

Research Article

Southern Appalachian urban forest response to three invasive plant removal treatments

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Abstract

Negative effects of non-native invasive plants have been well documented, but few studies have examined long-term impacts of non-native plant removal on both native and non-native plant community composition. This case study compared consequences of three non-native invasive removal methods (chemical, mechanical, and a combination of the two), applied to all exotic species, on native and non-native abundance, richness (total number of species), and community composition in two forested sites over six growing seasons. Important non-native vegetative components in pre-treatment and control plant communities included the vines English ivy (*Hedera helix* Linnaeus, 1753), Japanese honeysuckle (*Lonicera japonica* Thunberg, 1784), oriental bittersweet (*Celastrus orbiculatus* Thunberg, 1784), and clematis (*Clematis terniflora* De Candolle, 1817), and the shrub Chinese privet (*Ligustrum sinense* Lourero, 1790). In all removal treatments, non-native herbs, tree seedlings, and shrubs declined over six years, and native herbs' and tree seedlings' cover and richness increased. Time to implement treatments varied widely (844 person hours / ha for combination vs. 44 h / ha for chemical), but treatment effects only differed for native shrub density (highest in control treatment at one site), and native herb, shrub, and tree seedling richness (highest in mechanical and combination treatments at one site). Treatment did not affect cover or richness of non-native herb and tree seedlings, or shrub density and richness. Native species cover and richness increased as exotic species cover declined for all treatments in this study, suggesting that seed supplementation is not always necessary for community recovery. Spot-application of herbicides to foliage or girdled trees did not significantly hinder native plant community recovery, and no native species except poison ivy (*Toxicodendron radicans* (Linnaeus) Kuntze, 1891), which was intentionally removed, had its abundance or cover reduced by treatments. Even after treatment, clematis and Chinese privet remained important community components, demonstrating the difficulty in controlling these non-native species. Treatment effects were more pronounced at one site, perhaps due to imperfect selection of control plots, legacy land-use effects, or light limitation. This study supports the need for long-term treatment and measurement to accurately determine native plant community responses to non-native invasive removal.

Key words: chemical treatment, herbaceous plant, importance value, mechanical treatment, native plant, shrub, tree seedling

Introduction

Agricultural additions (Reichard and White 2001; Pimentel et al. 2005; Callaway and Maron 2006), combined with accidental introductions (Lehan et al. 2013), have led to the establishment of >1500 invasive exotic plants in the United States since 1800 (Miller 2010). Invasive exotic plants can affect nutrient and water cycles (reviewed by Ehrenfeld 2003), shift soil characteristics (Steinlein 2013; Greenwood and Kuhn 2014), reduce abundance and diversity of native plants (Vilà et al. 2011) and their seed banks (Gioria et al. 2014), decrease native

plants' fitness (reviewed by Jauni and Ramula 2015), drive native plants' evolution (Lau 2006; Oduor 2013), and depress rates of pollinator visitation (Montero-Castano and Vilà 2012). In addition, approximately 10% of non-native plants are ecosystem engineers (Richardson et al. 2000; Catford et al. 2009), capable of actively suppressing native plants or initiating changes in community composition (Heleno et al. 2010; Hanula and Horn 2011), succession (Corbin and D'Antonio 2012), or ecosystem function (Ehrenfeld 2010). The myriad negative influences of invasive non-native plants makes their removal a common restoration goal (Heleno et al. 2010).

Table 1. Importance values [(IV = relative density (proportion of total tree density) + relative dominance (proportion of total basal area) + relative frequency (proportion of plots in which species occurred); IV ranges from 0 to 3)] for all canopy trees (diameter at breast height >10 cm) at the two study sites, ranked from highest to lowest. Importance values rank species' contributions to overall community composition (McClanahan 1986). All canopy trees except *Ailanthus altissima* and *Prunus avium* were native. Nomenclature follows Wofford (1989).

Chestnut Ridge (CR)	IV	Pisgah Forest (PF)	IV
<i>Quercus alba</i>	0.455	<i>Pinus strobus</i>	1.234
<i>Liriodendron tulipifera</i>	0.368	<i>Prunus serotina</i>	0.409
<i>Robinia pseudoacacia</i>	0.337	<i>Quercus velutina</i>	0.233
<i>Carya glabra</i>	0.303	<i>Prunus avium</i>	0.204
<i>Quercus velutina</i>	0.227	<i>Ailanthus altissima</i>	0.131
<i>Prunus serotina</i>	0.197	<i>Pinus virginiana</i>	0.113
<i>Acer platanoides</i>	0.161	<i>Quercus falcata</i>	0.110
<i>Carya tomentosa</i>	0.137	<i>Quercus alba</i>	0.093
<i>Quercus rubra</i>	0.119	<i>Fraxinus americana</i>	0.074
<i>Acer rubrum</i>	0.113	<i>Quercus coccinea</i>	0.058
<i>Carya sp.</i>	0.108	<i>Liriodendron tulipifera</i>	0.053
<i>Quercus coccinea</i>	0.070	<i>Cornus florida</i>	0.046
<i>Cornus florida</i>	0.064	<i>Quercus rubra</i>	0.037
<i>Quercus prinus</i>	0.054	<i>Pinus echinata</i>	0.037
<i>Oxydendrum arboreum</i>	0.052	<i>Prunus pensylvanica</i>	0.035
<i>Nyssa sylvatica</i>	0.051	<i>Crataegus sp.</i>	0.030
<i>Pinus strobus</i>	0.045	<i>Quercus stellata</i>	0.022
<i>Morus rubrum</i>	0.045	<i>Viburnum prunifolium</i>	0.021
<i>Quercus falcata</i>	0.041	<i>Nyssa sylvatica</i>	0.021
<i>Prunus avium</i>	0.031	<i>Acer rubrum</i>	0.021
<i>Ailanthus altissima</i>	0.023	<i>Acer negundo</i>	0.021

Design gaps in many invasive removal studies mean that links between effective removal methods and native community responses are poorly understood. For example, most non-native plant removal projects target only one or a few species (Kettenring and Adams 2011). This approach streamlines removal processes, but it can also facilitate invasion by new species (e.g., Hanula et al. 2009; Loo et al. 2009), and it fails to consider species interactions (Wundrow et al. 2012; Kuebbing et al. 2014) or community dynamics (Zavaleta et al. 2001). In addition, most studies use small treatment plots (< 10 m²), removal and monitoring are limited in duration (< 1 y; Kettenring and Adams 2011), and benefits for native species are unclear (Kettenring and Adams 2011).

In this case study, we used three different methods to target removal of all non-native invasive plants from the herbaceous, shrub, and tree seedling communities of two heavily invaded urban forests; these forests are not contiguous with other wildlands, and are adjacent to high-density residential areas (see *Site Description*). Urban forest settings tend to be more susceptible to non-native plant invasions than wildland forests (Merriam 2003; Vidra et al. 2007) because fragmentation by roads and proximity to development facilitate plant invasions (Reichard and White 2001; Merriam 2003; Flory and Clay 2006; Hochstedler et al. 2007; Vidra et al. 2007; LaPaix et al. 2012). Our objectives were to test which

removal method was most effective in reducing the abundance and richness (number of species) of non-native invasive plants, to determine whether native plant communities increased in richness or abundance after treatments, and to identify important components of plant communities in two urban forests in the southern Appalachian Mountains, USA.

Materials and methods

Site description

This study was conducted in two forested areas on the University of North Carolina Asheville campus (UNCA, Buncombe County, NC, USA; elev. 650 m), with annual rainfall averaging 116 cm (NOAA NCDC 2015). Soils were similar between sites, consisting of deep to moderately deep Fannin-Lauada complexes (USDA NRCS 2015). Both study sites, Chestnut Ridge (CR) and Pisgah Forest (PF), are reforested areas with understories heavily dominated by non-native invasive species. Chestnut Ridge is a 24 ha fragment of *Quercus-Carya* (oak-hickory) forest (Table 1) used as a recreational camp until the mid-1960s (Melissa Acker, UNC Asheville Facilities Manager, personal communication; Heiman 2005), when it was acquired by the university. Since 1976, housing has been built on much of the land surrounding CR, and development pressures are expected to



Figure 1. Map of study sites Pisgah Forest (A) and Chestnut Ridge (B). Sampling areas are delimited by white boxes. At PF, controls were established immediately adjacent to one block, and across a small footpath from other blocks. This created a total of 5 sampling areas. At CR, controls were established immediately adjacent to other treatment areas, creating a total of 4 sampling areas. Imagery supplied by Google™ Maps.

intensify in the coming decades as rates of southern Appalachian urbanization increase (RENCI 2013). Pisgah Forest is a 20 ha fragment of abandoned dairy farm that was planted with native *Pinus strobus* Linnaeus, 1753 (eastern white pine) in the 1930s (M. Acker, personal communication; J. Horton, unpublished data; Heiman 2005), and this species remains dominant (Figure 1). PF is more closely associated with major roadways than CR (Figure 1).

Design and treatment

In 2008, three 25×50 m blocks [sizes standard for terrestrial plant studies (Kenkel and Podani 1991; Frelich and Reich 1995), but larger than those in most removal studies (Kettenring and Adams 2011)] were established in heavily invaded ($> 50\%$ cover of non-native species) areas at each site. Each block was divided into 3 equal 25×16.7 m plots. Blocks at PF were on flat ground, so treatments (chemical, mechanical, or combination) were assigned randomly to plots. At CR, blocks were arranged vertically down a slope, with one treatment plot assigned to each slope position (top, middle, bottom) across blocks. In 2009, three additional 25×16.7 m invaded but untreated control plots were installed at each site. At PF, control plots were established immediately adjacent to existing blocks for one block and across a small footpath for the other two blocks. At CR, control plots were installed in a single

25×50 m block adjacent and parallel to other blocks, so each slope position had a corresponding invaded control plot. The control plot was established towards the forest interior to avoid confounding effects of reintroductions (Figure 1).

