Southern Appalachian Forest Community Response to Three Methods of Exotic Invasive Removal

Sarah Farmer
Biology Department
The University of North Carolina at Asheville
One University Heights
Asheville, North Carolina 28804 USA

Faculty Advisors: Dr. Jennifer Rhode Ward, Dr. Jonathan Horton, and Dr. H. David Clarke

Abstract

Exotic plants often dominate areas to which they are introduced, and might ultimately alter community composition, ecosystem structure and function. This study evaluated the native plant community response to three different methods of exotic invasive removal – chemical, mechanical, and a combination of the two. The study was conducted on the campus of the University of North Carolina at Asheville over four consecutive summers (2008-2011). This study aimed to determine which treatment was most effective in reducing exotic presence and increasing native species abundance and richness, while also identifying species that were especially important in shaping the overall community composition. The cover and richness of native plants in the herbaceous community (all non-woody plants) and the tree seedling community (all tree species less than 0.2 m tall) increased significantly over all treatments during the study, while the exotic cover declined significantly. Differences among treatment methods were not significant. Important exotic drivers of community composition in the tree seedling, herbaceous, and shrub communities, included the exotic tree/shrub Ligustrum sinense (Chinese privet) and others. Future research should evaluate native community responses to removal of important exotic species identified in this study.

1. Introduction

Exotic plant introductions are, and historically have been, closely linked to human mobility, migration, and international trade. Since the 1800s, thousands of exotic plants have been introduced to the United States. While some exotic plant introductions were accidental, most were intentional, as exotic plants have been extensively used in agriculture, horticulture, and even restoration. Of all introduced plant species in the U.S., an estimated 5,000 species have escaped cultivation and become established in natural areas. Exotic plants that survive and reproduce with no human involvement for at least a decade are considered naturalized, and of these naturalized plants, a subset has become invasive, producing many offspring with the potential to spread over large areas. Exotic invasive plants can alter successional trajectories, displace native species, and change forest structure, although precise mechanisms by which they cause these responses are unclear.

Researchers have suggested that approximately 10% of alien plants can be deemed transformers or ecosystem engineers, capable of actively suppressing native plants and initiating change in community composition or ecosystem function. MacDougall and Turkington designate these exotic plants as drivers of ecological change, but also posit that exotic plants could perhaps more accurately be considered passengers of human mediated environmental degradation, including climate change, altered disturbance regimes, and fragmentation. Whether exotic invasive plants are drivers or passengers, their removal has become a common restoration goal.

The removal of exotic invasive plants does not necessarily lead to increased richness or abundance in the native plant understory. However, several studies have documented increases in native diversity and biomass after treatments which removed exotic invasives but did not replant native species. In some cases, however, native plant
responses have been more nuanced. For example, Heleno et al.\textsuperscript{8} found that native plant richness and seed production increased after exotic invasive plant removal, but invasive species had higher survival rates and faster growth than native plants. They interpreted this result as evidence that exotic invasive plants’ life history characteristics position them to be superior competitors for resources, and other researchers have reached similar conclusions\textsuperscript{1,15}.

Most exotic plant removal projects target only one or a few species for removal\textsuperscript{6,12,13,14}. While this approach streamlines the removal process, it can also facilitate invasion by new species. For example, Hanula et al.\textsuperscript{14} found that the exotic invasive grass \textit{Microstegium vimineum} (Japanese stilt grass) became more abundant after removal of \textit{Ligustrum sinense} (Chinese privet), and they suggested that the mechanical disruption of the litter layer facilitated the grass’s spread. Similarly, Vidra et al.\textsuperscript{6} found that, after initial removal of exotic invasive plants from study sites, native species richness did not increase, and exotic invasive plants like \textit{Elaeagnus umbellata} (autumn olive) and \textit{L. sinense} continued to dominate the seedling community.

In this study, we use three different treatment methods designed to remove exotic invasive plants from the herbaceous, mid-story and canopy layers of two heavily invaded urban forests. Our objectives were to determine which removal method was most effective in reducing the abundance and richness of exotic invasive plants, and to determine whether the native plant community increased in richness or abundance after treatment. Additionally, we identified both exotic and native species that drove community composition, as these data could inform future restoration efforts.

