *C. orbiculatus*, *Berberis thunbergii*, and *Rosa multiflora* (Leicht Young et al., 2007; Silander and Klepeis, 1999; Banadiak and Meiners, 2009). Increased light levels are most commonly indicated by lower canopy cover, but when this information is not available basal area may serve as a proxy by indicating open canopies (McNab and Loftis, 2002). The high light levels that allow invasives to thrive may be particularly prevalent in old fields and disturbed sites (Martin et al., 2009) as well as along roads (Mosher et al., 2009). However, many woody invaders in the Northeastern United States are also shade tolerant, and can persist and multiply at low light levels in intact forest, able to establish with only small increases in light level as occurs with canopy gap formation (Silander and Klepeis, 1999, Martin et al., 2009). Thus, forest invasion is possible and has been documented, but may only occur slowly as gaps form (Martin et al., 2009). In some cases, invasives may also start their growing season earlier than natives and can glean the extra light needed in an intact forest before the surrounding deciduous trees develop a full canopy, effectively cutting off the light source (Dreiss and Volin, 2013).

Dispersal of invasives is a major factor in determining their establishment. As with many plant species, the proximity of adult plants plays a large role as a seed source. Such a relationship has been documented in the case of *B. thunbergii*, where the majority of seedlings have been observed to occur within 1 meter of an adult *B. thunbergii* shrub

(Silander and Klepeis, 1999). However, roads and trails may also act as avenues of dispersal for seeds, which can be carried by vehicles in tires or transported by other anthropologic means (Parendes and Jones, 2000) and by animals and birds that utilize roads to travel (Flory and Clay, 2009). As many invasives are bird dispersed (Silander and Klepeis, 1999), fencing may also be indicative of dispersal range, as it provides perching area for birds (Lundgren et al., 2004).

Finally, diversity can impact patterns of species invasion. Though an increase in diversity has commonly been associated with a decrease in invasives (Van Roijven et al., 2003), the opposite has also been found. Though both theories are controversial, a number of recent studies have positively related invasive species presence to species richness, indicating potential similarities between invaders and resident species (Levine and D'Antonio, 1999). This has been demonstrated in particular with *R. multiflora* (Banasiak and Meiners, 2009).

In this study, I used data from six decades of surveys along with information on site characteristics to examine which factors help to explain the current distribution of several pervasive invasive plant species in the Bolleswood Natural Area of the Connecticut College Arboretum. In light of the trends found in past studies on invasive species, I proposed that invasive species in the Connecticut College Arboretum would be more prevalent in 2012 at disturbed sites with high moisture, pH, and other nutrients, as well as increased light levels. Additionally, I wanted to determine factors that influence invasion of an area over time, as this topic has not been extensively studied due to the lack of long-term studies concerning species growth and abundance. As has been documented, species composition in forests changes over time, especially with the introduction of invasives. Studies such as this one,

which have recorded species presence over decades, have the potential to reveal what factors influence that change.

Methods

Study Area

The Bolleswood Natural Area is composed of 65 hectares at the southwest corner of the Connecticut College Arboretum in New London, Connecticut. In 1952 the Board of Trustees designated it “for the express purpose of establishing long-term ecological studies” (Dreyer, 2013). Prior to this time, the western portion of the Bolleswood area was utilized for agricultural purposes. The rest of the area, though probably not cultivated, had been used for pasture, with the exception of some particularly rocky areas around the ravine. New London is located at the meeting place of the Thames River and Long Island Sound. Due to its coastal proximity, the climate is temperate, and the vegetation is primarily broad-leafed deciduous forests. Temperature averages -2.3°C in January and 21.8°C in July, the coldest and hottest months of the year, respectively. Additionally, the Arboretum is located on a hill, placing between 34 and 70 meters above sea level. The Bolleswood area is crosscut by a north-south ravine through which runs a stream. This allows for micro-climatic variation within the area due to differences in topography, temperature, and a number of other factors. The Bolleswood area is encircled by a chain link fence to reduce deer herbivory. The fence was constructed in sections, beginning in the mid-1960’s.

Field methods

Starting in 1952, a plant survey has been done every ten years in the Bolleswood area of the Connecticut College Arboretum. The most recent survey took place in the

summer of 2012. In 1952, four transects running east-west were laid out within the Bolleswood area (Fig. 1). Each transect was two plots wide, and was composed of contiguous plots from one end of the transect to the other. Each plot measured 3.05 meters by 3.05 meters, and every set of ten plots (5 X 2) was considered a section. The transects were of varying length, between 274.5 and 457.5 meters, featuring between 18 and 30 sections, and were located 122 meters apart. Three had offset portions at the end in order to stay in the middle of agricultural fields instead of at the edge. Using this system, a total of 890 plots were delineated and monitored. However, 20 plots in a lake and 4 plots located on a cliff were removed for the purposes of this study, leaving 866 plots.

Every 10 years, from 1952 to 2012, faculty and students monitored each plot for a number of different factors in the field. First and foremost, we recorded each plant species.

