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Independent Effects of Invasive Shrubs and Deer Herbivory on Plant Community Dynamics

Jeffrey S. Ward *, Scott C. Williams and Megan A. Linske

Department of Forestry and Horticulture, The Connecticut Agricultural Experiment Station, New Haven, CT 06511, USA; scott.williams@ct.gov (S.C.W.); megan.linske@ct.gov (M.A.L.)
* Correspondence: jeffrey.ward@ct.gov; Tel.: +1-203-974-8495

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Abstract: Both invasive species and deer herbivory are recognized as locally important drivers of plant community dynamics. However, few studies have examined whether their effects are synergistic, additive, or antagonistic. At three study areas in southern New England, we examined the interaction of white-tailed deer (*Odocoileus virginianus* Zimmermann) herbivory and three levels of invasive shrub control over seven growing seasons on the dynamics of nine herbaceous and shrub guilds. Although evidence of synergistic interactions was minimal, the separate effects of invasive shrub control and deer herbivory on plant community composition and dynamics were profound. Plant communities remained relatively unchanged where invasive shrubs were not treated, regardless if deer herbivory was excluded or not. With increasing intensity of invasive shrub control, native shrubs and forbs became more dominant where deer herbivory was excluded, and native graminoids became progressively more dominant where deer herbivory remained severe. While deer exclusion and intensive invasive shrub control increased native shrubs and forbs, it also increased invasive vines. Restoring native plant communities in areas with both established invasive shrub thickets and severe deer browsing will require an integrated management plan to eliminate recalcitrant invasive shrubs, reduce deer browsing intensity, and quickly treat other opportunistic invasive species.

Keywords: *Berberis*; non-native shrubs; keystone herbivore; *Odocoileus*; white-tailed deer

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1. Introduction

Many plant communities are currently under unprecedented stress from not only a changing climate, but also from the abrupt (in geological time-scales), nearly simultaneous landscape-scale changes in disturbance regimes [1], functional extirpation of major species following the introduction of non-native insects and diseases [2], wide-spread establishment of invasive plants [3], and severe herbivory by historically high deer densities [4,5]. Excessive deer herbivory and invasive plants are particularly problematic stressors of deciduous forests in eastern North America. Therefore, we examined their relative importance as drivers of plant community composition and dynamics to assist natural resources managers when deciding how to allocate limited resources available for active management. Throughout this paper, deer will refer to white-tailed deer (*Odocoileus virginianus* Zimmermann) and invasives will refer to non-native plants that have naturalized and disrupted native plant communities or ecosystem processes.

Deer have long been recognized as keystone herbivores [4] with multi-decadal legacy effects across trophic levels [5]. Many native forbs are lost at densities greater than 8 deer/km^2 [6,7]. While several studies reported deer herbivory did not affect total herbaceous cover [8–11], these studies did not separately examine cover of forbs, graminoids, and ferns. As deer density and resulting herbivory intensity increases, the relative dominance of graminoids and ferns also increases [12–14] while decreasing the relative dominance of forbs [15,16]. Deer herbivory can accelerate the proliferation of invasive species, especially in conjunction with canopy disturbances that increase light to understory plants [17]. Non-native species can benefit in areas of high deer abundances because of increased available growing space [18], seed transport [19], and unpalatability of some invasive species [20]. While unpalatable invasive species flourish where there is heavy deer browse [17], especially invasive grasses [10,14], growth of palatable invasive species can be severely depressed by herbivory [21,22].

Whether a specific invasive species is a passenger in a degraded system where it exploits underutilized growing space or whether it is an active driver that alters plant community composition depends on the species, the native plant community, and the disturbance regime [23]. Where the invasive species is a driver of plant community change, it can disrupt native species via several mechanisms including superior competitive ability (review in [24]), pollinator disruption [25], allelopathy [26], and altered patterns of herbivory or seed predation [27]. While invasive shrubs have been linked to depauperate native herbaceous and shrub strata [28–31], mixed results have been reported following removal of invasive shrubs including: increased native herbaceous cover [32,33], no change in herbaceous cover [34,35], and increased growth and fecundity of planted native annuals [36,37] and perennials [38]. Because a predominant invasive shrub often co-occurs with other non-native species, control of a particular invasive shrub species can have the undesired result of release and subsequent proliferation of other invasive species [37], especially in areas with high deer density [35].