Non-native invasive species removal methods (chemical, mechanical, and a combination of the two; *sensu* Miller et al. 2010) were randomly assigned to plots. Treatments were applied to all non-native species as well as the native liana *Toxicodendron radicans* Linnaeus (Kuntze) 1891 (poison ivy), which was removed because it can dominate urban forests following disturbance (Tessier 2010) and can have allelopathic effects on other native species (Ladwig et al. 2012). In the mechanical treatment, small (diameter at breast height < 5 cm) non-native plants were uprooted in early summer using hand-pulling, mattocks, and Weed Wrenches[®] to remove all roots; larger shrubs and trees were girdled, and vines were cut at ground level and uprooted to prevent re-sprouting. Mechanical treatments were applied in May 2008–12, prior to chemical treatments. In the chemical treatment, non-native plants were spot sprayed with 2% glyphosate plus non-ionic surfactant (Roundup[®]) in late May (2008–10). In the combination treatments, plots were treated mechanically in May from 2008–12, with glyphosate spot-spraying of re-emergent non-native plants in August (2008–10). Chemical spraying was not conducted after 2010 due to budget cuts and personnel losses.

Sampling procedures

Vegetative sampling occurred in May of each year (2008–2013 for treated plots and 2009–2013 for controls), prior to treatments. Sixteen 0.5 m² quadrats, divided into 50 squares, were randomly placed in each plot, excluding a 3 m un-sampled buffer to account for edge effects (e.g., Legee et al. 2010). Plants were identified to species level using nomenclature in Wofford (1989), except for *Carex* (sedge), *Poa* (grass), and some *Quercus* (oak) seedlings, which were grouped by genus. Percent cover was estimated visually by counting the number of squares in which each species occurred and multiplying by two. Quadrats were 0.25 m high, and non-woody plants with any aboveground biomass in the quadrat were classified as herbs. The tree seedling community, comprised of woody species < 0.25 m tall, included all trees along with the tree-like shrubs *Corylus americana* Walter, 1788 (American hazelnut), *Lonicera maackii* (Ruprecht) Herder, 1864 (bush honeysuckle), *Ligustrum sinense* (Chinese privet), and *Viburnum prunifolium* Linnaeus, 1753 (blackhaw). Mean species cover and richness (number of different species) of exotic and native plants were calculated for each plot and averaged across treatments.

Woody plants taller than 0.25 m with a dbh (diameter at breast height) less than 2.5 cm were defined as shrubs (USFS 2014). Shrub stem density was sampled within five 3 m² circular subplots, located randomly within plots but excluding the 3 m edge buffer. These circular subplots represented 3.5% of total plot area. Within plots, all woody plants with a dbh greater than or equal to 2.5 cm were identified and their diameters measured. Trees with a dbh > 10 cm were considered canopy trees (Horton et al. 2009), and their basal area was calculated as $A = \Pi(\text{dbh}/2)^2$; this value was then converted to m². Basal area was used to calculate density as $\sum(A) / 417.5 \text{ m}^2$, where 417.5 was total plot area. At each site, we calculated relative density (proportion of overall density attributed to each canopy tree species), relative dominance (proportion of total basal area for each canopy tree species), and relative frequency (proportion of plots in which each species occurred) of all canopy tree species in each plot, and summed those to determine Importance Values (Table 1).

Statistical analyses

Although some data were not normally distributed, we used generalized linear models and post hoc tests in analyses because these models are robust in analyzing non-normal count data (O'Hara and Kotze 2010). Because of differences in tree community structure, statistical analyses were done separately

for each site. To estimate the validity of controls established in 2009, community composition (native and non-native herb and seedling cover and richness, and shrub density and richness) of control plots was compared to that of plots established in 2008 (before treatment) using generalized linear models ANOVA. Generalized linear model repeated measures ANOVA was used to evaluate treatment effects on cover and richness of exotic and native plants in the herbaceous and tree seedling communities, and shrub density and richness in the shrub community. Responses were compared among treatments, including controls, from 2009–13. Because of differences in land use history and community composition (Table 1; Appendix 1), sites were analyzed separately. All analyses were performed with SAS 9.4 (SAS Institute, Cary, NC).

To visualize differences in species composition among treatments for the herbaceous, tree seedling, and shrub communities, we used non-metric multidimensional scaling (NMS) with Sorensen distance measures in PC-ORD (ver. 6.8; McCune and Mefford 2011), following procedures outlined by Peck (2010). These analyses were done separately for each site and included each treatment plot from 2008–2013 (2009–2013 for control plots). After initial runs using the autopilot function to determine the best number of axes, a final analysis was done by manually selecting the appropriate number of axes and running 250 iterations. Joint plots were used to determine species vectors associated with the spatial separation of plots in a 2D representation of the final analysis. No useable NMS ordination was found for shrub data from either site, likely because data were weakly structured, or because of the infrequent occurrence of several species (Peck 2010). Therefore, only ordinations of herbaceous and seedling communities are presented.

Results

Initial plot similarity

At CR, control and pre-treatment plots did not differ in any herbaceous, seedling or shrub community parameter (Table 2). At PF, non-native cover was lower, and native cover was lower or similar to, pre-treatment plots (Table 2). There, native shrub density and richness was higher in control plots than pre-treatment plots (Table 2).

Treatment effects, non-native cover and richness

Chestnut Ridge (CR). At CR, non-native herbaceous cover differed among treatments and years (Table 3). Control plots had consistently high non-native herbaceous cover throughout the course of the study

Table 2. Mean (± 1 S.E.) community parameters of treatment plots in 2008 (pre-treatment) and control plots in 2009. Superscripts denote significant differences among treatments for specific vegetation parameters at $P \leq 0.05$.

	Treatment			
	Control	Chemical	Mechanical	Combination
CR Herbs				
Native Cover	15.2 \pm 1.32	29.5 \pm 10.1	59.1 \pm 17.3	33.3 \pm 6.3
Non-Native Cover	80.5 \pm 11.9	67.4 \pm 30.8	59.1 \pm 19.3	33.3 \pm 6.3
Native Richness	9.0 \pm 1.7	12.3 \pm 4.4	17.7 \pm 3.5	18.7 \pm 1.2
Non-Native Richness	5.0 \pm 0.0	3.7 \pm 0.3	3.7 \pm 0.3	5.0 \pm 0.6
PF Herbs				
Native Cover	12.7 \pm 3.2 ^b	24.0 \pm 1.0 ^{ab}	27.7 \pm 3.1 ^a	9.6 \pm 4.5 ^b
Non-Native Cover	32.6 \pm 10.0 ^b	40.5 \pm 6.3 ^{ab}	36.3 \pm 3.9 ^{ab}	78.5 \pm 15.5 ^a
Native Richness	12.3 \pm 3.5	10.0 \pm 1.5	10.3 \pm 1.8	9.0 \pm 0.6
Non-Native Richness	4.3 \pm 1.2	7.3 \pm 0.7	6.3 \pm 0.9	6.3 \pm 0.3
CR Seedlings				
Native Cover	3.3 \pm 1.6	2.8 \pm 1.0	4.8 \pm 0.7	6.0 \pm 0.6
Non-Native Cover	2.8 \pm 2.8	0.4 \pm 0.4	0.1 \pm 0.4	1.3 \pm 0.9
Native Richness	3.7 \pm 0.9	3.0 \pm 1.0	5.3 \pm 0.9	6.0 \pm 0.6
Non-Native Richness	0.7 \pm 0.7	0.3 \pm 0.3	0.7 \pm 0.3	2.0 \pm 0.6
PF Seedlings				
Native Cover	4.7 \pm 1.8	5.2 \pm 3.2	6.3 \pm 2.6	3.2 \pm 1.7
Non-Native Cover	1.6 \pm 1.2	9.2 \pm 3.5	7.8 \pm 4.2	10.9 \pm 3.5
Native Richness	6.0 \pm 1.0	3.0 \pm 0.6	3.0 \pm 0.6	3.3 \pm 1.5
Non-Native Richness	1.3 \pm 0.9	1.7 \pm 0.3	1.7 \pm 0.3	1.3 \pm 0.3
CR Shrubs				
Native Density	0.6 \pm 0.3	1.1 \pm 0.1	2.2 \pm 0.5	1.3 \pm 0.5
Non-Native Density	0.5 \pm 0.3	5.1 \pm 3.4	5.8 \pm 2.9	4.5 \pm 0.3
Native Richness	4.3 \pm 1.8	4.0 \pm 0.6	5.0 \pm 0.6	6.0 \pm 0.6
Non-Native Richness	3.0 \pm 0.6	3.0 \pm 0.6	3.3 \pm 0.3	3.0 \pm 0.6
PF Shrubs				
Native Density	3.3 \pm 1.6 ^a	0.1 \pm 0.1 ^b	0.4 \pm 0.3 ^b	0.7 \pm 0.3 ^{ab}
Non-Native Density	1.0 \pm 0.1	5.7 \pm 0.9	6.2 \pm 1.3	7.2 \pm 2.6
Native Richness	8.3 \pm 2.7 ^a	1.0 \pm 0.6 ^b	2.0 \pm 1.2 ^{ab}	3.0 \pm 0.6 ^{ab}
Non-Native Richness	4.0 \pm 0.6	4.3 \pm 0.3	4.0 \pm 0.6	4.3 \pm 0.3

(Figure 2A). In 2008, pre-treatment, removal plots also had high non-native cover. In the mechanical and combination treatments, non-native cover decreased over time, while in the chemical treatment, non-native cover increased after an initial decline. Overall, non-native cover was highest in the control, intermediate in the chemical, and lowest in mechanical and combination treatments, and these trends persisted through 2013 (Figure 3A); however, non-native richness did not differ among treatments (Table 3; Figure 3C).