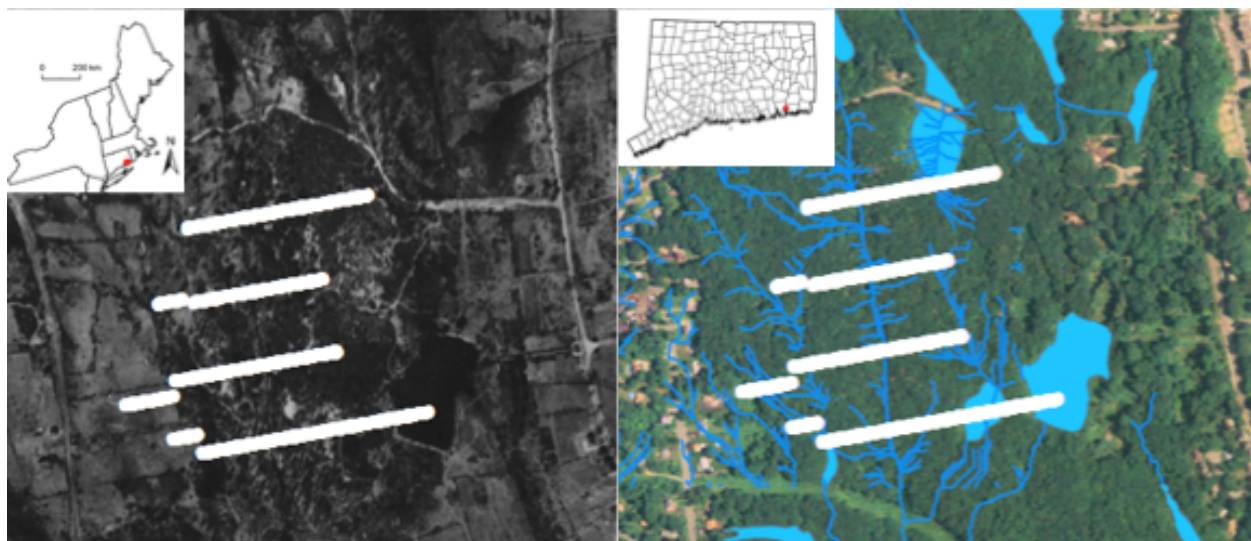


Figure 1. Image of the transects in the Bolleswood Natural Area. The image on the left is of a 1934 aerial photograph, showing land use, with an inset showing the location of the Connecticut College Arboretum within New England. The image on the right is from a 2006 aerial photograph, showing water features (streams, swamps and open water) in blue, indicating where along the transects there may be more moisture, with an inset showing where the Connecticut College Arboretum is within the state of Connecticut. In both insets, the Arboretum location is indicated by a red dot.

We identified all trees and shrubs of more than 5 centimeters diameter at breast height (DBH) separately, and tagged all such trees. We classified all trees and shrubs less than 5 centimeters DBH as being <2.5 cm or >2.5 cm at breast height. We then placed all plants less than 5 centimeters DBH in one of four height classes, less than 2 centimeters, at least 2 centimeters and under 60 centimeters, and at least 60 centimeters and less than 1.8 meters. For plants below breast height, we counted the number of stems in each height class. Then we estimated the overall cover of each species below breast height present within the plot. If individuals were less than 2 centimeters tall, we did not count their stems, but only recorded a cover estimate. We also estimated and recorded the percentage cover of rock, moss, lichen, and leaf litter in each plot.

Beginning in 1992, canopy cover for each plot was recorded. In 1992 and 2002, canopy cover was estimated visually. In 2012, however, we took a canopy photo with a hemispherical lens in the center of each plot approximately 1 meter above the ground. We then analyzed each canopy photo using the computer program Hemiview 2.1 (Delta-T Devices) to determine the percentage of open canopy in each plot.

In 2012, we collected soils samples from each plot. Soil samples were taken from three areas within the plot, to account for variation within the plot. Soil was taken from below a depth of approximately 10 centimeters after clearing large leaf litter deposits and any roots. In some plots that were particularly rocky, covered in roots, or swampy, fewer than three samples were taken for logistical reasons. In the lab, we dried samples and recorded percent moisture by mass. Each sample was then frozen to preserve its integrity for further analysis. We used a small portion of each sample to measure the organic matter using a loss on ignition test.

For nutrient analysis, soil samples for each plot were combined based on section, Combined samples were sent to the Cornell Nutrient Analysis Laboratory. The lab tested for pH, P, Ca, and NO₃ in milligrams per kilogram.

Target Species

Individual species were chosen for analysis based on a number of factors. Only species listed on the official list of invasive species for Connecticut (Connecticut Invasive Plants Council, 2011) were considered. From the list, I selected species that showed an increase in abundance in the Bolleswood Natural Area during the span of the study. We selected *Celastrus orbiculatus*, *Berberis thunbergii*, *Rosa multiflora*, and *Ligustrum spp.* for individual analysis, along with the presence of all invasives included on the official list of invasive plants of Connecticut. *Ligustrum spp.* includes several species of which *L. vulgare* is the most common, but not all specimens could be identified to the species level. All selected species except for *R. multiflora* were also noted forest invaders (Martin et al., 2009).