2. Methods

2.1 Site History

The study was conducted on the campus of the University of North Carolina Asheville, which is situated in Buncombe County in the Blue Ridge Mountains. The approximate elevation is 650 m\textsuperscript{16}, and precipitation is evenly distributed throughout the year\textsuperscript{17}. The main soil types in the study area are Biltmore loam, Tate loam, Micaville-Brownwood complexes, and Fannin Lauada-Urban land complexes\textsuperscript{16}. All of these soils are deep or moderately deep and well drained\textsuperscript{19}, making them suitable for supporting a broad range of plant life.

We chose to work in an urban forest because these areas tend to be more susceptible to exotic plant invasions\textsuperscript{6,18}. In the southeastern United States, urbanization\textsuperscript{6} and fragmentation\textsuperscript{12} facilitate plant invasions, and urban forests are also bisected by roads and developed areas, making them closer to sources of exotic propagules\textsuperscript{4,7,18}. Both of our study sites, Chestnut Ridge (CR) and Pisgah Forest (PF), are reforested areas whose understories were heavily dominated by exotic invasive plants, as is typical of many urban forests\textsuperscript{6}. Chestnut Ridge is a 24 hectare (ha) \textit{Quercus-Carya} (oak-hickory) forest (Table 1) that was used as pastureland (Melissa Acker, UNC Asheville landscape architect, personal communication). Anthropogenic disturbance on CR was less intense than on PF. Much of the area around CR has been converted from forested land to residential and industrial areas since 1976 (Figure 1), and some experts expect these pressures to intensify over the coming decades\textsuperscript{19}.

![Image of land use changes from 1976 to 2010](image)

Figure 1. Changes in historical and recent land use in the Chestnut Ridge (CR) area. Dark brown areas represent forested land; light areas represent developed land\textsuperscript{19}. Approximate locations of study plots are outlined in black.
Pisgah Forest is a 20 ha re-forested area dominated by *Pinus strobus* (Eastern white pine) (Table 1). The site was once a dairy farm (Acker, personal communication), and is more closely associated with transportation corridors than CR (Figure 2). Historically and presently, development pressures have been more intense in this area than on CR.

Table 1. Importance values for dominant trees on each study site. Importance values rank species’ contributions to overall composition

<table>
<thead>
<tr>
<th>Species</th>
<th>Importance Value</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Quercus alba</em></td>
<td>0.404</td>
</tr>
<tr>
<td><em>Carya glabra</em></td>
<td>0.338</td>
</tr>
<tr>
<td><em>Liriodendron tulipifera</em></td>
<td>0.291</td>
</tr>
<tr>
<td><strong>Pinus strobus</strong></td>
<td>1.128</td>
</tr>
<tr>
<td><strong>Prunus serotina</strong></td>
<td>0.382</td>
</tr>
<tr>
<td><strong>Quercus velutina</strong></td>
<td>0.154</td>
</tr>
</tbody>
</table>

Figure 2: Changes in historical and recent land use in the Pisgah Forest (PF) area of the UNC Asheville campus. Dark brown areas represent forested land; light areas represent developed land. Approximate locations of study sites are outlined in black.

### 2.2 Design and Treatment

In 2008, three 25 x 50 m blocks were established at each site. Plot sizes are standard for terrestrial plant studies; the three initial blocks covered 2.4% of the total forested area on CR and 4.0% of the total area on PF. Each block was divided into 3 equal subplots of 25 x 16.7 m. Pre-treatment vegetation surveys were conducted in early summer of 2008, and treatments were implemented later that season. In 2009, three 25 x 16.7 m control plots (untreated) were installed at each site. All plots were surveyed in the fall of 2008 and every subsequent summer and fall. Fall data were deemed less reliable than summer data because in some years, sampling occurred after many herbaceous species had senesced. Thus, fall data were not analyzed in this study.