In the seedling layer, there were no differences among treatments or years for non-native cover and richness (Table 3; Figures 2E, 3G). Non-native shrub density and richness varied among treatments, and richness varied among years (Table 3; Figure 2I). Overall, both non-native density and richness were highest in the control and lower in all treatments, and these trends persisted until 2013 (Figures 3I, 3K).

Pisgah Forest (PF). Treatments were less effective at PF than at CR, with no effects on non-native or

native herbaceous cover (Figure 2C, 3B) and richness (Figure 3D), or seedling cover (Figures 2G, 3H) and richness (Table 3). Non-native shrub density did not differ among treatments (Table 3; Figures 2K, 3L). Non-native shrub richness was highest in the control compared to other treatments, while native shrub richness was also highest in the control, intermediate in the mechanical and combination, and lowest in the chemical treatment (Table 3; Figure 3L).

Treatment effects, native cover and richness

Chestnut Ridge (CR). Native herb cover did not differ among treatments but did vary among years, increasing over time (Table 3; Figure 2B). While native herbaceous cover was highest in mechanical and combination treatments, these differences were not significant (Figure 3A). Native herbaceous richness, however, was statistically higher in the mechanical and combination treatments, intermediate in the chemical treatment, and lowest in the control (Table 3).

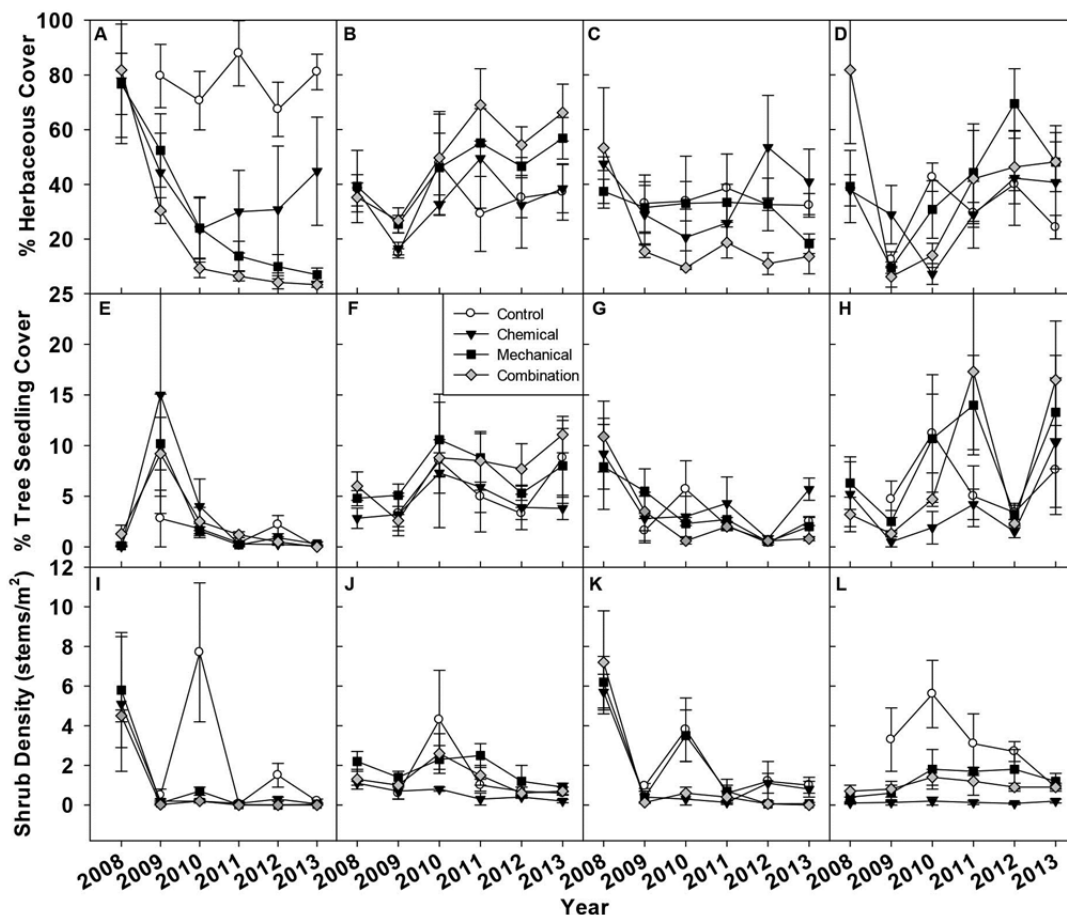


Figure 2. Mean (± 1 S.E.): percent cover of non-native and native herbs at Chestnut Ridge (A and B) and Pisgah Forest (C and D); percent cover of non-native and native tree seedlings at CR (E and F) and PF (G and H); and density of non-native and native shrubs at CR (I and J) and PF (K and L) from 2009–2011. Removal treatments (chemical, mechanical and combination) were initiated in summer 2008; chemical treatments were repeated in 2009 and 2010, while mechanical treatments were repeated from 2009–2012. All treatments were applied after annual vegetative sampling. Results of statistical analyses are reported in Table 3.

In the seedling layer, native richness increased over the course of the experiment and was highest in mechanical and combination treatments, intermediate in the chemical treatment, and lowest in the control treatment; these trends persisted in 2013 (Figure 3E). Native shrub density did not differ among treatments, but did among years, while native richness differed among both treatments and years (Table 3; Figure 2J). Native shrub richness was highest in the mechanical and combination treatments, intermediate in the control, and lowest in the chemical treatment, and this trend persisted in 2013 (Figure 3I).

Pisgah Forest (PF). There were no effects of treatments on native herbaceous cover and richness (Table 3; Figures 2D, 3F) or tree seedling cover and

richness (Table 3; Figures 2H, 3F). Native shrub density was higher in the control than other treatments (Table 3; Figure 2L). Native shrub richness was highest in the control, intermediate in the mechanical and combination treatments, and lowest in the chemical treatment (Table 3; Figure 3J). Total species richness was equivalent between sites (CR: 105, with 84 native + 21 invasive; PF: 107, with 85 native + 22 invasive).

Community composition

The NMS ordination of the herbaceous layer recommended a three axis solution for each site, but graphs were qualitatively similar, so only two axes are shown for each (Figure 4). At both sites, control

Table 3. Degrees of freedom (df), F-values, and P-values resulting from generalized linear model repeated measures analyses of variance measuring effects of treatment, year, and their interaction on plant community parameters at each site.

	Treatment			Year			Year * Treatment		
	df	F	P	df	F	P	df	F	P
Chestnut Ridge									
Non-Native Herb Cover	3	8.91	0.006	4	10.15	0.007	12	2.19	0.003
Native Herb Cover	3	1.22	0.363	4	12.52	< 0.001	12	0.62	0.789
Non-Native Herb Richness	3	1.14	0.391	4	0.90	0.468	12	1.44	0.206
Native Herb Richness	3	9.70	0.005	4	3.55	0.036	12	0.93	0.943
Non-Native Seedling Cover	3	0.79	0.535	4	6.94	0.023	12	1.17	0.378
Native Seedling Cover	3	1.34	0.327	4	4.29	0.010	12	0.54	0.857
Non-Native Seedling Richness	3	0.70	0.575	4	11.57	< 0.001	12	2.30	0.031
Native Seedling Richness	3	8.07	0.008	4	16.21	< 0.001	12	0.85	0.559
Non-Native Shrub Density	3	7.37	0.011	4	5.08	0.051	12	3.75	0.056
Native Shrub Density	3	2.00	0.192	4	5.33	0.032	12	1.11	0.400
Non-Native Shrub Richness	3	7.46	0.011	4	14.35	< 0.001	12	3.16	0.009
Native Shrub Richness	3	6.45	0.016	4	8.23	< 0.001	12	0.96	0.505
Pisgah Forest									
Non-Native Herb Cover	3	3.78	0.059	4	0.49	0.740	12	0.84	0.613
Native Herb Cover	3	0.68	0.586	4	16.92	< 0.001	12	1.76	0.100
Non-Native Herb Richness	3	1.85	0.217	4	2.93	0.036	12	0.42	0.943
Native Herb Richness	3	0.45	0.723	4	7.95	0.001	12	2.63	0.026
Non-Native Seedling Cover	3	0.98	0.447	4	3.00	0.039	12	1.57	0.161
Native Seedling Cover	3	0.91	0.477	4	7.24	0.001	12	1.32	0.268
Non-Native Seedling Richness	3	0.33	0.806	4	0.41	0.745	12	0.70	0.699
Native Seedling Richness	3	3.49	0.070	4	0.61	0.606	12	1.72	0.145
Non-Native Shrub Density	3	2.54	0.130	4	5.39	0.021	12	2.15	0.117
Native Shrub Density	3	14.25	0.001	4	2.20	0.145	12	1.31	0.315
Non-Native Shrub Richness	3	5.42	0.025	4	1.49	0.248	12	2.69	0.034
Native Shrub Richness	3	14.46	0.001	4	4.94	0.003	12	1.41	0.213

plots clustered together, overlapping somewhat with treatments. The community composition spread of mechanical, chemical, and combination plots diverged over time, with repeated treatments. Herbaceous cover was variable across treatments and years for most species, and was generally low (Appendix 1); however, at CR, species vectors indicated that cover of non-natives *Celastrus orbiculatus* (oriental bitter-sweet) and *Lonicera japonica* (Japanese honeysuckle) were important in clustering control plots. Cover of both of these species remained relatively constant in control and chemical treatments over the course of this study, while they declined in the mechanical and combination treatment (Table 4). NMS ordination also identified the native species *Maianthemum racemosum* Link, 1821 (false lily of the valley), *Parthenocissus quinquefolia* (Linnaeus) Planchon, 1887 (Virginia creeper), and *Phytolacca americana* Linnaeus (pokeweed), as important in plots' arrangement in NMS space. *Parthenocissus quinquefolia* cover was relatively constant in all treatments, including the control, while *M. racemosum* cover remained relatively constant in the control and the mechanical treatments and increased in the chemical

and combination treatment (Table 4). Cover of *P. americana* was variable across treatment and year.