Variable selection

I analyzed data based on species presence in 2012 on both an individual plot and a section level to incorporate both site and soil characteristics. I also analyzed invasion based on historical data in each survey period of the study. Each test used the variable indicated in Table 1.

Age class was categorized as 1, 2, 3, or 4. Age class 1 was areas dominated by old fields in 1952, age class 2 was areas dominated by shrubs in 1952, age class 3 was areas dominated by young, transitional forest in 1952, and age class 4 was areas dominated by mature forest in 1952 (Goodwin and Niering, 1962). These age categories were assigned to

Table 1. Site variables included in the analyses of invasive species presence on the individual plot and section level in 2012, as well as historical analysis over the period of the study.

Presence in 2012	Section presence in 2012	Historical presence 1952-2002
Age class 1	Age class	Age class 1
Age class 2		Age class 2
Age class 3		Age class 4
Drainage class	Drainage class	Drainage class
Soil moisture	Soil moisture	
Organic content of soil	pH of soil	
	P in soil	
	Ca in soil	
	NO3 in soil	
Canopy cover	Canopy cover	Canopy cover
Aspect	Aspect	Aspect
Slope	Slope	Slope
Elevation	Elevation	Elevation
Distance from fences	Distance from fences	Distance from fences
Distance from trails	Distance from trails	Distance from nearest specimen in previous year
	Basal area	Basal area
		Total richness

each plot based on the map drawn by Goodwin and Niering (1962). Hence, the lower the age class, the more recently the plot was disturbed by human activity.

Drainage class ranged from 1 to 6, with 1 being the most saturated and 6 being excessively drained (Goslee et al. 2005). Drainage was based on topography, whereas moisture was based on direct measurement of moisture in soil obtained in the field.

Elevation was calculated based on the Connecticut DEM, and aspect and slope (in degrees) were calculated from the DEM using ArcMap 9.3 (ESRI Corp.) Cosine of the aspect (hereafter aspect) was categorized as ranging from -1 (north facing) to 1 (south facing).

We calculated the proximity of each plot to trails and fences using ArcMap 9.3 (ESRI Corp.)

Statistical analysis

I calculated the correlations between all of the dependent variables using SPSS Statistics 20 (IBM). Any variables with a correlation of more than 0.8 were eliminated.

For each species and each analysis type (plots and sections in 2012 and new invasions in each year), I created general linear models using the `glmulti` function in the program R version 2.15.2 (R Core Team). The `glmulti` functions tests all possible variable combinations for each model and selects the one with the lowest AIC. This allows for the removal of variables that do not strongly improve the model.

In the presence in 2012 and section presence in 2012 models, species presence or absence was the dependent variable. Species presence was indicated by 0 (absent) or 1 (present) at the individual plot level and as the proportion of plots the species were present in for the section level. In the historical presence model, the new appearance of an invasive species in a plot was the dependent variable. A new presence was indicated by a 1, while no presence was indicated by a 0. All plots that had been invaded in previous years, and hence were not newly invaded, were not included in the model.

One factor post hoc ANOVAs were also conducted in SPSS Statistics 20 (IBM) between age class and all variables utilized for the 2012 data set, and again between age class and total richness in each year of the study.

Results

Of the 866 plots included in analysis, 100 contained *R. multiflora*, 29 contained *B. thunbergii*, 67 contained *C. orbiculatus*, 42 contained *Ligustrum spp.*, and 106 contained at least one of the species on the official list of invasive plants in Connecticut in 2012, either of the four target species or another species on the list, hereafter referred to as “all invasives”.

I found a number of general patterns among species present in plots in 2012. All species were more likely to occur in moister soils as measured directly and all but *Ligustrum spp.* were more common in less well drained plots. There was a moderate correlation ($r=0.372$) between drainage class and soil moisture content, as would be expected. (Table 2). All studied species were more likely to occur in the youngest (age 1) plots than historically mature forest (age 4), and *R. multiflora*, *C. orbiculatus*, and all invasives were more likely to occur in historical shrubland (age 2) than historically mature forest. Organic matter was not significant for any species. Other variables, however, were inconsistent among species (Table 2). The only species affected by canopy cover was *C. orbiculatus*, which was more likely to occur where there was less sky visible and hence more canopy cover. *R. multiflora* and *B. thunbergii* were more likely to occur on north facing slopes. *R. multiflora* and all invasives were more common on steeper slopes.

Table 2. Significant variables in plots (3X3 m) where invasive species were present in 2012. All models had 865 total degrees of freedom. The numbers indicate the coefficients for the variables that were included in the multivariate logistic regressions models. Cells with a dash indicate no significance.