In contrast to the extensive literature on the separate effects of deer herbivory and invasive species on plant communities noted above, few studies have examined their interactive effects, if any, especially for invasive shrubs. These reports differ on the relative importance of these stressors on native plants and whether their effects were synergistic. Where Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder) was controlled, planted jewelweed (*Impatiens capensis* Meerb) was larger and produced more fruits when protected from herbivory [37]. In contrast, growth, survival, and fecundity of several native herbaceous species did not differ between sites with and without a complex of invasive species (shrub/forb/graminoid), but growth of taller plants was negatively impacted by deer herbivory [39]. Exclusion of deer herbivory, but not removal of Japanese honeysuckle (*Lonicera japonica* Thunb.), affected growth of trillium (*Trillium* spp.) [40]. In a study that examined the response of different native guilds (growth forms), Amur honeysuckle removal and deer exclusion increased abundance of annuals and spring perennials [41]. They also reported that deer exclusion increased the abundance of all guilds except summer perennials. Interestingly, the study concluded that the deer/invasive interaction effect was only significant for spring perennials where deer herbivory did not allow recovery following removal of the invasive shrub. These short-term studies indicate the influence of deer browse/invasive shrub interaction vary depending on which native species was examined in the study.

As noted above, few studies have examined whether the effects of invasive shrubs and deer herbivory on plant communities are synergistic, additive, or antagonistic; and those studies were limited to two years [37,39–41]. Our general hypothesis was that the cover dynamics of some plant guilds (defined below) would not be independent of deer herbivory and levels of invasive shrub control. We investigated the effects of differing combinations of deer herbivory and invasive shrub control to address several questions: (1) What are the individual effects of two stressors (deer herbivory, invasive shrubs) on distinct guilds—vegetation layers or growth forms including graminoids, forbs, shrubs, and vines? (2) For each guild, are the effects of these two stressors additive, synergistic, or antagonistic? (3) What are the short-term (seven growing seasons) net effects of these two stressors on plant community structure and dynamics? (4) How do these findings help natural resource managers decide which, if any, actions to implement?

2. Materials and Methods

2.1. Study Areas

Three study areas were established in geographically separate locations across Connecticut in January 2007: a South Central Connecticut Regional Water Authority property in the town of North Branford (Tommy's Path 41°22′10″ N, 72°46′19″ W); one in western Connecticut on the Centennial Watershed State Forest that is jointly managed by the Aquarion Water Company, The Nature Conservancy, and the Connecticut Department of Energy and Environmental Protection-Forestry Division in the town of Redding (Egypt 41°17′02″ N, 73°22′01″ W); and a site in northeastern Connecticut on the University of Connecticut Forest in Storrs (Storrs 41°49′24″ N, 72°15′07″ W). Forest management was negligible, except at Tommy's Path where ~70% of the upper canopy was removed during a salvage harvest of eastern hemlock (*Tsuga canadensis* L. (Carrière)) in the early 1990s. The remaining upper canopy of Tommy's Path was primarily sugar maple (*Acer saccharum* Marsh.) with mixed oak (*Quercus* spp.), white ash (*Fraxinus americana* L.), American beech (*Fagus grandifolia* Ehrh.), and scattered yellow-poplar (*Liriodendron tulipifera* L.). Upper canopies at Storrs and Egypt were characterized by a predominance of white ash, red maple (*Acer rubrum* L.), mixed oak, yellow-poplar, and some black cherry (*Prunus serotina* Ehrh.). The understories of study areas were dominated by medium to dense infestations of non-native woody species including Japanese barberry (*Berberis thunbergii* DC), multiflora rose (*Rosa multiflora* Thunb.), Oriental bittersweet (*Celastrus orbiculatus* Thunb.), winged euonymus (*Euonymus alatus* (Thunb.), Siebold), and wine raspberry (*Rubus phoenicolasius* Maxim.). Native woody understory species included Allegheny blackberry (*Rubus allegheniensis* Porter), northern spicebush (*Lindera benzoin* L.), and American witchhazel (*Hamamelis virginiana* L.).

2.2. Experimental Design and Treatments

This research originated as part of a project investigating the effectiveness of different techniques to control Japanese barberry [42]. At each of the study areas, three 30 m × 30 m plots were established where all non-native woody species were treated either three times, I_3, initial mechanical cutting in March followed by directed flame treatments of any new ramets (sprouts) of only non-native species with propane torches in July and again in October (intensive control); once, I_1, single mechanical cutting in March (partial control); or were not treated, I_0 (details below). Treatments were randomly assigned within study areas and were conducted during the first year only.

The initial mechanical cutting was accomplished using a hydraulically driven, rotary wood shredder mounted to a tracked compact loader. As with any economically feasible control treatment in areas with dense invasive shrubs, many smaller (diameter < 10 cm) native seedlings and saplings were also cut during this step. Brush saws then were used to cut stems of non-native species missed by the rotary wood shredder such as stems adjacent to trees, stone walls, or large rocks. Mechanical treatments were completed before leafout in April 2007. Rootstocks of nearly all invasives produced new ramets several weeks into the growing season. Herbicide was not used to eradicate invasive shrubs because its use was prohibited on one study area over concerns of possible drinking water contamination. Instead, new ramets of invasive shrubs were heat treated in July 2007 using directed flame from a 100,000 BTU backpack propane torch on intensive treatment (I_3) subplots. Any rootstocks of non-native species that developed new ramets after the first flame treatment were treated with directed flame for a second time in early October 2007.