The cover of two vines, the native *Toxicodendron radicans* and the non-native *L. japonica*, were important in the separation of herbaceous control plots in NMS space at PF. Cover of *L. japonica* remained relatively constant across years in the control plot, while it declined in the treatment plots (Table 4). This decline was greater in the chemical and combination than the mechanical treatment. Cover of *T. radicans* was highest in the control plots and declined in the treatment plots (Table 4), where it was intentionally removed. The cover of two natives, *P. americana* and *P. quinquefolia*, and the non-native *Clematis terniflora* (clematis) were important in the spatial separation of treated plots (Figure 4). Cover of *P. quinquefolia* increased in the combination treatment but was relatively constant in the control, chemical, and mechanical treatments.

The NMS ordination of the seedling layer recommended a three axis solution for CR and a two axis solution for PF. Because different graphs for each site were qualitatively similar no matter which axes were chosen for CR, only two axes are shown

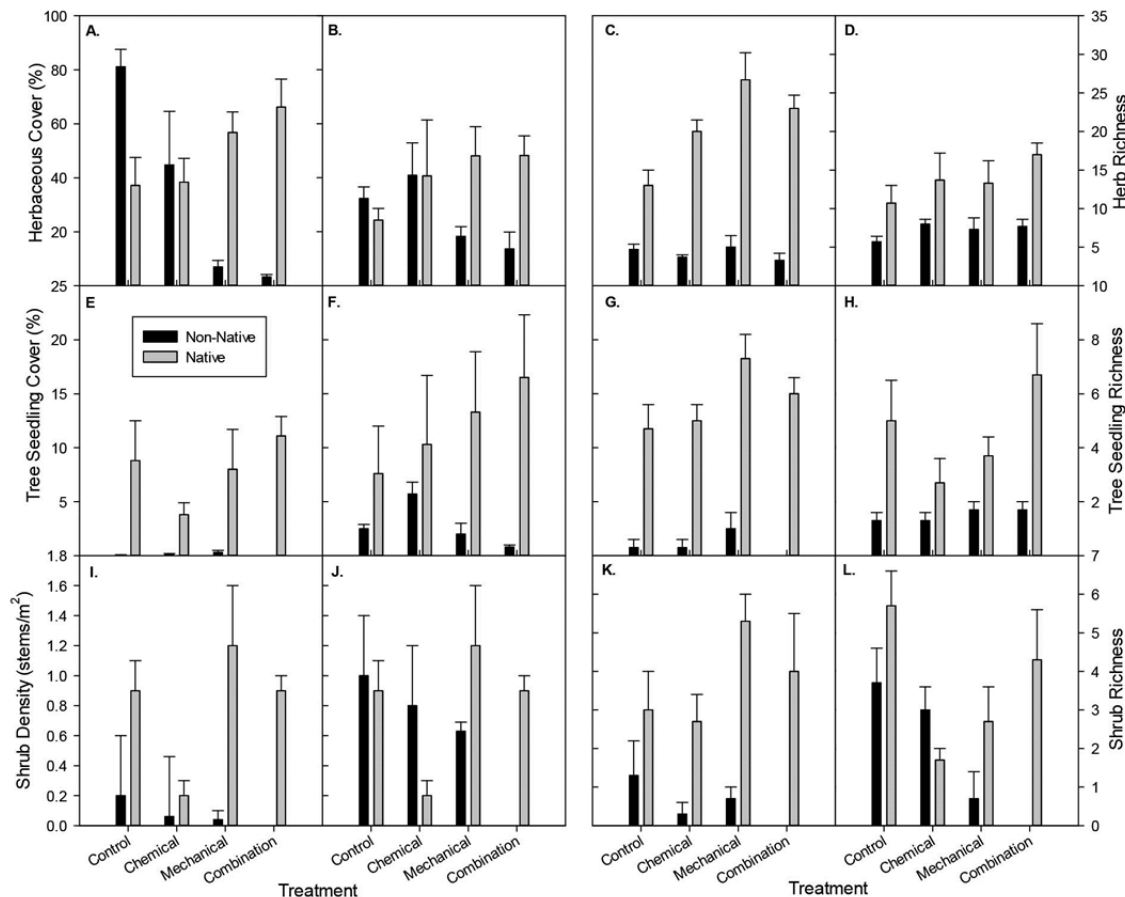


Figure 3. Mean (± 1 S.E.) values in 2013, after five years of removal treatments (chemical, mechanical, and combination). Data are for native and non-native herbaceous cover and richness at Chestnut Ridge (A and C, respectively) and Pisgah Forest (B and D, respectively); native and non-native seedling cover and richness at CR (E and G) and PF (F and H); and native and non-native shrub density and richness at CR (I and K) and PF (J and L). Removal treatments (chemical, mechanical and combination M+C) were initiated in summer 2008; chemical and combination treatments were repeated in 2009 and 2010, while mechanical treatments were repeated from 2009–2012. All treatments were applied after annual vegetative sampling. Results of statistical analyses are reported in Table 3.

(Figure 5); there was still no clear separation of treatments at either site. *Fraxinus americana* Linnaeus, 1753 (white ash) was an important component of the seedling community at both sites, with relatively stable cover throughout the study duration (Table 5). At CR, two additional native species, *Acer rubrum* Linnaeus, 1753 (red maple) and *Liriodendron tulipifera* Linnaeus, 1753 (tulip tree), were important in the separation of individual plots, but these did not separate by treatment. Cover of these two species was variable but relatively constant over the duration of the study (Table 5). At PF, the native *Prunus serotina* Ehrhart, 1784 (black cherry) and non-native *Ligustrum sinense* (Chinese privet) were also important in the separation of plots, but, similarly to CR, there was no separation of treatments. Cover of *P. serotina* was relatively constant across treatments and years. Cover

of *L. sinense* was relatively constant in the control and chemical treatments but decreased over time in the mechanical and combination treatments (Table 5).

Discussion

CR controls were better representations of pre-treatment conditions than PF controls. Inter-site differences in control plot suitability might have influenced final analyses, and comparisons between CR controls and treatments are likely more robust than those for PF. Thus, site-specific community differences could be confounded by these comparisons.

Non-native cover in herb and tree seedling communities declined with repeated treatment, but there were no differences among treatments. Lack of treatment effects could be due to the overall richness

Table 4. Mean (\pm 1 st. err.) cover of species identified by non-metric multidimensional scaling joint plots as being important in spatially separating treatment plots in ordination space at each site. Control plots were not present in 2008 and are denoted as not applicable (“na”). Species absence in a particular treatment \times year combination is denoted by “np” (not present).