Variable	<i>R.</i>			<i>Ligustrum</i>	All invasives
	<i>multiflora</i>	<i>B. thunbergii</i>	<i>C. orbiculatus</i>	<i>spp.</i>	
Age 1	31.243	21.433	5.503	23.622	7.171
Age 2	28.809	-	3.731	-	4.938
Age 3	28.978	17.537	2.638	18.371	4.669
Moisture	2.787	3.283	2.597	3.490	3.156
Drainage	-0.634	-0.501	-0.502	-	-1.109
Organic matter	-	-	-	-	-
Open canopy	-	-	-2.752	-	-
Cosine aspect	-1.142	-0.905	-	-	-
Slope	0.095	-	-	-	0.082
Elevation	0.186	-	0.035	-	0.088
Distance from fence	-0.008	-	-	0.007	0.006
Distance from trails	0.024	-0.007	-	-	0.019
Residual degrees of freedom	855	859	856	861	856
Null Deviance	619.7	254	471.6	336.1	643.8
Residual Deviance	131.4	132.4	233	133.8	201.3
AIC	153.4	146.4	247	143.8	221.3

Although slope is a factor in determining drainage, there was only a moderate correlation ($r = 0.385$) between them. *R. multiflora*, *C. orbiculatus*, and all invasives were more likely to occur at higher elevations. *R. multiflora* was more likely to occur closer to the fence, whereas all invasives and *Ligustrum spp.* were more likely to occur farther from the fence. *R. multiflora* and all invasives were more likely to occur near trails, while *B. thunbergii* was more likely to occur away from trails. Thus, for all species, forest age and moisture played a significant role in determining the presence of invasives, and drainage was significant for most species, but all other variables differed in their significance.

By far, each species invaded more of the historically agricultural plots (age 1; Table 3). Historically shrubland plots (age 2) were only invaded by *R. multiflora*, *C. orbiculatus*, and all invasives, whereas historically young forest plots (age 3) were invaded by all species. Historically mature forest plots (age 4) have only been invaded by *C. orbiculatus*.

Patterns at the larger-scale (section data) for 2012, were similar to the plot-level patterns for age, soil moisture, drainage class, and aspect (Table 4). However, some patterns emerged that were not evident in the individual plot analysis. *C. orbiculatus*, *Ligustrum spp.*, and all invasives were more likely to occur closer to the trails. All other variables that were previously included in individual plot analysis, however, were

Table 3. Percentage of plots of each age class invaded by each species and number of plots found in each age class.

	Age 1	Age 2	Age 3	Age 4
Plots in class	86	30	185	565
<i>R. multiflora</i>	89.5%	20.0%	9.1%	0.0%
<i>B. thunbergii</i>	27.9%	0.0%	2.7%	0.0%
<i>C. orbiculatus</i>	58.1%	20.0%	4.8%	0.4%
<i>Ligustrum spp.</i>	45.3%	0.0%	1.6%	0.0%
All invasives	89.5%	20.0%	10.8%	0.5%

Table 4. Significant variables in sections (6X15m) where invasive species were present in 2012. All models had 86 total degrees of freedom. The numbers indicate the coefficients for the variables that were included in the multivariate logistic regressions models. Cells with a dash indicate no significance. Open canopy was not included for *Ligustrum spp.* because it destabilized the model.

Variable	<i>R. multiflora</i>	<i>B. thunbergii</i>	<i>C. orbiculatus</i>	<i>Ligustrum spp.</i>	All invasives
Age class	-2.150	-1.588	-1.598	-4.310	-4.875
Moisture	9.503	9.148	4.996	-	11.960
Drainage	-0.764	-0.944	-0.466	-	-
Open canopy	6.021	-	-	N/A	-26.950
Distance from fence	-	-	-	-	-0.047
Distance from trails	-	-	-0.005	-0.020	-0.060
Cosine Aspect	-2.235	-2.362	-	-	-4.254
Slope	-	-	-	0.205	-0.232
Elevation	-	-	-	-	-
pH	2.285	-	2.157	9.879	24.110
P	-	-	-0.053	-	0.183
Ca	-	-	-	-0.006	-
NO3	-	-	-	-	-
Basal	-	-	-	-	<0.001
Residual degrees of freedom	80	82	80	76	76
Null	501.3	163.7	307.8	251.9	513.8
Residual	55.7	41.1	51.2	1.75	11.3
AIC	97.8	72.4	105.8	45.0	58.6

inconsistent among species. Soil pH and nutrients, as well as basal area, were added to the section analysis, but none showed a consistent pattern except for pH. *R. multiflora*, *C. orbiculatus*, *Ligustrum spp.*, and all invasives were more likely to occur in areas with higher pH. *C. orbiculatus* appeared where there was less phosphorus, whereas all invasives appeared where there was more. *Ligustrum spp.* was more likely to be found where there were lower calcium levels.

Several site characteristics beyond forest age were different in age 1 plots than older plots.. Age 1 plots showed higher levels of moisture, organic matter, pH, Ca, and NO3 and lower levels of P (Table 5).

All invasive species, since their introduction, continually invaded new plots over time (Table 6). For historical analysis, years with less than 5 new appearances for a species

Table 5. The mean of all variables by age class for 2012 and significant values from a one-way ANOVA. In each row, any means sharing letters are not significantly different from each other, based on LSD *post-hoc* tests.