After completing the mechanical mowing treatment, half of each treatment area was protected from deer herbivory with a fence (F-fenced exclosure) and half was left exposed to deer herbivory (U-unprotected). This provided the opportunity to examine the separate and interactive effects of invasive species control and deer herbivory on the composition of ground and shrub layers. Each subplot designated to be protected from herbivory was surrounded by a 2.3 m-tall polyethylene fence. Fences were attached to pressure-treated wooden posts at corners with steel supports between posts. Fences were staked to the ground and affixed to PVC (polyvinyl chloride)-coated aluminum strand wire between the top of all posts. Fences were periodically checked for damage and repaired as needed. Thus, there were six treatment combinations I_3F, I_3U, I_1F, I_1U, I_0F, and I_0U. It should be noted that the last treatment combination (I_0U) was the control; i.e., invasive shrubs were not treated and deer herbivory was not excluded.

2.3. Vegetation Sampling

Pretreatment estimates of invasive shrub cover in study areas were completed using one-hundred 0.25 m^2 sample points per plot in a 10 × 10 grid at 5 m spacing. This sampling technique was also used to examine changes in cover of invasive species in immediately adjacent forests with dense and minimal invasive infestations to examine recruitment of invasive shrubs in areas with minimal infestations. Sample points were spaced at larger 10 m intervals as sampling was part of a study examining the relationship between invasive shrubs and the density of blacklegged ticks (*Ixodes scapularis* Say).

To intensively monitor the impact of invasive shrub control and deer herbivory at the individual species level, two rows of five vegetation sampling points were established in May 2007 within each of the six treatment subplots at each of the three study areas. Sampling points (n = 180) were spaced at 5-m intervals, were 5 m from subplot edges, and permanently demarcated with plastic pipes. Cover of all herbaceous species, vines, and woody shrubs was estimated within a 4 m^2 circular plot centered on permanent points. Each 4 m^2 circular plot was divided into four 1 m^2 quadrants. Within each quadrant, cover of individual species was estimated to be 0% (not present), <2%, 10%, 25%, 50%, 75%, or 100%. Quadrant values for individual species were averaged to obtain the sample point estimate. Data from the five sample points within each row were pooled to avoid potential pseudo-replication (i.e., there were two replicates per treatment combination per study site). Measurements were repeated in the late summer in 2008, 2009, 2010, 2012, and 2013 to cover the first seven growing seasons after initial treatments. Measurements were not completed in 2011 because of a lack of funding.

2.4. Deer Density

Tommy's Path and Egypt were included in aerial snow counts of deer in 2004 and 2008, respectively. At each location, a total count of all animals was completed with the double observer method [43,44] using a helicopter with a pilot and two experienced observers. Observers maintained a 100-m search distance on either side of the aircraft throughout the survey while the pilot maintained an approximate altitude of 60 m and air speed of 40 km/h. Based on previous experience [43], we assumed two experienced observers had an 80% detection function, but adjusted values in areas that were difficult to visually penetrate because of dense evergreen cover.

2.5. Statistical Analyses

We identified 107 genera during the study. Because species differed among study areas and to simplify analysis, species were assigned guilds based on life forms and life histories [41,45,46]. Herbaceous species were assigned to one of five guilds: annuals/biennials, short perennial forbs (<20 cm tall), tall perennial forbs (>20 cm tall), ferns, and graminoids. The graminoids guild included all grasses, sedges, and rushes. Four additional guilds were recognized: invasive and native woody shrubs, and native and invasive woody vines.

To examine the effects of invasive control and deer exclusion, repeated measures analysis of variance of cover (SYSTAT 13, San Jose, CA, USA) was used for each guild with years (growing seasons) since initial treatment as the within subjects factor; and study area, invasive control treatment (I_0, I_1, I_3), deer exclusion (F, U), and invasive-by-deer interactions as between subject factors. Reported P-values are those after applying the conservative Greenhouse-Geisser Epsilon correction for deviations from compound symmetry (i.e., non-sphericity) [47]. All cover values were arcsine transformed prior to analysis to normalize the distribution [48]. To determine if the cover of a given guild differed among treatments after seven growing seasons, a three-factor ANOVA (study area, deer exclusion, invasive control) was used. When appropriate, Tukey's HSD (honest significant difference) test was used to test for differences of guild cover values among invasive shrub control treatments or invasive shrub-by-deer exclusion interactions.