Chestnut Ridge							
Species	Treatment	2008	2009	2010	2011	2012	2013
<i>Celastrus orbiculatus</i>	Control	na	9.8 \pm 3.5	9.8 \pm 3.5	11.7 \pm 2.2	15.4 \pm 4.6	3.9 \pm 1.7
	Chemical	3.3 \pm 1.2	4.7 \pm 0.1	3.3 \pm 1.4	8.9 \pm 0.4	5.3 \pm 2.0	4.8 \pm 2.2
	Mechanical	8.5 \pm 3.2	3.4 \pm 0.5	6.7 \pm 3.5	2.1 \pm 1.1	1.6 \pm 1.1	1.3 \pm 0.4
	Combination	11.2 \pm 1.4	3.5 \pm 0.6	2.5 \pm 1.2	3.3 \pm 2.0	1.8 \pm 1.1	0.1 \pm 0.1
<i>Lonicera japonica</i>	Control	na	54.9 \pm 5.1	54.9 \pm 5.1	68.8 \pm 11.1	47.2	68.4 \pm 9.4
	Chemical	27.4 \pm 26.0	10.6 \pm 1.4	0.9 \pm 0.0	5.3 \pm 1.8	2.9 \pm 2.9	12.1 \pm 7.3
	Mechanical	58.5 \pm 20.4	19.8 \pm 8.3	14.4 \pm 7.0	10.4 \pm 4.7	6.2 \pm 3.7	3.6 \pm 1.8
	Combination	40.8 \pm 5.3	8.3 \pm 3.4	1.6 \pm 0.8	1.1 \pm 0.3	0.7 \pm 0.1	1.8 \pm 0.9
<i>Maianthemum racemosum</i>	Control	na	8.8 \pm 8.8	14.4 \pm 12.1	10.6 \pm 8.8	6.2 \pm 6.2	7.0 \pm 7.0
	Chemical	8.3 \pm 6.7	1.7 \pm 1.2	12.3 \pm 6.3	18.1 \pm 10.7	21.8 \pm 4.1	12.6 \pm 5.4
	Mechanical	13.5 \pm 1.8	2.8 \pm 1.2	9.5 \pm 0.2	10.5 \pm 6.3	7.6 \pm 4.0	11.7 \pm 5.1
	Combination	9.0 \pm 6.3	3.1 \pm 0.4	16.4 \pm 9.9	15.7 \pm 7.4	13.2 \pm 7.7	17.5 \pm 7.0
<i>Parthenocissus quinquefolia</i>	Control	na	8.9 \pm 2.4	8.9 \pm 2.4	8.8 \pm 2.4	9.0 \pm 2.0	5.3 \pm 1.1
	Chemical	3.4 \pm 1.8	4.9 \pm 1.2	5.3 \pm 1.1	9.4 \pm 3.4	5.4 \pm 4.7	8.6 \pm 3.9
	Mechanical	4.9 \pm 0.7	2.8 \pm 0.6	6.7 \pm 3.3	5.5 \pm 1.1	4.8 \pm 1.5	5.0 \pm 0.3
	Combination	6.6 \pm 1.0	4.3 \pm 0.5	3.9 \pm 1.1	5.7 \pm 2.2	5.9 \pm 1.4	5.3 \pm 1.3
<i>Phytolacca americana</i>	Control	na	0.2 \pm 0.2	0.2 \pm 0.2	np	np	np
	Chemical	np	1.1 \pm 1.1	np	3.0 \pm 3.0	np	np
	Mechanical	np	2.0 \pm 0.8	5.3 \pm 5.1	0.1 \pm 0.1	0.6 \pm 0.1	np
	Combination	0.1 \pm 0.0	3.1 \pm 2.8	np	np	np	np
Pisgah Forest							
Species	Treatment	2008	2009	2010	2011	2012	2013
<i>Clematis terniflora</i>	Control	na	4.0 \pm 0.8	1.3 \pm 0.5	0.4 \pm 0.1	2.1 \pm 0.4	0.2 \pm 0.2
	Chemical	6.5 \pm 2.1	6.1 \pm 4.1	2.2 \pm 1.3	5.3 \pm 2.5	9.0 \pm 0.8	6.2 \pm 2.7
	Mechanical	6.0 \pm 1.6	4.8 \pm 0.7	17.9 \pm 11.3	13.7 \pm 0.2	14.4 \pm 1.7	5.0 \pm 0.8
	Combination	3.7 \pm 2.0	1.8 \pm 0.6	1.7 \pm 0.7	4.6 \pm 2.0	6.6 \pm 3.4	3.2 \pm 1.8
<i>Lonicera japonica</i>	Control	na	25.9 \pm 10.7	18.7 \pm 2.3	28.9 \pm 11.4	10.9 \pm 1.7	15.6 \pm 2.1
	Chemical	8.8 \pm 0.9	2.3 \pm 1.6	1.9 \pm 1.6	1.1 \pm 0.5	4.0 \pm 3.0	3.4 \pm 1.2
	Mechanical	12.2 \pm 4.3	9.5 \pm 1.1	6.6 \pm 3.0	7.5 \pm 3.1	4.7 \pm 2.9	7.9 \pm 1.8
	Combination	11.5 \pm 8.0	3.7 \pm 1.4	1.6 \pm 0.4	3.5 \pm 1.4	0.8 \pm 0.1	3.2 \pm 2.2
<i>Parthenocissus quinquefolia</i>	Control	na	2.6 \pm 1.7	7.2 \pm 2.3	7.7 \pm 2.0	6.0 \pm 2.0	4.3 \pm 1.8
	Chemical	8.7 \pm 4.1	0.6 \pm 0.2	2.4 \pm 0.9	4.3 \pm 3.1	8.0 \pm 3.3	5.0 \pm 2.1
	Mechanical	12.4 \pm 0.7	2.6 \pm 0.9	7.3 \pm 3.9	10.6 \pm 5.9	14.2 \pm 2.8	9.6 \pm 2.3
	Combination	1.0 \pm 0.8	3.5 \pm 2.7	7.0 \pm 4.5	14.8 \pm 6.5	15.0 \pm 9.3	13.8 \pm 5.7
<i>Phytolacca americana</i>	Control	na	np	np	np	np	np
	Chemical	np	1.4 \pm 1.4	1.6 \pm 1.6	4.9 \pm 1.2	4.5 \pm 2.1	np
	Mechanical	np	np	0.8 \pm 0.6	2.4 \pm 1.6	2.8 \pm 2.8	0.7 \pm 0.7
	Combination	np	0.2 \pm 0.2	0.3 \pm 0.1	1.6 \pm 1.6	2.0 \pm 2.0	0.8 \pm 0.8
<i>Toxicodendron radicans</i>	Control	na	3.1 \pm 0.8	17.6 \pm 6.3	14.5 \pm 5.2	16.7 \pm 5.8	10.4 \pm 5.5
	Chemical	1.5 \pm 0.5	np	np	0.4 \pm 0.4	1.1 \pm 0.1	0.1 \pm 0.1
	Mechanical	1.5 \pm 0.5	np	0.8 \pm 0.8	1.3 \pm 0.1	2.2 \pm 1.2	0.6 \pm 0.3
	Combination	4.9 \pm 4.8	0.1 \pm 0.1	1.5 \pm 1.1	0.1 \pm 0.1	0.6 \pm 0.1	1.3 \pm 0.7

in the exotic community, which included 49 different species whose most effective removal method might differ (Flory and Clay 2009) by phenology (Wolkovich and Cleland 2010; Godoy and Levine 2014) or interactions with surrounding invaded areas (Davies and Sheley 2007). Species-specific differences in optimal removal method were revealed by NMS data, which showed that mechanical treatment is necessary to control *C. orbiculatus* and *L. sinense*, and that both mechanical and chemical treatment might be needed for *L. japonica* removal.

Treatments did not reduce non-native richness because they failed to completely exclude established non-native species, particularly *C. orbiculatus* and *H. helix*. This implies that propagules from outside study plots recruited continually into treated sites (e.g., Simberloff 2009) or that soil seed banks persisted (e.g., Van Clef and Stiles 2001). Sites' land use histories could have also rendered them susceptible to repeated non-native plant invasion, with former agricultural sites like PF particularly vulnerable (Kulmatiski et al. 2006; Kuhman et al. 2011). Non-

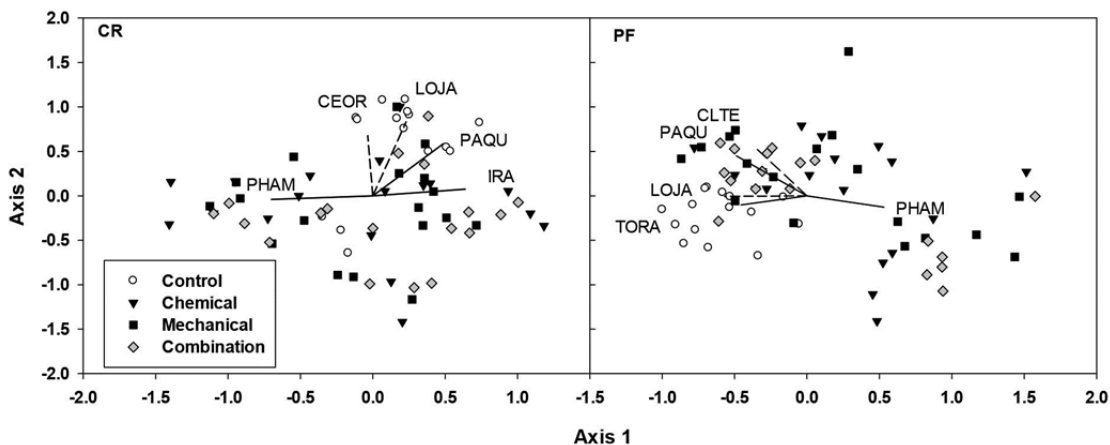


Figure 4. Non-metric multidimensional scaling (NMS) ordination result, showing a two axis solution for herbaceous species composition in four treatments (control, chemical, mechanical, and combination) at Chestnut Ridge (A) and Pisgah Forest (B). Important species vectors from joint plots are overlaid. Solid lines represent native species and dashed lines represent non-native species. CLTE – *Clematis terniflora*, CEOR – *Celastrus orbiculatus*, LOJA – *Lonicera japonica*, MARA – *Maianthemum racemosum*, PAQU – *Parthenocissus quinquefolia*, PHAM – *Phytolacca americana*, TORA – *Toxicodendron radicans*.

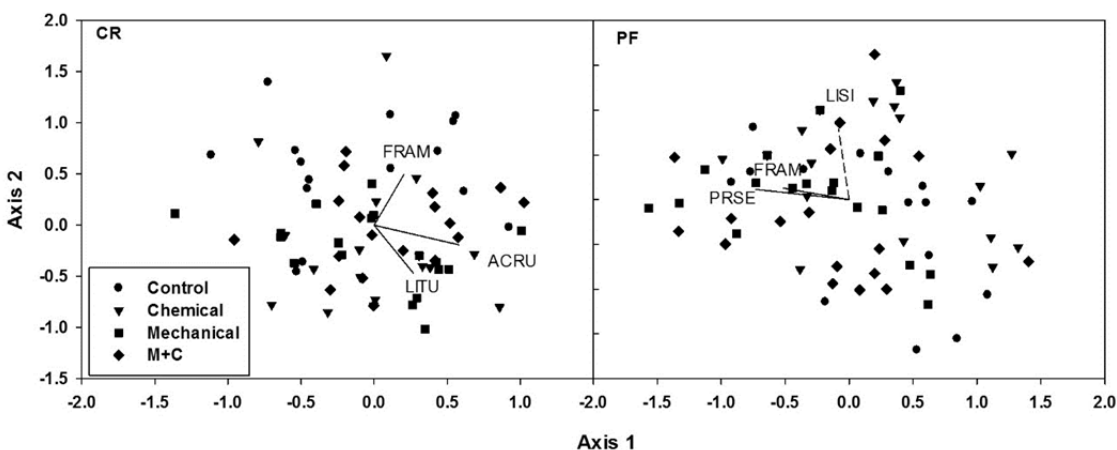


Figure 5. Non-metric multidimensional scaling (NMS) ordination result, showing a two axis solution to seedling species composition in four treatments (control, chemical, mechanical, and combination) at Chestnut Ridge (A) and Pisgah Forest (B). Important species vectors from joint plots are overlaid. Solid lines represent native species, and dashed lines represent non-native species. ACRU – *Acer rubrum*, FRAM – *Fraxinus americana*, LISI – *Ligustrum sinense*, LITU – *Liriodendron tulipifera*, PRSE – *Prunus serotina*.

native removal efforts typically target only a few species (Hochstedler et al. 2007; Vidra et al. 2007; Flory and Clay 2009; Hanula et al. 2009), but studying single species in isolation can make results less relevant to ecosystem restoration or conservation efforts (Heleno et al. 2010; Kuebbing et al. 2013). Thus, the multi-species approach taken in this study could be particularly applicable for land managers (*sensu* Glen et al. 2013).