Plots were randomly assigned to treatment condition: mechanical removal of invasives, chemical removal of invasives, and a combination of the two. Mechanical treatment was conducted in May - July of each year and involved uprooting exotic plants by hand and with shovels, mattocks, and Weed Wrenches. Exotic shrubs and trees were uprooted when possible or otherwise girdled. Exotic plants in the chemical treatment plots were tagged, and 5% glyphosate (herbicide) with a non-ionic surfactant was applied via foliar spot spraying in late summer. Due to budget restrictions, the last year of chemical treatment was 2010.
2.3 Sampling Procedures

The herbaceous layer was defined as any woody plant less than 0.2 m tall and all non-woody plants, regardless of height. To sample the herbaceous layer, sixteen 0.5 m² quadrats were randomly sampled in each subplot. A 3 m buffer was left unsampled around each plot to account for edge effects. Quadrats were divided into 50 squares to allow percent cover counts. All herbaceous plants with any aboveground biomass in, over, or under the quadrat were included in the quadrat. Most plants were identified to species level, but species-level identification was not possible in some cases [ex: *Quercus* (oaks) seedlings, *Carex* (sedges), and *Poa* (grasses)]. Nomenclature was according to Wofford24. Mean species cover, and richness of exotic and native species, were calculated for each subplot.

Tree seedling abundance and richness data were analyzed as part of the herbaceous layer, then sorted into a new category and analyzed separately. This category included all trees, along with woody plants such as the native understory species *Cornus florida* (Eastern flowering dogwood), *Amelanchier arborea* (common serviceberry), and *Viburnum prunifolium* (blackhaw), and the exotic tree/shrub *Ligustrum sinense* (Chinese privet). Plants classified by USDA PLANTS25 as shrubs were excluded.

We defined the shrub layer as woody plants taller than 0.2 m and with a diameter at breast height (dbh) less than 2.5 cm. Shrub stem density was sampled with five 3 m² circular sample zones, which were randomly located within subplots, excluding a 3 m buffer around each plot. Woody plants with a dbh more than 2.5 cm were counted as trees and identified to species, and their dbhs were recorded.

In 2013, a canopy analyzer (LAI-2200, LiCor Biosciences, Lincoln, NE) was used to measure leaf area index (LAI), a proxy for light levels. LAI was measured at two heights to approximate the height of the herbaceous layer (0.2 m above ground level) and the shrub layer (1 m above ground level). Five randomly selected points per plot were sampled in each layer. Data were obtained during the month of July, when leaves were fully expanded, and in mornings, evenings, or under uniformly cloudy skies. In each site the sensor was directed to the southwest before logging a data point.

2.4 Statistical Analyses

Mean percent cover data from the herbaceous and tree seedling community, and mean stem density from the shrub community, were analyzed using non-metric multidimensional scaling (NMS) in PC-ORD version 6.0826 following procedures outlined by Peck27. In each layer, the number of axes was determined with a stress test, conducted by running the ordination on autopilot 3 times and comparing the recommended number of axes with scree plots. Stress is a measurement of how much adjustment ordination scores require in order to achieve monotonicity, and ordinations with final stress values greater than ~ 15 are only useful in deducing general trends27. Vector overlays, describing species’ influence over community composition, were included for ordinations with low stress values.

Because control plots were not established until 2009, statistical analyses across all years and treatment groups were not possible. To determine whether community composition on 2008 pre-treatment plots was equivalent to composition on 2009 control plots, NMS was used. Establishing that the plant communities in these two conditions and years were similar allowed the 2008 pre-treatment data to function as a proxy for control data. These ordinations were conducted for the tree seedling, herbaceous and shrub layers.

Once initial ordinations confirmed that the 2008 pre-treatment plots had similar community composition as the 2009 control plots, the community composition on the two sites through the years 2008 – 2011 was compared. This was done to identify pre-treatment compositional differences between CR and PF. Ordinations were successful for the tree seedling and herbaceous communities, but those comparing shrub communities generated one-dimensional solutions, which often indicate the presence of outliers29. Outlier analysis confirmed that numerous outliers were present in the full shrub dataset, causing it to be weakly structured29. Other ordination problems can be due to variables of drastically unequal weight30. Sparse datasets can also cause problems with NMS, but even after adjusting for sparsity, successful ordinations for the comparison of shrub communities of the two sites, as well as ordinations comparing tree seedling and shrub treatment groups, were not successful. However, ordinations for herbaceous treatment groups on both sites for the years 2008 – 2011 were created.

Repeated measures ANOVA was conducted in SAS 9.228 to evaluate treatment effects on cover of the exotic and native communities in the herbaceous layer and tree seedling community. Because there were no control data in 2008, separate analyses were conducted for controls plus treatment over the years 2009 – 2011, and for treatments only over the years 2008 – 2011. LAI data were analyzed with an ANOVA in SAS 9.228 to determine whether light levels varied across plots.
Mean shrub stem densities were non-normal, even after transformations, so treated plots were pooled over the years 2009 – 2011 and compared to shrub density in control plots with the non-parametric Kruskal-Wallis test in SAS 9.228. Time was not a factor in this test. Average scores were used for ties. Because richness data were discrete, non-continuous integers, they were analyzed in the same way.