3. Results

3.1. Pre-Treatment Invasive Cover

Pre-treatment invasive shrub cover (58% ± 5%) did not differ between study areas ($F_{2,6} = 3.24$, $p = 0.11$) or between areas that received different invasive control treatments ($F_{1,6} = 0.01$, $p = 0.93$). Japanese barberry accounted for 83% of invasive shrub cover prior to treatments. Other invasive woody species observed within the study areas included shrubs (multiflora rose and wine raspberry) and vines (Japanese honeysuckle and Oriental bittersweet). A full list of species within each guild can be found in Appendix A.

3.2. Deer Density

Results from the 2004 aerial survey that included Tommy's Path estimated a mean density of 16 deer/km^2. The 2008 aerial survey of the area including Egypt estimated a mean density of 12 deer/km^2. Deer density in the immediate vicinity of research plots at Egypt was likely equal to that of Tommy's Path due to proximity to residences that function as a quasi-refuge from hunting. As the result of a survey of ecological damage, pellet presence, and visual sightings in comparison to the other study areas, we estimated the Storrs deer density to be lower than Egypt; approximately 10 deer/km^2. This density was consistent with the Connecticut Department of Energy and Environmental Protection estimate for this deer management zone [49].

3.3. Changes in Cover over Time

It is notable that the cover values of all guilds, both woody and herbaceous, were remarkably stable where conditions remained unchanged over the seven growing seasons of the study (i.e., where deer were not excluded and where invasive shrubs were not controlled) (Figures 1 and 2). Similarly, excluding deer from areas with untreated invasive shrubs also had a minimal effect on changes of cover for all guilds (Figures 1 and 2). Invasive shrub cover did not change in the immediately adjacent forests with either dense or minimal invasive infestations (Figure 3). Cover values of woody (Figure 1) and herbaceous guilds (Figure 2) over the seven growth seasons were not independent of either invasive control, herbivory exclusion, or both (Table 1). However, invasive × exclosure and invasive × exclosure-by-year interactions were not significant for all guilds (p-values 0.081–0.998), except for the tall perennial forb invasive × exclosure interaction ($p = 0.015$).

Table 1. Repeated measures analysis of variance of invasive control treatments and deer herbivory exclusion using an exclosure on guild cover changes during seven growing seasons after initial treatments. p-values are shown below.

Guild	Between Subjects		Within Subjects (Factor-by-Year)	
	Invasive	Exclosure	Invasive	Exclosure
Invasive shrub	<0.001 ***	0.247	0.007 **	0.305
Native shrub	0.004 **	<0.001 ***	0.009 **	0.018 *
Invasive vine	0.672	0.011 *	0.046 *	0.026 *
Native vine	0.098	0.009 **	0.001 ***	0.255
Graminoid	<0.001 ***	0.012 *	0.257	<0.001 ***
Tall perennial forb	0.017 *	0.150	0.069	0.621
Short perennial forb	<0.001 ***	0.216	0.038 *	0.111
Annual/biennial	0.010 **	0.443	0.205	<0.001 ***

* Different at $p \leq 0.05$; ** different at $p \leq 0.01$; *** different at $p \leq 0.001$.

Guild cover values were dynamic during the seven growing seasons after invasive species control (invasive shrubs, native vines, short perennial forbs), deer exclusion (graminoids, annual/biennials), or both (native shrubs, invasive vines). Cover of woody guilds other than invasive shrubs increased dramatically over seven growing seasons where deer were excluded and where invasive shrubs were intensively controlled (Figure 1); cover increases were more modest where invasive shrubs were only mowed and outside of exclosures where deer herbivory was not limited.