Variable	Age 1	Age 2	Age 3	Age 4	p	F
Drainage	4.000	4.000	4.281	4.327	0.115	1.984
Moisture	0.620 ^a	0.524 ^b	0.482 ^b	0.419 ^c	0.000	39.911
Organic matter	0.771 ^a	0.626 ^b	0.529 ^b	0.405 ^c	0.000	51.317
Open canopy	0.184 ^a	0.159 ^a	0.126 ^b	0.158 ^a	0.000	10.816
Slope	5.205 ^c	3.273 ^d	7.567 ^b	9.540 ^a	0.000	14.391
Elevation	174.343 ⁿ	181.955 ^a	169.483 ^c	169.888 ^c	0.000	6.600
Aspect	0.463 ^a	0.481 ^a	0.090 ^b	0.197 ^b	0.000	11.043
Distance from fence	221.425 ^c	379.897 ^b	407.328 ^b	497.447 ^a	0.000	101.438
Distance from trails	276.360 ^a	94.655 ^b	96.880 ^b	111.369 ^b	0.000	245.341
pH	3.941 ^a	3.530 ^b	3.54 ^b	3.462 ^b	0.000	9.673
P	15.036	16.820	22.139	22.308	0.732	0.430
Ca	432.482	103.791	240.866	279.307	0.325	1.172
NO3	1.963 ^a	0.000 ^b	0.348 ^b	0.385 ^b	0.000	14.023
Basal area	1837.508	1494.673	3181.084	2781.423	0.160	1.766

Table 6. Number of plots that were newly invaded by each species in each study year. Plots were newly invaded if the species had not occurred in that plot in any prior survey.

Year	<i>R. multiflora</i>	<i>B. thunbergii</i>	<i>C. orbiculatus</i>	<i>Ligustrum spp.</i>	All invasives
1952	18	14	0	1	36
1962	2	4	0	0	16
1972	7	6	0	0	31
1982	34	9	55	4	48
1992	36	24	20	18	19
2002	13	13	36	23	35
2012	24	7	14	11	17

were not included. Years with less than 10 new appearances were included, but the number of data points was included in parentheses next to the year (Tables 7 and 9). The actual number of new occurrences on the transects in every year is indicated in Table 6.

Canopy cover was included in analysis for all years for which it was recorded, but this information was only available in 1992, 2002, and 2012. For all other years, it was hoped that basal area could act as a proxy for canopy cover, but with only a weak correlation of 0.277 in 2012, it was not practical to presume such a substitution.

Although there were no variables that consistently indicate presence of *B. thunbergii*, there were several overall patterns. First, *B. thunbergii* appears more commonly

in plots of the youngest age class (age 1), as shown in the 1972, 1992, and 2002 analysis (Table 7). *B. thunbergii* also occurred in plots with higher total species richness in 1972, 1982, 1992, and 2002. Finally, it also invaded plots closer to the fence in 1952 and to plots where it was found in the previous study in 1982, 1992, and 2012.

The only consistent factors in invasion of plots by *C. orbiculatus* are the youngest age class (age 1) and total richness (Table 8). *C. orbiculatus* occurred more frequently in plots of the youngest age class (age 1) in 1982, 1992, and 2012, and more frequently in plots with greater total species richness in 1992, 2002, and 2012. *C. orbiculatus* also occurs closer to the fence in 1982 but closer to specimens found in the previous study year in 1992 and 2002.

Table 7. Significant variables in historical analysis of *B. thunbergii*. The numbers indicate the coefficients for the variables that were included in the multivariate logistic regressions models. Cells with a dash indicate no significance. There was not enough data to analyze patterns in 1962.

Variable	1952	1972 (6)	1982 (9)	1992	2002	2012 (7)
Drainage	-	-	-	-	-	-0.998
Age 1	-	21.708	-	1.807	3.981	-
Age 2	6.681	-	-	-	-	-
Age 3	-	-	-	-	-	-
Total Richness	-	0.214	0.402	0.527	0.185	-
Cosine Aspect	-	-	-	-	-	-1.661
Slope	-	-	-	-	-	-
Elevation	-0.059	-0.099	-	0.122	-	0.207
Distance from previous year	-	-	-0.006	-0.010	-	-0.051
Distance from fence	-0.013	-	-	-	-	-
Basal Area	-	-	-	-	<0.001	-
Canopy Cover	-	-	-	0.040	-	-
Degrees of Freedom	865 Total; 862 Residual	847 Total; 844 Residual	841 Total; 839 Residual	856 Total; 851 Residual	808 Total; 805 Residual	867 Total; 863 Residual
Null	143.300	71.370	99.600	218.900	141.300	81.43
Residual	70.920	36.680	60.690	69.920	77.770	47
AIC	78.920	44.680	66.690	81.920	85.770	57

Table 8. Significant variables in historical analysis of *C. orbiculatus*. *C. orbiculatus* did not appear in the transects until 1982. The numbers indicate the coefficients for the variables that were included in the multivariate logistic regressions models. Cells with a dash indicate no significance.