Variation in treatment effects on native richness could be due to differences in land use history between sites (Cramer et al. 2008) or to individual

species' responses (Flory and Clay 2009; Johnson and Davies 2014). For instance, NMS data showed that *M. racemosum* increased after chemical removal of non-natives, and cover of *P. americana* grew following tree fall; thus, abundance of the latter is likely influenced by light availability rather than treatment (Luken et al. 1997). In all CR treatments, native richness increased over time; this could be attributed to germination from the seed bank, which can persist for more than a year in southern Appalachian tree species measured in this study (Lambers et al. 2005). Native seed banks can endure even in

Table 5. Mean (\pm 1 st. err.) density of shrub-sized (> 25 cm height and < 2.5 cm diameter at breast height) woody plants identified by non-metric multidimensional scaling joint plots as being important in spatially separating treatment plots in ordination space at each site. Control plots were not present in 2008 and are denoted as not applicable (“na”). Species absence in a particular treatment x year combination is denoted by “np” (not present).

Chestnut Ridge		2008	2009	2010	2011	2012	2013
Species	Treatment						
<i>Acer rubrum</i>	Control	na	0.13 \pm 0.06	0.06 \pm 0.01	np	0.02 \pm 0.02	0.02 \pm 0.02
	Chemical	0.11 \pm 0.11	np	0.08 \pm 0.08	0.06 \pm 0.01	np	0.02 \pm 0.02
	Mechanical	0.11 \pm 0.01	0.02 \pm 0.02	0.02 \pm 0.02	0.06 \pm 0.01	np	np
	Combination	np	0.02 \pm 0.02	0.10 \pm 0.03	0.16 \pm 0.03	0.02 \pm 0.02	0.06 \pm 0.01
<i>Fraxinus americana</i>	Control	na	0.02 \pm 0.02	0.72 \pm 0.60	0.36 \pm 0.04	0.13 \pm 0.04	0.28 \pm 0.08
	Chemical	np	0.02 \pm 0.02	np	0.06 \pm 0.01	0.04 \pm 0.04	np
	Mechanical	np	0.22 \pm 0.16	0.02 \pm 0.02	0.15 \pm 0.06	0.02 \pm 0.02	np
<i>Liriodendron tulipifera</i>	Control	na	np	0.06 \pm 0.01	0.10 \pm 0.03	np	0.04 \pm 0.04
	Chemical	0.11 \pm 0.01	np	0.03 \pm 0.03	0.06 \pm 0.01	0.02 \pm 0.02	0.10 \pm 0.03
	Mechanical	0.21 \pm 0.06	0.25 \pm 0.04	0.57 \pm 0.38	0.45 \pm 0.11	0.30 \pm 0.30	0.21 \pm 0.14
	Combination	0.18 \pm 0.04	0.22 \pm 0.04	0.47 \pm 0.31	0.28 \pm 0.13	0.02 \pm 0.02	0.50 \pm 0.26
Pisgah Forest							
Species	Treatment						
<i>Fraxinus americana</i>	Control	na	0.35 \pm 0.22	0.36 \pm 0.36	0.06 \pm 0.01	0.29 \pm 0.22	0.36 \pm 0.11
	Chemical	0.14 \pm 0.04	0.02 \pm 0.02	np	0.15 \pm 0.15	np	0.24 \pm 0.10
	Mechanical	0.90 \pm 0.58	1.06 \pm 0.22	0.61 \pm 0.44	0.87 \pm 0.32	1.36 \pm 1.02	0.96 \pm 0.32
	Combination	0.58 \pm 0.27	0.17 \pm 0.06	0.55 \pm 0.21	0.59 \pm 0.34	0.30 \pm 0.11	0.60 \pm 0.18
<i>Ligustrum sinense</i>	Control	na	0.57 \pm 0.14	1.08 \pm 0.57	0.68 \pm 0.24	0.55 \pm 0.37	0.75 \pm 0.24
	Chemical	2.85 \pm 0.72	0.57 \pm 0.17	0.29 \pm 0.22	1.36 \pm 0.71	0.76 \pm 0.70	1.11 \pm 0.57
	Mechanical	2.53 \pm 0.90	0.96 \pm 0.30	1.66 \pm 0.91	0.64 \pm 0.57	np	0.10 \pm 0.03
	Combination	3.50 \pm 2.08	0.08 \pm 0.01	0.32 \pm 0.25	0.36 \pm 0.30	0.04 \pm 0.04	0.06 \pm 0.06
<i>Prunus serotina</i>	Control	na	0.22 \pm 0.03	1.51 \pm 0.75	0.22 \pm 0.11	0.40 \pm 0.24	0.28 \pm 0.11
	Chemical	np	0.02 \pm 0.02	np	0.02 \pm 0.02	np	0.02 \pm 0.02
	Mechanical	0.18 \pm 0.05	0.19 \pm 0.10	0.02 \pm 0.02	0.16 \pm 0.06	0.10 \pm 0.03	0.21 \pm 0.07
	Combination	0.64 \pm 0.34	0.17 \pm 0.17	0.17 \pm 0.08	0.11 \pm 0.04	0.21 \pm 0.21	0.06 \pm 0.01

the presence of heavy invasion (Biggerstaff and Beck 2007; Robertson and Hickman 2012), although they might be depressed in previously-invaded areas (Gioria et al. 2014) and restrict urban forest regeneration (Vidra et al. 2007; Overdyck and Clarkson 2012). Native increases could also reflect seed recruitment from outside the study plots (Robinson and Handel 2000) or from established native plants within plots, but recruitment was not measured in this study. Although greater richness and cover of native species do not preclude additional invasion (Stohlgren et al. 2003), these factors might create higher-quality habitat (Martin and Murray 2011; Bezemer et al. 2014).

Not all non-native invasive removal studies have observed such persistent increases in native species (Hochstedler et al. 2007; Pavlovic and Frohnapple 2009; Kettenring and Adams 2011). For example, Vidra et al. (2007) measured few post-treatment increases in native richness and cover with either one initial removal treatment or repeated removal of non-natives every two weeks for 16 months, and suggested three mechanisms to explain this lack of recovery. The understory environment might be

mismatched to the native species in the seed bank, or native seed dispersal might be limited, or native propagules might be outcompeted by an influx of non-native propagules. The lack of native recovery in Vidra et al.'s (2007) repeated treatment is surprising because their treatments spanned two growing seasons, a minimal but sufficient amount of time for evaluating restoration projects (Heleno et al. 2010). Our study spanned six complete growing seasons, and its longer duration of both non-native removal and native recovery could explain why results differed so dramatically from those of Vidra et al. (2007), who treated similar sites.

Several researchers have suggested that revegetation or seed supplementation is necessary to restore native plant communities (Martinez and Dornbush 2013), because of depauperate native seed banks (Gioria et al. 2014) or because exotic removal processes harm native species (Heleno et al. 2010; Kettenring and Adams 2011). However, our study demonstrates that reductions in exotic species abundance and increases in native abundance are not mutually exclusive, at least in this system. Removal treatments might have harmful effects on some sensitive non-

target species (Suckling and Sforza 2014), but they do not necessarily preclude the re-creation of native plant communities.

In the absence of sustained removal treatments, capacity for re-invasion at these sites, particularly from adjacent sites (*sensu* Davies and Sheley 2007, Vidra and Shear 2008), is high. For instance, cover of *C. terniflora*, a common component of fragmented forests (Schulz and Gray 2013), was relatively constant in this study and did not change with removal treatments. *Ligustrum sinense* also persisted over treatments and years. This shrub is known to negatively impact forest regeneration and can cause decreased native species richness and abundance (Hanula et al. 2009; Hart and Holmes 2013). It is also readily dispersed by vertebrate vectors, particularly birds, especially in winter when other food sources are scarce (Greenberg and Walter 2010). The higher importance of this species at PF likely reflects the greater proximity to residential development, where *L. sinense* might have been planted horticulturally and where bird abundance (Mason et al. 2007) is higher.

Mechanical removal of non-native invasive species required more than 800 person-hours / ha in the first year of treatment, reflecting the labor-intensive nature of this approach (Catford et al. 2009; Kettenring and Adams 2011). Chemical-only treatments, for comparison, took only 44 person-hours / ha to implement. Although the time investment for mechanical treatments decreased in subsequent years, it was always at least ten times greater than chemical treatment times. Because there were no treatment effects on non-native species, and treatment effects on native species were limited, future work might focus on the most cost-effective solutions to re-establishing native communities. While herbicides can harm non-target species (e.g., Crone et al. 2009), these effects were not observed consistently in our study. Cover of some but not all native species declined after initial treatments in 2008, the year in which non-native cover was highest and the most spot-spraying was done (Table 4). With proper planning, managers could use chemical treatments for initial reductions in exotic cover, which could then be sustained manually. The recovery of non-native communities in chemical plots following cessation of herbicide application in 2010 emphasizes the importance of sustaining treatments over long time periods. Managers should further explore native community responses to targeted removal of non-native species identified in this study as important community members, and also aim to identify and mitigate factors maintaining exotic plant richness.