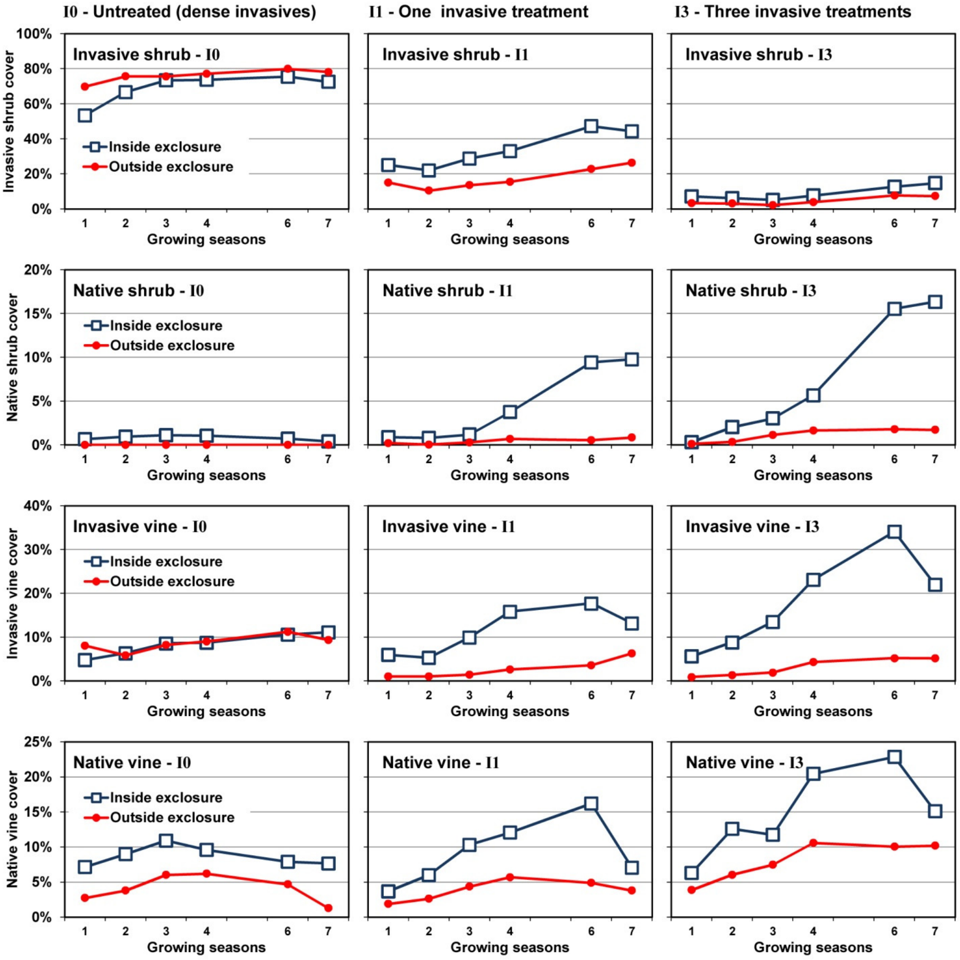

Figure 1. Changes in cover (least square means) of woody guilds over seven growing seasons (years) after initial treatment by deer herbivory exclusion and invasive shrub control method. Standard error estimates for seventh year shown in Table 2. I0—invasives not controlled, I1—invasives mowed, I3—invasives mowed and then treated twice with directed flame from propane torches.

The cover of all herbaceous species was increased by invasive shrub control (Figure 2). The increase in graminoid cover was both higher and more persistent outside the exclosures. In contrast, cover of tall perennial forbs and annual/biennials was usually higher inside the exclosure where deer herbivory was excluded. It is also worth noting the forb cover peaked 1–2 years (annual/biennials) or 3–5 years after invasive shrub control (perennial forbs).

After seven growing seasons, invasive shrub cover differed among invasive control treatments ($F_{2,18} = 66.49$, $p < 0.001$) with cover remaining high where untreated, recovering where only mowed, and still low in areas that had been mowed and then treated twice with propane torches (Table 2, Figure 1). Cover of native shrubs ($F_{2,18} = 3.92$, $p = 0.039$) and invasive vines ($F_{2,18} = 4.28$, $p = 0.030$) after seven growing seasons differed by the interaction of invasive × exclosure treatments. Their cover was negligible outside of exclosures, but increased rapidly inside exclosures where invasive shrubs were controlled. Native vine cover differed by invasive control treatment ($F_{2,18}$ = 19.35, p < 0.001) and exclosures ($F_{1,18}$ = 21.06, p < 0.001), but not their interaction ($F_{2,18}$ = 1.89, p = 0.180).