Variable	1982	1992	2002	2012
Drainage	-	-	-	-
Age 1	24.037	4.420	-	1.934
Age 2	24.022	-	-	-
Age 3	18.274	-	-	1.428
Total Richness	-	0.268	0.323	0.245
Cosine Aspect	-1.493	-	-	-
Slope	-	-	-	-
Elevation	0.167	-0.066	0.049	0.035
Distance from previous year	-	-0.009	-0.010	-
Distance from fence	-0.010	-	-	-
Basal Area	-0.001	-0.002	<0.001	-
Canopy Cover	-	-0.048	-	-
	889 Total; 882	810 Total; 804	790 Total; 786	812 Total; 808
Degrees of Freedom	Residual	Residual	Residual	Residual
Null	412.800	187.600	292.800	141.500
Residual	114.100	59.730	160.500	109.900
AIC	130.100	73.730	170.500	119.900

R. multiflora occurred more commonly in plots of the youngest age class (age 1) in 1952, 1972, 1982, 1992, and 2012, and in plots of historical shrubland in 1952, 1972, and 1982 (Table 9). It also was more likely to invade areas with higher species richness in 1952, 1972, 1982, 2002, and 2012. It occurred more commonly in plots closer to those where it was found during the previous study in 1992, 2002, and 2012, though in 1972 it was found farther from areas where it was found the previous year.

Ligustrum spp. was consistently more likely to be found in areas of higher species richness in all years where models were run, and farther from the fence in the 1992 and 2002 (Table 10).

Table 9. Significant variables in historical analysis of *R. multiflora*. There was not enough data to analyze patterns in 1962. The numbers indicate the coefficients for the variables that were included in the multivariate logistic regressions models. Cells with a dash indicate no significance.

Variable	1952	1972 (7)	1982	1992	2002	2012
Drainage	1.138	14.094	-	-1.081	-	-
Age 1	25.630	49.429	19.671	4.416	-	2.244
Age 2	26.930	-	-	-	-	9.821
Age 3	20.380	21.048	17.617	-	-	-
Total Richness	0.177	0.423	0.453	-	0.341	0.184
Cosine Aspect	-	-	-	-1.202	-	-
Slope	-	-	0.107	-	-	0.131
Elevation	-	-	-	0.068	-	0.230
Distance from previous year	-	0.011	-	-0.015	-0.143	-0.030
Distance from fence	0.012	-	-	-	-	-0.021
Basal Area	0.001	-	-	-	-0.001	-
Canopy Cover	-	-	-	-	-	-16.178
	865 Total; 858 Residual	845 Total; 840 Residual	838 Total; 834 Residual	805 Total; 800 Residual	765 Total; 762 Residual	789 Total; 781 Residual
Degrees of Freedom						
Null	175.100	81.070	284.600	294.200	131.800	215.000
Residual	70.890	35.000	127.200	102.300	47.470	84.790
AIC	86.890	47.000	137.200	114.300	55.470	102.800

Invasives overall consistently invaded in plots of the youngest age class (age 1) in 1952, 1972, 1982, 1992, and 2002, and in areas closer to where species were found in the previous study in 1962, 1972, 1982, 1992, and 2012 (Table 11). They were also found in areas closer to the fence in 1972, 1982, and 2012. Though the pattern based on species richness is not consistent across all years, invasives were more likely to occur in areas of higher total richness in 1962, 1972, 1982, 1992, and 2002, though the opposite was shown in 1952.

Species richness varied by age class in all years (Table 12). There was higher total richness per plot in all years except for 1952 in age 1 plots than in any other age plot. In 1952, there was higher species density in age 2 only.

Table 10. Significant variables in historical analysis of *Ligustrum spp.* There was not enough data to analyze patterns in 1952, 1962, 1972, or 1982. The numbers indicate the coefficients for the variables that were included in the multivariate logistic regressions models. Cells with a dash indicate no significance.

Variable	1992	2002	2012
Drainage	-	-4.245	-
Age 1	37.110	-39.165	2.053
Age 2	-	44.253	-
Age 3	-	-39.416	18.790
Total Richness	0.170	0.236	0.490
Cosine Aspect	-	-	-
Slope	-	-	0.132
Elevation	0.284	-0.436	-
Distance from previous year	-	-0.165	-
Distance from fence	0.034	0.021	-
Basal Area	-0.001	-	0.000
Canopy Cover	-	-	-
Degrees of Freedom	860 Total; 855 Residual	842 Total; 834 Residual	858 Total; 853 Residual
Null	174.900	211.000	117.700
Residual	65.400	68.800	56.390
AIC	77.400	86.800	68.390

Age 1 plots have a higher total richness in all years except for 1952 and these differences were significant in all plots (Table 12).

Discussion

The patterns found in present and historical analysis are similar to patterns found in some previous studies, but different from others. As expected, invasive presence in 2012 was most commonly found in the youngest landscape, areas that were fields in 1952, and thus showed more recent anthropogenic disturbance, though natural disturbance would have played a role in all plots over the study period (Johnson et al., 2006; Mosher et al., 2009; Von Holle and Motzkin, 2007). In this study, age class indicated the age of the

Table 11. Significant variables in historical analysis of invasives overall. The numbers indicate the coefficients for the variables that were included in the multivariate logistic regressions models. Cells with a dash indicate no significance.