3. Results

3.1 Similarities and Differences in Community Composition

Non-metric multidimensional scaling (NMS) showed that the tree seedling community varied greatly between the sites (Figure 3). Because these ordinations compared pre-treatment conditions on study plots in 2008 with untreated control plots in 2009, they showed that prior to treatment, CR and PF were distinct, and also indicated that the community composition in control and treatment plots of each site were comparable. The final stress for this ordination was 11.05, so species-level observations are appropriate to make from this ordination. Prior to treatment, native species were important drivers of community composition in the tree seedling layer. The only exotic invasive driver of community composition in this layer is *L. sinense*, and the directionality of the species vector shows that it is especially influential in the PF area. A three-dimensional solution was recommended for the tree seedling ordination, but because graphs were qualitatively similar, only two axes are shown.

Ordinations comparing the herbaceous layer composition in 2008 pre-treatment plots and 2009 control plots showed a similar difference in composition among sites (Figure 4). A two-dimensional solution was recommended for this ordination, and the final stress value was 13.18. In addition to showing site differences, this ordination confirmed that the treatment and control plots are fairly similar and can thus be treated as equivalent. The ordination also shows that prior to treatment, the most important community drivers were all exotic invasive species. *Ligustrum sinense, Lonicera japonica* (Japan honeysuckle), and *Hedera helix* (English ivy) are important on both sites.

Trends in the shrub layer were similar to those observed in the herbaceous and seedling communities, as the sites are fairly distinct and pre-treatment plots are similar in composition (Figure 5). However, native and exotic species both influenced pre-treatment community composition in this layer, and their influence is fairly equal, as evidenced by the symmetry of the species vector and the comparable lengths of each vector. A two-dimensional solution was recommended, and the final stress was 13.67.

![Figure 3. NMS results for the tree seedling communities of Chestnut Ridge (CR) and Pisgah Forest (PF) for the treatment groups in 2008 and control group in 2009. The vector overlay shows important species. Vectors for invasive species are solid, and native species’ vectors are dashed.](image-url)
Figure 4. NMS results for the herbaceous communities of Chestnut Ridge (CR) and Pisgah Forest (PF) for the treatment groups in 2008 and control group in 2009. The herbaceous layer includes all woody plants and shrubs less than 0.2 m tall, so some tree seedling data is included in this ordination. The vector overlay shows important species. Vectors for invasive species are solid, and native species’ vectors are dashed.

Figure 5. NMS results for the shrub communities of Chestnut Ridge (CR) and Pisgah Forest (PF) for the treatment groups in 2008 and control group in 2009. The vector overlay shows important species. Vectors for invasive species are solid, and native species’ vectors are dashed.

Further ordinations used NMS to compare community composition between the two sites over the course of the experiment. These ordinations used data from 2008 – 2011 and confirmed that the plant communities on the two studies sites were compositionally distinct throughout the course of the experiment. A three-dimensional solution was recommended for the tree seedling ordination, but graphs were qualitatively similar, so only two axes are shown (Figure 6). The final stress for the ordination was 15.63, which makes species-level interpretation less reliable. Nevertheless, the ordination suggests that L. sinense and C. glabra are important potential drivers of community composition in the tree seedling layer both before (Figure 3) and after treatment (Figure 6). The ordination also shows that the composition of
tree seedling communities on CR is more variable, as symbols for CR are dispersed over a wider area than the symbols for PF.

Ordination results for the herbaceous layer confirm that the community composition differs between the two sites over the duration of the experiment (Figure 7). A two-dimensional solution was recommended, and the final stress was 22.35. Because of the high stress, no species vectors are shown. A successful ordination comparing the shrub communities of both sites across these years was not attainable.

![Figure 6](image6.png)

**Figure 6.** NMS results for the tree seedling communities of Chestnut Ridge (CR) and Pisgah Forest (PF) over the years 2008 – 2011. The vector overlay shows important species. Vectors for invasive species are solid, and native species’ vectors are dashed.