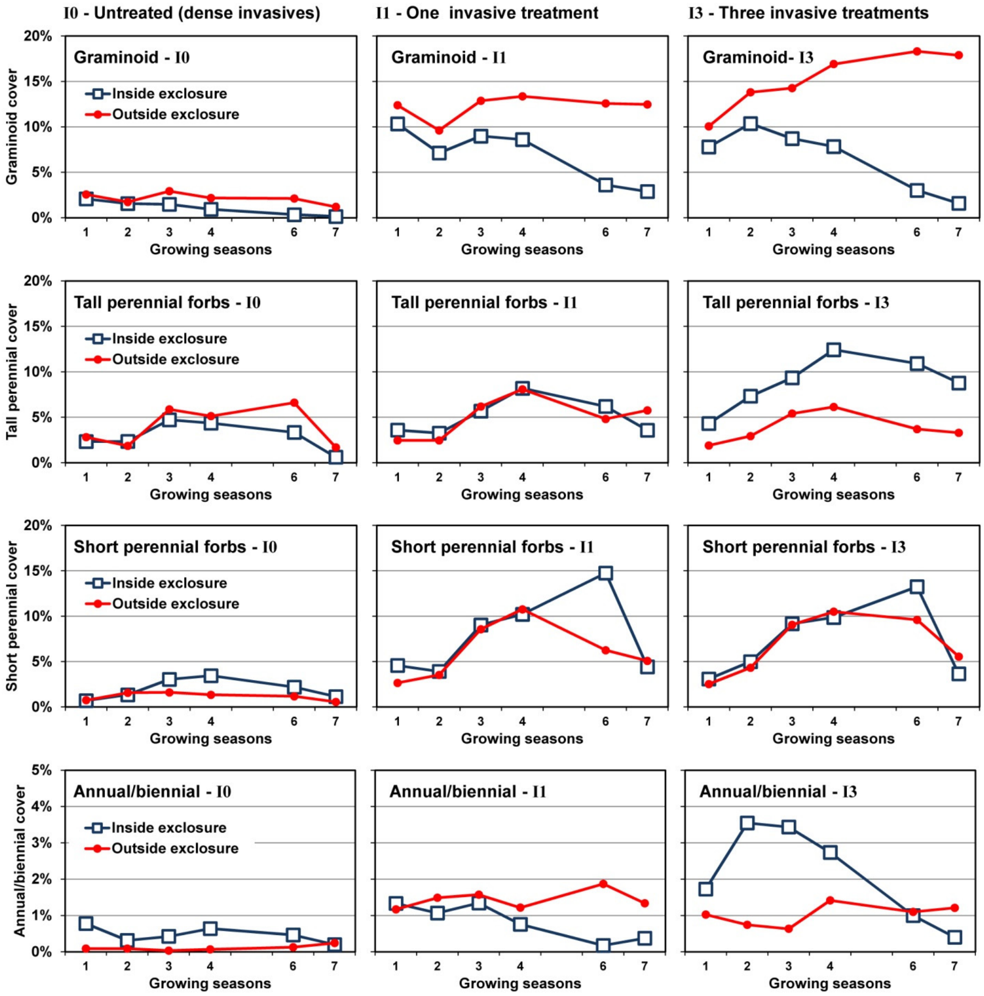

Figure 2. Changes in cover (least square means) of herbaceous guilds over seven growing seasons (years) after initial treatment by deer herbivory exclusion and invasive shrub control method. Standard error estimates for seventh year shown in Table 2. I0—invasives not controlled, I1—invasives mowed, I3—invasives mowed and then treated twice with directed flame from propane torches.

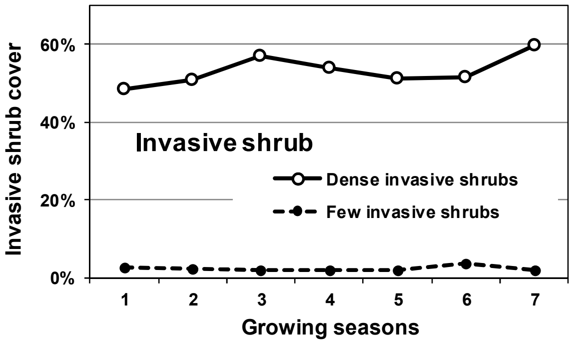

Figure 3. Changes in cover (least square means) over time of invasive shrubs in immediately adjacent forests with dense and minimal invasive shrubs.

Table 2. Means (±SE) vegetation cover (%) by guild seven growing season seasons after invasive control treatments in southern New England.

	Invasive Control Treatments					
	I0-Dense		**I1-Partial**		**I3-Controlled**	
Invasive shrub	75.4 (9.6)	a *	35.1 (6.4)	b	10.7 (7.5)	c
Native shrub	0.1 (0.4)	b	4.1 (4.6)	a	7.3 (4.4)	a
Invasive vine	10.3 (4.4)	a	9.5 (4.6)	a	12.3 (8.5)	a
Native vine	3.8 (2.5)	b	5.3 (2.4)	b	12.5 (2.1)	a
Graminoid	0.5 (0.3)	b	6.9 (4.4)	a	7.7 (3.6)	a
Tall perennial forb	1.1 (1.0)	b	4.6 (1.5)	a	5.7 (1.4)	a
Short perennial forb	0.8 (0.4)	b	4.8 (1.3)	a	4.6 (1.8)	a
Annual/biennial	0.2 (0.2)	a	0.8 (0.4)	a	0.8 (0.6)	a
Fern	1.9 (1.4)	a	0.5 (0.9)	a	1.6 (3.2)	a

* Values within a row followed by the same letter were not significant at $p = 0.05$ using Tukey HSD test.

Cover of graminoids and perennial forbs after seven growing seasons were higher where invasive shrubs had been treated (Table 2, Figure 2). Cover of tall perennials was increased by invasive shrub control ($F_{2,18} = 14.27$, $p < 0.001$), especially inside exclosures. Both inside and outside of deer exclosures, partial and intensive control of invasive shrubs resulted in at least a three-fold increase of short perennial forb cover ($F_{2,18} = 35.45$, $p < 0.001$). While annuals/biennial cover initially increased after invasive shrub treatments inside the exclosures, the decline several years later, likely a response to shading by taller perennials and shrubs, resulted in no difference among treatments after seven growing seasons ($F_{2,18} = 1.83$, $p = 0.189$). Fern cover did not differ among invasive control treatments or by herbivory exclusion (not shown).