Variable	1952	1962	1972	1982	1992	2002	2012
Drainage	0.522	-0.627	-	-	-	-	-
Age 1	4.716	-	18.641	2.339	4.622	2.249	3.987
Age 2	6.672	-	-	-	-	3.553	1.904
Age 3	2.371	-1.113	16.308	-	-	2.186	2.157
Total Richness	-1.303	0.218	0.362	0.384	0.586	0.209	0.390
Cosine Aspect	-1.303	-0.897	-	-	-	-0.583	-
Slope	-	-	-	-	-	-	0.0482
Elevation	-0.045	0.048	-	0.076	-	-	-
Distance from previous year	-	-0.006	-0.034	-0.008	-0.006	-	-
Distance from fence	-	-	-0.009	-0.007	-	-	-
Basal Area	-	-	-	-	-	0.000	<-0.001
Canopy Cover	-	-	-	-	-0.044	-	-
		845	842	816	772	764	799
Degrees of Freedom	865 Total; 858 Residual	Total; 839 Residual	Total; 837 Residual	Total; 811 Residual	Total; 768 Residual	Total; 758 Residual	Total; 793 Residual
Null	299.500	158.700	265.600	365.200	178.400	284.300	164.6
Residual	151.400	117.200	81.930	123.900	72.700	194.200	115.5
AIC	167.400	131.200	93.930	135.900	82.700	208.200	129.5

Table 12. The mean total richness in each age class for every year of the study and significant values from a one-way post hoc ANOVA. In each row, any means sharing letters are not significantly different from each other.

Year	Age 1	Age 2	Age 3	Age 4	p	F
1952	13.663 ^b	17.533 ^a	11.784 ^c	7.140 ^d	0.000	171.470
1962	11.395 ^a	8.533 ^b	10.076 ^{ab}	5.471 ^c	0.000	156.531
1972	8.581 ^a	7.467 ^a	7.405 ^a	3.650 ^b	0.000	167.482
1982	9.581 ^a	5.400 ^c	6.924 ^b	3.547 ^d	0.000	170.039
1992	12.849 ^a	9.800 ^b	9.605 ^b	5.297 ^c	0.000	204.340
2002	13.733 ^a	10.567 ^b	9.822 ^b	5.958 ^c	0.000	172.495
2012	10.767 ^a	9.000 ^b	7.551 ^c	5.227 ^d	0.000	119.676

landscape in 1952. Therefore, in years after 1952, age class is indicative of the forest age relative to 1952 and not the absolute age of the forest. Thus, age class may actually serve as an indicator of the significant impact of land use and not of forest age. As with the individual plot data from 2012, younger forests displayed a far greater likelihood of being

invaded from year to year, though the magnitude of the difference generally declined. This implies the importance of land use history in addition to age class, as even with more current invasion trends, species tend to come into areas that were more recently used agriculturally, even though those areas are over 50 years old in 2012. Distance from the fence, in regards to disturbance, did not appear to exert a significant impact on invasive presence, probably because the fence only ran along the edges of the natural area and only impacted a small area to either side of the fence. Similarly, trails would be indicative of disturbance in only a small area to either side, so would not have had a widespread impact on disturbance.

Soil characteristics had a strong influence on species invasion in both 2012 and historical analysis. All of the species analyzed in 2012 were more common in moister soil on the individual plot level, and all but *Ligustrum spp.* showed this pattern on the section level, and with a slightly weaker but still prevalent drainage correlation, the relation between these two variables is supported. Though drainage is based on topography, while soil moisture includes the effects of soil texture and organic matter, less well-drained soil is generally moister (Lundgren et al., 2004). However, both aspects of moisture appear to be important as they are both retained in the model. The only other soil characteristic that was consistent among the species was a higher level of pH. We can postulate that either the agricultural areas had higher pH levels from previous activity (Compton and Boone, 2000), or that invasive presence changed the pH of the soil in which is appeared. Though not specifically documented for pH, invasive species have been shown to change soil characteristics where they grow (Dassonville et al., 2008). However, the plots that were fields in 1952 show higher levels of pH, Ca, and NO₃, which may be remaining from their

recent past as agricultural fields as has been found elsewhere (Compton and Boone, 2012), implying that it was agriculture use and not invasive presence that changed the soil characteristics. These plots also show higher moisture levels, which though not associated with past agricultural use directly may indicate moisture as one of the reasons invasives preferentially invade historically agricultural plots. Unfortunately, the only soil characteristic available for historical analysis was drainage, which did not show any consistent trends among species.

With no variables pertaining to topography having a major effect on plots with species presence in 2012 or in historical analysis, it is impossible to either support or refute hypotheses in relation to site specifications; however, site specifications appear to be generally weak indicators in other studies as well. Due to the low range of elevation in the study area, the elevation variable may be more indicative of relative topographic differences than of absolute elevation change. Though aspect and slope are not consistently significant in any of the analyses, it is worth noting where the coefficients are significant, invasives always occur on higher, north facing slopes. With moisture and drainage as such significant factors, we might expect more consistent significance with slope, as this is one determinant of drainage, but nonetheless, drainage and slope only show a moderate correlation. Therefore, while direct measures of soil moisture are better indicators of invasive presence, the indirect measure of slope may be a proxy in cases where direct information is not available.