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References

- Bezemer T, Harvey J, Cronin J (2014) Response of native insect communities to invasive plants. *Annual Review of Entomology* 59: 119–141, <http://dx.doi.org/10.1146/annurev-ento-011613-162104>
- Biggerstaff M, Beck C (2007) Effects of English ivy (*Hedera helix*) on seed bank formation and germination. *American Midland Naturalist* 157: 250–257, [http://dx.doi.org/10.1674/0003-0031\(2007\)157\[250:EOEIHJ\]2.0.CO;2](http://dx.doi.org/10.1674/0003-0031(2007)157[250:EOEIHJ]2.0.CO;2)
- Callaway RM, Maron JL (2006) What have exotic plant invasions taught us over the past 20 years? *Trends in Ecology and Evolution* 21: 369–374, <http://dx.doi.org/10.1016/j.tree.2006.04.008>
- Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* 15: 22–40, <http://dx.doi.org/10.1111/j.1472-4642.2008.00521.x>
- Corbin JD, D'Antonio CM (2012) Gone but not forgotten? Invasive plants' legacies on community and ecosystem properties. *Invasive Plant Science and Management* 5: 117–124, <http://dx.doi.org/10.1614/IPSM-D-11-00005.1>
- Cramer VA, Hobbs RJ, Standish SJ (2008) What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology and Evolution* 23: 104–112, <http://dx.doi.org/10.1016/j.tree.2007.10.005>
- Crone E, Marler M, Pearson D (2009) Non-target effects of broadleaf herbicide on a native perennial forb: a demographic framework for assessing and minimizing impacts. *Journal of Applied Ecology* 46: 673–682, <http://dx.doi.org/10.1111/j.1365-2664.2009.01635.x>
- Davies K, Sheley R (2007) A conceptual framework for preventing the spatial dispersal of invasive plants. *Weed Science* 55: 178–184, <http://dx.doi.org/10.1614/WS-06-161>
- Ehrenfeld J (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6: 503–523, <http://dx.doi.org/10.1007/s10021-002-0151-3>
- Ehrenfeld J (2010) Ecosystem consequences of biological invasions. *Annual Review of Ecology and Systematics* 41: 1, <http://dx.doi.org/10.1146/annurev-ecolsys-102209-144650>
- Flory SL, Clay K (2006) Invasive shrub distribution varies with distance to roads and stand age in eastern deciduous forests in Indiana, USA. *Plant Ecology* 184: 131–141, <http://dx.doi.org/10.1007/s11258-005-9057-4>
- Flory SL, Clay K (2009) Invasive plant removal method determines native plant community responses. *Journal of Applied Ecology* 46: 434–442, <http://dx.doi.org/10.1111/j.1365-2664.2009.01610.x>
- Frellich LE, Reich PB (1995) Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecological Monographs* 65: 325–346, <http://dx.doi.org/10.2307/2937063>
- Gioria M, Jarosik V, Pysek P (2014) Impact of invasions by alien plants on soil seed bank communities: emerging patterns. *Perspectives in Plant Ecology* 16: 132–142, <http://dx.doi.org/10.1016/j.ppees.2014.03.003>

- Glen AS, Atkinson R, Campbell K, Hagen E, Holmes N (2013) Eradicating multiple invasive species on inhabited islands: the next big step in island restoration? *Biological Invasions* 15: 2589–2603, <http://dx.doi.org/10.1007/s10530-013-0495-y>
- Godoy O, Levine J (2014) Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. *Ecology* 95: 726–736, <http://dx.doi.org/10.1890/13-1157.1>
- Greenberg CH, Walter ST (2010) Fleshy fruit removal and nutritional composition of winter-fruited plants: a comparison of non-native invasive and native species. *Natural Areas Journal* 30: 312–321, <http://dx.doi.org/10.3375/043.030.0306>
- Greenwood P, Kuhn N (2014) Does the invasive plant, *Impatiens glandulifera*, promote soil erosion along the riparian zone? an investigation on a small watercourse in northwest Switzerland. *Journal of Soils and Sediments* 14: 637–650, <http://dx.doi.org/10.1007/s11368-013-0825-9>
- Hanula JL, Horn S (2011) Removing an exotic shrub from riparian forests increases butterfly diversity and abundance. *Forest Ecology and Management* 262: 674–680, <http://dx.doi.org/10.1016/j.foreco.2011.04.040>
- Hanula JL, Horn S, Taylor JW (2009) Chinese privet (*Ligustrum sinense*) removal and its effect on native plant communities of riparian forests. *Invasive Plant Science and Management* 2: 292–300, <http://dx.doi.org/10.1614/IPSM-09-028.1>
- Hart JL, Holmes BN (2013) Relationships between *Ligustrum sinense* invasion, biodiversity, and development in a mixed bottomland forest. *Invasive Plant Science and Management* 6: 175–186, <http://dx.doi.org/10.1614/IPSM-D-12-00050.1>
- Heiman K (2005) Environmental assessment and finding of no significant impact. Consulting Report for the University of North Carolina Asheville, 10 pp
- Heleno R, Lacerda I, Ramos JA, Memmott J (2010) Evaluation of restoration effectiveness: community response to the removal of alien plants. *Ecological Applications* 20: 1191–1203, <http://dx.doi.org/10.1890/09-1384.1>
- Hochstedler WW, Bradford SS, Gorchov DL, Saunders LP, Stevens MH (2007) Forest floor plant community response to experimental control of the invasive biennial, *Alliaria petiolata* (garlic mustard). *The Journal of the Torrey Botanical Society* 134: 155–165, [http://dx.doi.org/10.3159/1095-5674\(2007\)134\[155:FFPCRT\]2.0.CO;2](http://dx.doi.org/10.3159/1095-5674(2007)134[155:FFPCRT]2.0.CO;2)
- Horton JL, Clinton BD, Walker JF, Beier CM, Nilsen ET (2009) Variation in soil and forest floor characteristics along gradients of ericaceous, evergreen shrub cover in the southern Appalachians. *Castanea* 74: 340–352, <http://dx.doi.org/10.2179/08-016R3.1>
- Jauni M, Ramula S (2015) Meta-analysis on the effects of exotic plants on the fitness of native plants. *Perspectives in Plant Ecology, Evolution, and Systematics* 17: 412–420, <http://dx.doi.org/10.1016/j.ppees.2015.06.002>
- Johnson DD, Davies KW (2014) Effects of integrating mowing and Imazapyr application on African rue (*Peganum harmala*) and native perennial grasses. *Invasive Plant Science and Management* 7: 617–623, <http://dx.doi.org/10.1614/IPSM-D-13-00019.1>
- Kenkel NC, Podani J (1991) Plot size and estimation efficiency in plant community studies. *Journal of Vegetation Science* 2: 539–544, <http://dx.doi.org/10.2307/3236036>
- Kettenring KM, Adams CR (2011) Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. *Journal of Applied Ecology* 48: 970–979, <http://dx.doi.org/10.1111/j.1365-2664.2011.01979.x>
- Kuebbing SE, Nu-éz M, Simberloff D (2013) Current mismatch between research and conservation efforts: the need to study co-occurring invasive plant species. *Biological Conservation* 160: 121–129, <http://dx.doi.org/10.1016/j.biocon.2013.01.009>
- Kuebbing SE, Classen A, Simberloff D (2014) Two co-occurring invasive woody shrubs alter soil properties and promote subdominant invasive species. *Journal of Applied Ecology* 51: 124–133, <http://dx.doi.org/10.1111/1365-2664.12161>
- Kuhman T, Pearson S, Turner G (2011) Agricultural land-use history increases non-native plant invasion in a southern Appalachian forest a century after abandonment. *Canadian Journal of Forest Research* 41: 920–929, <http://dx.doi.org/10.1139/x11-026>
- Kulmatiski A, Beard KH, Stark JM (2006) Soil history as a primary control on plant invasion in abandoned agricultural fields. *Journal of Applied Ecology* 43: 868–876, <http://dx.doi.org/10.1111/j.1365-2664.2006.01192.x>
- Ladwig L, Meiners S, Pisula N, Lang K (2012) Conditional allelopathic potential of temperate lianas. *Plant Ecology* 213: 1927–1935, <http://dx.doi.org/10.1007/s11258-012-0087-4>
- Labbers J, Clark J, Lavine M (2005) Implications of seed banking for recruitment of southern Appalachian woody species. *Ecology* 86: 85–95, <http://dx.doi.org/10.1890/03-0685>
- LaPaix R, Harper K, Freedman B, Fraser L (2012) Patterns of exotic plants in relation to anthropogenic edges within urban forest remnants. *Applied Vegetation Science* 15: 525–535, <http://dx.doi.org/10.1111/j.1654-109X.2012.01195.x>
- Lau J (2006) Evolutionary responses of native plants to novel community members. *Evolution* 60: 56–63, <http://dx.doi.org/10.1111/j.0014-3820.2006.tb01081.x>
- Leege LM, Thompson JS, Parris DJ (2010) The responses of rare and common trilliums (*Trillium reliquum*, *T. cuneatum*, and *T. maculatum*) to deer herbivory and invasive honeysuckle removal. *Castanea* 75: 443–443, <http://dx.doi.org/10.2179/09-048.1>
- Lehan N, Murphy J, Thorburn L, Bradley B (2013) Accidental introductions are an important source of invasive plants in the continental United States. *American Journal of Botany* 100: 1287–1293, <http://dx.doi.org/10.3732/ajb.1300601>
- Loo S, Mac Nally R, O'Dowd D, Lake P (2009) Secondary invasions: implications of riparian restoration for in-stream invasion by an aquatic grass. *Restoration Ecology* 17: 378–385, <http://dx.doi.org/10.1111/j.1526-100X.2008.00378.x>
- Luken JO, Kudes LM, Tholemeier TC (1997) Response of understory species to gap formation and soil disturbance in *Lonicera maackii* thickets. *Restoration Ecology* 5: 229–235, <http://dx.doi.org/10.1046/j.1526-100X.1997.09727.x>
- Martin LJ, Murray BR (2011) A predictive framework and review of the ecological impacts of exotic plant invasions on reptiles and amphibians. *Biological Reviews* 86: 407–419, <http://dx.doi.org/10.1111/j.1469-185X.2010.00152.x>
- Martinez JA, Dornbush ME (2013) Use of a native matrix species to facilitate understory restoration in an overbrowsed, invaded woodland. *Invasive Plant Science and Management* 6: 219–230, <http://dx.doi.org/10.1614/IPSM-D-12-00062.1>
- Mason J, Moorman C, Hess G, Sinclair K (2007) Designing suburban greenways to provide habitat for forest breeding birds. *Landscape and Urban Planning* 80: 153–164, <http://dx.doi.org/10.1016/j.landurbplan.2006.07.002>
- McClanahan TR (1986) The effect of a seed source on primary succession in a forest ecosystem. *Vegetatio* 65: 175–178, <http://dx.doi.org/10.1007/BF00044817>
- McCune B, Mefford MJ (2011) PC-ORD. Multivariate analysis of ecological data. Version 6.08. MjM Software, Gleneden Beach, OR, USA
- Merriam RW (2003) The abundance, distribution and edge associations of six non-indigenous, harmful plants across North Carolina. *The Journal of the Torrey Botanical Society* 130: 283–291, <http://dx.doi.org/10.2307/3557546>
- Miller JH, Manning ST, Enloe SF (2010) A management guide for invasive plants in southern forests. General Technical Report SRS-13. United States Department of Agriculture Forest Service Southern Research Station, Asheville, NC, 120 pp
- Montero-Castano A, Vilà M (2012) Impacts of landscape alteration and invasions on pollinators: a meta-analysis. *Journal of Ecology* 100: 884–893, <http://dx.doi.org/10.1111/j.1365-2745.2012.01968.x>
- National Oceanic and Atmospheric Administration, National Climatic Data Center (NOAA, NCDC) (2015) Climate Data Online, <https://www.ncdc.noaa.gov/cdo-web/> (accessed June 2015)
- Oduor AM (2013) Evolutionary responses of native plant species to invasive plants: a review. *New Phytologist* 200: 986–992, <http://dx.doi.org/10.1111/nph.12429>