Where invasive shrubs were treated, graminoid cover averaged 15% seven growing seasons after treatment compared with 2% inside exclosures (Figure 2). Excluding deer herbivory using exclosures did cause long-term increases in cover of herbaceous guilds. Indeed, graminoid cover was notably higher outside the exclosures provided that the invasive shrubs had been at least mowed. ($F_{1,18} = 48.91$, $p < 0.001$). Inside the exclosures, graminoid cover quickly increased following invasive shrub control, but then rapidly declined as it was shaded out by taller perennials and shrubs.

3.4. Plant Community Composition

Seven growing seasons after initial treatments and erection of exclosures to exclude deer herbivory, total vegetation cover did not differ among invasive control treatments ($F_{2,28} = 0.65$, $p = 0.530$) nor by herbivory levels ($F_{3,28} = 2.16$, $p = 0.115$). However, there was a marked difference in the plant community composition among the treatment combinations. While it was expected that total invasive woody cover (shrubs and vines) would differ among levels of invasive shrub treatments and be higher where invasive shrubs were not treated ($F_{2,28} = 19.53$, $p < 0.001$), an unanticipated observation was that total invasive woody cover was slightly higher ($F_{3,28} = 3.12$, $p = 0.042$) inside than outside exclosures, especially where invasive shrubs were treated (Figure 4).

Total native woody cover (shrubs and vines) differed by both invasive shrub control ($F_{2,28} = 4.63$, $p = 0.018$) and herbivory exclusion ($F_{3,28} = 4.65$, $p = 0.009$). However, native woody cover was only higher where both invasive shrubs had been controlled and within exclosures (Figure 4). Just treating invasive shrubs or just excluding herbivory did not increase native woody cover. In contrast, invasive shrub control by itself was sufficient to increase herbaceous cover seven growing seasons after initial treatments (Figure 5). However, composition of the herbaceous layer differed greatly between inside and outside exclosures. Perennial forbs predominated inside and a graminoid/fern complex predominated outside exclosures.

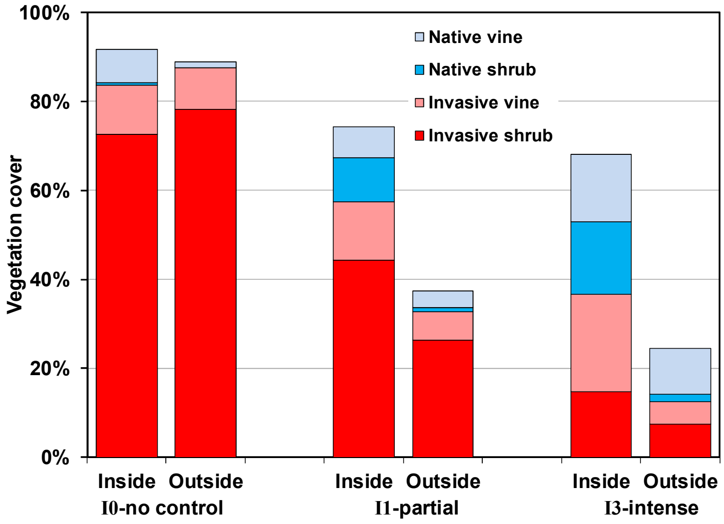

Figure 4. Distribution of observed cover (%) among woody species guilds seven growing seasons after initial treatment by invasive control (I0—invasives not controlled, I1—invasives mowed, I3—invasives mowed and then treated twice with directed flame from propane torches) and herbivory exclusion (inside or outside exclosures) treatments.

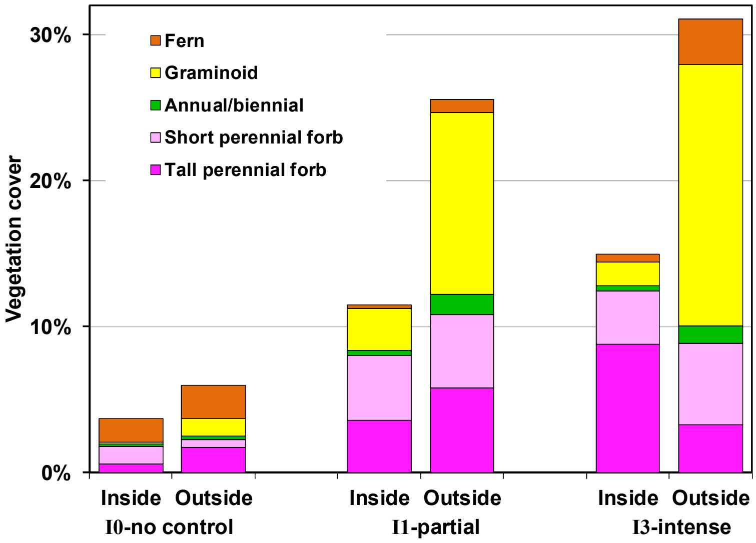

Figure 5. Distribution of observed cover (%) among herbaceous species guilds seven growing seasons after initial treatment by invasive control (I0—invasives not controlled, I1—invasives mowed, I3—invasives mowed and then treated twice with directed flame from propane torches) and herbivory exclusion (inside or outside exclosures) treatments.