Though greater light availability has commonly been associated with invasive species presence, this study did not consistently find light availability to be a strong factor. This supports the potential of the studied species as forest invaders. Though our 2012

analysis did not show canopy gaps, it is possible that in previous years in which canopy cover was estimated visually, small canopy gaps were not consistently detected, or that canopy gaps opened up in the years between when the study was conducted and were not evident at the survey time. There is also a possibility that in a deciduous forest such as in the study area, invasive species took advantage of higher light levels before the canopy was fully developed during each growing season (Dreiss and Volin, 2013). As the survey was conducted in the summer when the canopy was full, it was not possible to examine such a relationship. There is also little evidence of light influence historically, as data on canopy cover is not available before 1992, thus limiting the ability to test for the significance of light. In the few places that canopy cover did appear as a significant factor, species were more likely to occur where there was less canopy cover, providing weak but positive evidence of the impact of light abundance on presence. *R. multiflora* is the only species found, on the section level, in areas of higher canopy cover, suggesting, contrary to prior study, that it is a forest invader (Martin et al., 2009). We had hoped that basal area could be used as a proxy for canopy cover, but based on the weak positive correlation between canopy cover and basal area in 2012, the relationship is not strong enough to utilize. In the few places where basal area is significant, its significance is inconsistent and is not consistently negative or positive. Thus, it is impossible to detect if increased light levels in earlier study years were instrumental in invasive species establishment, which given previous studies seems like a relevant factor (Mosher et al., 2009).

Our data suggests that dispersal from parent plants is stronger than that from either the fence or trails. The data from 2012, which only included analysis based on distance from trails and fences, show significance in some species. However, the patterns are

inconsistent, though there is some evidence that species occur closer to fences and trails. As the studied species are bird dispersed (Silander and Klepeis, 1999), it is somewhat surprising that there is not a more significant relationship based on distance from the fence. However, in examining the historical data, it becomes clear that distance from the fence is a more significant factor in early years, with distance from the nearest adult becoming significant later on. This suggests that distance from the fence, which indicates both the edge of the natural area and potential bird perching area, may have played a larger role in initial establishment of invasives. In the early years, there may have also been fewer perching spots for birds besides the fence, but as the forest matured they had other perching spots available. Then, when significant seed sources existed within the study area, parent plants took over as a dispersal source.

Historical analysis also included total richness from each year, which was not considered in the 2012 presence analysis. For every species in almost every year, invasives were more likely to occur in plots with a higher total richness. This supports the pattern found in other studies where invasives were more likely to occur in plots that already host greater native species richness, providing evidence for the similarities between native and invasive species (Levine and D'Antonio, 1999). In all years except for 1952, greater total species richness occurs in age 1 plots, and in each year a strong correlation between younger age class and species richness is found. As age class and richness are the two most significant variables in historical analysis, with the clear relationship that total richness shows in relation to age class, it is clear that age class may influence total richness and thus be indicative of it. However, it is not clear if invasion is driven by age class or total richness.

Both current species distribution and historical invasion trends show similar patterns among the analyzed species. In species presence in 2012, age class and soil characteristics emerge as the most important factors, and including historical analysis emphasizes the importance of dispersal factors and total richness, while reiterating the importance of age class. Essentially, the most predictive variables in presence analysis are the youngest forest age class and higher soil moisture, lower drainage class, and higher pH. Thus, my original hypothesis is supported except for the lack of significance of soil nutrients and light levels. In historical analysis, the importance of younger forest, dispersal characteristics with early emphasis on fencing location and later transition to the importance of adult plants as seed dispersers, and total richness emerge as trends. These factors, though not significant in all models, are generally predictive across species and time. However, a clear relationship becomes evident between the youngest age class and higher moisture, pH, and total richness. Thus, it appears that age class may be indicative of not only absolute forest age, but also an indirect indicator of these other factors as a result of its historical land use. By examining all of these factors, with particular regard to historically agricultural sites, it may become possible to relatively accurately predict areas prone to invasion and target areas where future invasion may occur for removal of potential invasives.

The study at hand shows the importance of long term studies across a large area in drawing conclusions pertaining to invasion trends. Long term studies such as this one show the importance of having historical data on invasion, particularly as different factors were important in historical analysis than in presence analysis. Additionally, large study areas allow for a large data set that becomes particularly relevant when invasion trends occur

slowly, with relatively few plots invaded in a given year. Without such studies, it would be impossible to see the emerging trend of the importance of age class as an indirect indicator of other variables relevant to invasion. In order to continue monitoring invasion trends, particularly as they may change in the future, it is thus necessary to continue large scale, long term studies and to begin new ones in order to understand the factors that affect invasion in different areas and throughout time.

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