![Figure 7](image7.png)

**Figure 7.** NMS results for the herbaceous communities of Chestnut Ridge (CR) and Pisgah Forest (PF) over the years 2008 – 2011. Because of the high final stress value, species level interpretations are not appropriate, so vector overlays are not included.

Ordinations comparing the effect of individual treatments and controls on community composition were only possible for the herbaceous community. This ordination shows that community composition on control plots remained very similar, while treatment plots have become more distinct, and more unlike the control plots (Figure 8), suggesting that community composition has changed in the treatment plots over time. A two-dimensional solution was recommended, and the final stress value was 19.92, so no species vector overlays are shown.
3.2 Changes in abundance and richness over time

Over the course of treatment, exotic cover decreased while native cover increased. These trends were seen whether control data were included or not. Analyses were conducted for controls plus treatment over the years 2009–2011, and for treatment only (no controls) over the years 2008–2011. Because NMS results indicate that 2008 pre-treatment condition can be treated as equivalent to 2009 control plots (Figures 3-5), and because control plots in the herbaceous community have changed very little over time (Figure 8), only results from analysis of 2008–2011 are included in this study.

In both sites, the native seedling cover increased significantly ($P < 0.0001$, $F = 11.12$, $df = 4/48$), while the cover of exotic seedlings decreased significantly ($P < 0.0001$, $F = 7.68$, $df = 4/48$; Figure 9). However, there were no significant differences in these responses among treatments. The percent cover of exotic seedlings on PF before treatment (2008) was much higher than the percent cover of native seedlings at that site, and much higher than the cover of exotic seedlings on CR (Figure 9). In both sites, a decrease in native cover was observed the year after treatment (2009), but in subsequent years the native seedling cover increased.

Similar trends were observed in the herbaceous community (Figure 10). The native herbaceous cover increased significantly over time at both sites ($P = <0.0001$, $F = 23.29$, $df = 1/12$), and exotic herb cover decreased significantly ($P = 0.0002$, $F = 11.04$, $df = 3/36$). However, the herbaceous community was heavily invaded prior treatment, and in 2008 the percent cover of exotic invasive herbs was greater than the cover of native herbs. Since 2009, native cover has increased across all treatments, and there were no significant differences among treatments. There were no significant differences in LAI at the height of the herb layer between treatment plots and controls, and no differences between sites.

Shrub density distribution between treatment groups and controls differed significantly (Table 2), indicating that the increase in native shrub density on treatment plots of both sites was significant. Prior to treatment, native shrub density was much lower than exotic density, but by 2011, native density increased significantly (Figure 11). Exotic shrub density was not affected by treatment (Table 2). There were no significant differences in LAI at the shrub layer’s height between treatment plots and controls, and no differences between sites.

In both the tree seedling and shrub communities, native richness increased significantly over the years 2009–2011 with treatment when compared to the controls (Table 3). The native herb community on CR also exhibited significant increased richness. Species richness among the exotic community was not significantly affected by treatments.
Figure 9. Mean percent cover (± 1 S.E) of native and exotic seedlings on Chestnut Ridge (left) and Pisgah Forest right. The seedling community included all woody plants (except shrub species) that were less than 0.2 m tall.
Figure 10. Mean percent cover (± 1 S.E.) of native and exotic herbs on Chestnut Ridge (left) and Pisgah Forest (right). The herbaceous community included all woody plants less than 0.2m and all non-woody plants, regardless of height.
Figure 11. Mean shrub stem density (± 1 S.E.) of native and exotic shrubs on Chestnut Ridge (left) and Pisgah Forest (right). The overall increase in native shrub stem density was significant.

Table 2. Kruskal-Wallis test statistic (DF = 3) for differences in mean shrub stem density between treated plots and control plots over the years 2009 - 2011. Data were pooled across these years and time was not a factor. **Bold** indicates significant values.

<table>
<thead>
<tr>
<th></th>
<th>Chestnut Ridge</th>
<th>Pisgah Forest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native stem density</td>
<td><strong>H = 12.5703</strong></td>
<td><strong>H=34.1856</strong></td>
</tr>
<tr>
<td></td>
<td><em>P</em> = 0.0057</td>
<td><em>P</em> = 0.0001</td>
</tr>
<tr>
<td>Exotic stem density</td>
<td><strong>H= 5.9020</strong></td>
<td><strong>H=2.4412</strong></td>
</tr>
<tr>
<td></td>
<td><em>P</em> = 0.1165</td>
<td><em>P</em> = 0.4860</td>
</tr>
</tbody>
</table>
Table 3. Kruskal-Wallis test statistic (DF = 3) for differences in richness between treated plots and control plots over the years 2009 - 2011. Data were pooled across these years and time was not a factor. **Bold** indicates significant values.