- O'Hara RB, Kotze DJ (2010) Do not log-transform count data. *Methods in Ecology and Evolution* 1: 118–122, <http://dx.doi.org/10.1111/j.2041-210X.2010.00021.x>
- Overdyck E, Clarkson B (2012) Seed rain and soil seed banks limit native regeneration within urban forest restoration plantings in Hamilton City, New Zealand. *New Zealand Journal of Ecology* 36: 1–14
- Pavlovic N, Frohnapple K (2009) Effect of removal of *Hesperis matronalis* (dame's rocket) on species cover of forest understory vegetation in NW Indiana. *American Midland Naturalist* 161: 165–176, <http://dx.doi.org/10.1674/0003-0031-161.1.165>
- Peck JE (2010) Multivariate analysis for community ecologists: step-by-step using PC-ORD. MjM Software Design, Gleneden Beach, OR, USA
- Pimentel D, Lach L, Zuniga R, Morrison D (2005) Environmental and economic costs of non-indigenous species in the United States. *BioScience* 50: 53–65, [http://dx.doi.org/10.1641/0006-3568\(2000\)050\[0053:EAECON\]2.3.CO;2](http://dx.doi.org/10.1641/0006-3568(2000)050[0053:EAECON]2.3.CO;2)
- Reichard SH, White P (2001) Horticulture as a pathway of invasive plant introductions in the United States. *BioScience* 51: 103–113, [http://dx.doi.org/10.1641/0006-3568\(2001\)051\[0103:HAPOIJ\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2001)051[0103:HAPOIJ]2.0.CO;2)
- Renaissance Computing Institute (RENCI) (2013) Buncombe County Multi-Hazard Risk Tool. Asheville, NC, USA, http://www1.nemac.unca.edu/Renci/MultiHazardRiskTool/bunc_hazard_tool_public.html (accessed June 2015)
- Richardson DM, Pyšek P, Rejmánek MG, Panetta FD, West CJ (2000) Naturalisation and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6: 93–107, <http://dx.doi.org/10.1046/j.1472-4642.2000.00083.x>
- Robertson S, Hickman K (2012) Aboveground plant community and seed bank composition along an invasion gradient. *Plant Ecology* 213: 1461–1475, <http://dx.doi.org/10.1007/s11258-012-0104-7>
- Robinson G, Handel S (2000) Directing spatial patterns of recruitment during an experimental urban woodland reclamation. *Ecological Applications* 10: 174–188, [http://dx.doi.org/10.1890/1051-0761\(2000\)010\[0174:DSPORD\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2000)010[0174:DSPORD]2.0.CO;2)
- Schulz B, Gray A (2013) The new flora of northeastern USA: quantifying introduced plant species occupancy in forest ecosystems. *Environmental Monitoring and Assessment* 185: 3931–3957, <http://dx.doi.org/10.1007/s10661-012-2841-4>
- Simberloff D (2009) The role of propagule pressure in biological invasions. *Annual Review of Ecology and Systematics* 40: 81–102, <http://dx.doi.org/10.1146/annurev.ecolsys.110308.120304>
- Steinlein T (2013) Invasive alien plants and their effects on native microbial soil communities. *Progress in Botany* 74: 293–319, http://dx.doi.org/10.1007/978-3-642-30967-0_11
- Stohlgren TJ, Barnett DT, Kartesz JT (2003) The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology and the Environment* 1: 11–14, [http://dx.doi.org/10.1890/1540-9295\(2003\)001\[0011:TRGRPO\]2.0.CO;2](http://dx.doi.org/10.1890/1540-9295(2003)001[0011:TRGRPO]2.0.CO;2)
- Suckling D, Sforza R (2014) What magnitude are observed non-target impacts from weed biocontrol? *PLoS ONE* 9: e84847, <http://dx.doi.org/10.1371/journal.pone.0084847>
- Tessier J (2010) Effect of forest harvest on the vegetation of an urban park. *Northeastern Naturalist* 17: 273–284, <http://dx.doi.org/10.1656/045.017.0210>
- United States Department of Agriculture, Natural Resources Conservation Service [USDA NRCS] (2015) Web Soil Survey, <http://www.nrcs.usda.gov/wps/portal/nrcs/main/soils/survey/> (accessed June 2015)
- United States Forest Service [USFS] (2014) Forest Inventory and Analysis, <http://www.nrs.fs.fed.us/fia/data-tools/state-reports/glossary/default.asp> (accessed June 2014)
- Van Clef M, Stiles E (2001) Seed longevity in three pairs of native and non-native congeners: assessing invasive potential. *Northeastern Naturalist* 8: 301–311, <http://dx.doi.org/10.2307/3858486>
- Vidra RL, Shear TH, Stucky JM (2007) Effects of vegetation removal on native understory recovery in an exotic-rich urban forest. *The Journal of the Torrey Botanical Society* 134: 410–419, [http://dx.doi.org/10.3159/1095-5674\(2007\)134\[410:EOVRON\]2.0.CO;2](http://dx.doi.org/10.3159/1095-5674(2007)134[410:EOVRON]2.0.CO;2)
- Vidra RL, Shear TH (2008) Thinking locally for urban forest restoration: a simple method links exotic species invasion to local landscape structure. *Restoration Ecology* 16: 217–220, <http://dx.doi.org/10.1111/j.1526-100X.2008.00387.x>
- Vilà M, Espinar J, Hejda M, Hulme P, Jarosik P, Maron J, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14: 702–708, <http://dx.doi.org/10.1111/j.1461-0248.2011.01628.x>
- Wofford EB (1989) Guide to the Vascular Plants of the Blue Ridge. Athens, GA: University of Georgia Press, 400 pp
- Wolkovich EM, Cleland EE (2010) The phenology of plant invasions: a community ecology perspective. *Frontiers in Ecology and the Environment* 9: 287–294, <http://dx.doi.org/10.1890/100033>
- Wundrow E, Carillo J, Gabler C, Horn K, Siemann E (2012) Facilitation and competition among invasive plants: a field experiment with alligatorweed and water hyacinth. *PLoS ONE* 7: e48444, <http://dx.doi.org/10.1371/journal.pone.0048444>
- Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* 16: 454–459, [http://dx.doi.org/10.1016/S0169-5347\(01\)02194-2](http://dx.doi.org/10.1016/S0169-5347(01)02194-2)

Supplementary material

The following supplementary material is available for this article:

Appendix 1. Mean cover of all native and non-native species, by treatment and site, from 2008–2013.

This material is available as part of online article from:

http://www.reabic.net/journals/mbi/2016/Supplements/MBI_2016_Farmer_etal_Appendix1.xls