<table>
<thead>
<tr>
<th>Category</th>
<th>Layer</th>
<th>Chestnut Ridge</th>
<th>Pisgah Forest</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Herbs</strong></td>
<td>Native</td>
<td>H = 24.5842</td>
<td>H = 5.3488</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P = 0.0001</td>
<td>P = 0.1480</td>
</tr>
<tr>
<td></td>
<td>Exotic</td>
<td>H = 3.5517</td>
<td>H = 4.0961</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P = 0.3141</td>
<td>P = 0.2513</td>
</tr>
<tr>
<td><strong>Tree Seedlings</strong></td>
<td>Native</td>
<td>H = 20.0953</td>
<td>H = 14.6462</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P = 0.0002</td>
<td>P = 0.0021</td>
</tr>
<tr>
<td></td>
<td>Exotic</td>
<td>H = 4.4026</td>
<td>H = 0.8223</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P = 0.2211</td>
<td>P = 0.8441</td>
</tr>
<tr>
<td><strong>Shrubs</strong></td>
<td>Native</td>
<td>H = 13.0815</td>
<td>H = 34.7882</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P = 0.0045</td>
<td>P = 0.0001</td>
</tr>
<tr>
<td></td>
<td>Exotic</td>
<td>H = 10.2930</td>
<td>H = 2.1769</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P = 0.0162</td>
<td>P = 0.5365</td>
</tr>
</tbody>
</table>

4. Discussion

In 2008, plant communities in the CR and PF study plots were dominated by exotic invasive species. Over the four years of treatments, native abundance and richness increased significantly in all layers. Not all exotic invasive removal studies have found such dramatic and consistent increases\(^\text{29}\). For example, Vidra et al.\(^\text{6}\) observed few post-treatment increases in native richness and cover, and attributed changes in post-treatment community composition to absence of the exotic invasives. However, the treatment groups where Vidra et al.\(^\text{6}\) did observe increases in native richness were plots in which exotic invasive shrubs had been repeatedly removed (by clipping off aboveground portions) every two weeks throughout two complete growing seasons. While other researchers have found that two years is a minimal but sufficient amount of time for evaluation of restoration projects\(^\text{8}\), had our study concluded after two growing seasons, the overall native increases in the herbaceous community would not have been observed, as overall native cover declined after initial treatment. Our study spanned four complete growing seasons, so its longer duration, and repeated treatments, could explain why our findings differed so dramatically from Vidra et al.\(^\text{6}\) despite similar site conditions.

Overall, the exotic cover declined significantly with repeated treatment. Treatments did not reduce exotic richness, but native richness did increase over the course of treatment. While native richness does not preclude invasion by exotic species\(^\text{30}\), it could indicate heterogeneity of habitats, and could provide higher-quality forage and cover for wildlife. Native richness on PF was lower, and this may be due to its land use history as a dairy farm. Pisgah Forest was also replanted with *Pinus strobus* (white pine), and although LAI did not differ between sites over the summer, PF’s greater canopy cover could affect spring ephemerals and other members of the herbaceous plant community. Furthermore, PF’s history as an abandoned agricultural site could make it more susceptible to exotic plant invasion, as some researchers have found that soil history is a more powerful explanatory factor for plant community assemblage than restoration or exotic plant invasion treatments\(^\text{31}\).

Richness data from the exotic and native communities suggests that propagule pressure from outside the study sites is an important influence on community composition. Although exotic cover declined, exotic richness did not decrease significantly in any layer, implying that propagules from outside the study plots are continually introduced into the treated sites. The increase in native richness could be attributed to germination from the seedbank, although seedbanks for the CR and PF types of forests are not especially long-lived\(^\text{6}\), or it could reflect propagule pressure from outside the study plots.

All removal methods were effective in reducing exotic abundance, but there were no significant differences among treatments. This lack of difference could reflect overall richness in the exotic community, as there were 49 different exotic species across the two study sites, and each exotic invasive species would likely have unique phenology and responses to treatment. Land managers already exploit phenological differences by removing the exotic shrub *Lonicera maackii* (Amur honeysuckle) later in the growing season, as native plants senesce earlier than *L. maackii*\(^\text{32}\). As other researchers have pointed out, identifying phenological trends in exotic invasive plants may be a promising way to identify optimal treatment times\(^\text{33}\).
In contrast to Flory and Clay’s findings, different removal methods did not appear to influence native composition in the herbaceous layer of CR or PF. However, Flory and Clay’s study only removed Microstegium vimineum (Japanese stiltgrass), and as this particular species was never a significant component of the herbaceous community on our study sites, findings may not be directly relatable. Perhaps more meaningfully, Flory and Clay evaluated treatment effectiveness and costs, and concluded that grass-specific herbicide application was superior to non-specific herbicide or handweeding because of the combined efficacy and affordability. Many researchers have noticed that mechanical removal of exotic invasives is quite expensive and labor-intensive, and in our study, mechanical removal across the twelve plots (mechanical and combination of mechanical and chemical) required almost 400 hours of labor in the first year of treatment. Although the time investment required to mechanically remove exotic invasives became lower with each subsequent year of treatment, it was consistently at least ten times higher than the amount of time required for herbicide application. Herbicide application in the first year of treatment only required 22 hours to treat the six subplots that were treated solely with chemicals. Herbicides can harm non-target species, and environmental concerns over its widespread and/or long-term use have been raised. However, controlling invasive plants can require long-term commitment and continual monitoring, and chemical treatments could be used to reduce exotic cover to a level that would be sustainable for longer term manual maintenance.

Although most removal efforts target only a few invasive species for removal, recent studies have pointed out that when species are singled out from their communities and studied in isolation, findings become less relevant to conservation efforts. This study was not designed to examine interactions between species, but NMS results do show how individual species influence overall community composition. The species most frequently identified as a driver of community composition is the exotic tree/shrub L. sinense. Other important exotic drivers of composition include A. altissima, L. japonica, and H. helix.

Ligustrum sinense has been shown to negatively impact forest regeneration and cause decreased plant species richness and abundance and is also readily dispersed by birds and other vertebrates, especially in winter when other food sources for birds are rare. Seed dispersal is one of the basic foundational steps of the invasion process, and both L. sinense and H. helix appear to take advantage of seasonal fluctuations in available wildlife forage. Additionally many exotic invasive plants in urban forests are introduced through horticultural activities, and L. sinense and H. helix have both been used for landscaping purposes.

Ailanthus altissima is also an important driver of community composition in the seedling community of both plots. This exotic tree usually colonizes open areas, like fields, roadsides, and forest edges and does not normally persist in the understory of mature forests. However, because CR and PF are relatively small tracts of forested area, surrounded by roads and developed areas, they have a higher proportion of edge habitats to interior forest area. These edge habitats may be especially susceptible to invasion by A. altissima and other edge-adapted species. Ailanthus altissima is a prolific seed-producer, and once established in the understory, can grow more rapidly than native saplings to reach the canopy in the event of gap formation. Ailanthus altissima can also reproduce via clonal ramets, which may be more likely to populate the understory. Mature A. altissima is an inconsequential component of the overstory in CR and PF (Importance values of 0.05 on CR and 0.01 on PF). However, its importance in the treated plots of the herbaceous community indicates that clonal ramets or seeds from outside the study plots are persisting despite continued treatment.

Several researchers have suggested that revegetation is sometimes necessary because the process of controlling exotic species harms native species. However, our study shows that reduction in exotic species abundance and increases in native abundance are not mutually exclusive and that while treatments may have harmful effects on non-target species, they do not necessarily reduce fitness or reproductive ability in native species. Future studies should explore native community responses to removal of exotic species identified in this study as important drivers of community composition, and also aim to identify dispersal pathways or other factors that may be maintaining these plant communities.

5. Acknowledgements

Thanks to the many students who have participated in gathering data for this project, including those enrolled in BIOL 211 (Principles of Botany). Special thanks to the students who conducted the initial sampling in 2008, and to Karissa Keen, Jake Francis, Megan Rayfield, Kristin Emery, Katherine Culatta, Andrew Watson, and Gwendolyn Casebeer. Funding was provided by the Undergraduate Research Program and National Science Foundation CCLI grant (DEB# 0942776).
6. References