4. Discussion

Novel plant communities with admixtures of persistent native species and species introduced from disjunct geographical regions comprise an ever-increasing proportion of the landscape that often result in changes to ecosystem structures and functions [50–52], especially when coupled with historically high deer densities, anthropogenically-dominated disturbance regimes, and a changing climate. Our study found that plant community composition and dynamics were influenced by both deer herbivory and invasive shrubs. Excluding deer herbivory had a minimal effect on the cover of any guild where invasive shrubs were not treated. However, where invasive shrubs were treated, the presence or absence of deer herbivory had a profound influence on the composition and dynamics of the plant community for the subsequent seven years. These differences can initiate legacy effects that persist for decades [5].

4.1. Invasive Shrub Thickets

Minimal changes were observed in the areas where invasive shrubs were not controlled, whether or not deer were excluded (I_0F and I_0U), suggesting that well-established, invasive shrubs have formed relatively stable, alternative plant communities [53]. The legacy effect of chronic herbivory can result in plant communities dominated by recalcitrant invasive shrubs that will likely persist for decades, even if deer densities are reduced. Similarly, established native shrubs were found to be highly resistant to herbaceous plant and tree seedling establishment [54]. Depressed native herbaceous species metrics have been associated with other invasive shrubs including Amur honeysuckle [30,38], Tatarian honeysuckle (*Lonicera tatarica* L.) [28], and Chinese privet (*Ligustrum sinense* Lour.) [33]. Light intercept by early season leaf expansion of invasive shrubs may be particularly detrimental for spring ephemerals and native annuals [36].

Treatments did not kill all invasive shrubs. Survival of Japanese barberry clumps, which as noted above accounted for 83% of invasive shrub cover, ranged from 65% to 88% for clumps that ranged in size from 90 cm to $\geq$180 cm, respectively, when only mowed [55]. The surviving invasive shrubs demonstrated a remarkable ability to recover from treatments that killed all aboveground tissues. Within two years of mowing, surviving barberry clumps were 80% of the size of untreated clumps and continued to grow throughout the four subsequent years. The full recovery of root carbohydrate reserves within one month of leafout for barberry [56] undoubtedly contributed to its ability to form vigorous new ramets after loss of aboveground tissues. The capacity of barberry to exhibit positive growth under very low light conditions [57,58], coupled with its phenology of leaves that expand before and senesce later than native species [59] also contributed to its rapid recovery after cessation of treatments that removed aboveground tissues.

The lack of a deer browse effect on invasive plant cover and dynamics in our study supports the Enemy Release Hypothesis (ERH) that when an exotic plant species becomes established in a native ecosystem, the introduced plant may experience a decrease in regulation from native herbivores and other generalist enemies, which can result in a rapid increase in their abundance and distribution as herbivory impacts continue to negatively affect native species [60]. Similarly, non-exclosure studies in forested landscapes have also linked higher deer populations to an increased proportion of invasives relative to natives [61,62]. While some studies have reported that non-native species become invasive because they are competitively superior to natives in acquiring limiting resources (review in [24]), our study suggests that toleration of chronic herbivory can sometimes be the major factor facilitating invasive species dominance, as implied by the enemy release hypothesis. Recovery of invasive shrubs cover following treatment was independent of deer herbivory exclusion (i.e., the increase in cover during the seven years following partial (I_1) or intense (I_3) control was similar inside and outside of exclosures). Therefore, it is not that invasive growth is higher in areas with high deer herbivory—indeed growth of invasives is often depressed relative to unbrowsed plants [22,42]—rather that invasive shrubs are the only taller, woody species that tolerated chronic herbivory and continued to grow in our study.

4.2. Deer Herbivory

Once the competitive interference of the invasive shrubs thickets was reduced, our study found that plant community composition and structure was directly influenced by whether or not they were subject to deer herbivory. Relative to areas protected from herbivory, areas outside exclosures had higher absolute graminoid cover and higher relative invasive shrub cover, but fewer native shrubs, vines, or forbs. These observations support the hypothesis that deer are a keystone species that regulate plant community composition and structure [4], and thereby indirectly influence invertebrate and vertebrate species that utilize specific habitats and food availability [7,63].

Our findings corroborate the view that deer herbivory is functionally a chronic disturbance agent, especially at high densities [64,65]. This chronic disturbance caused by severe herbivory would negatively impact native shrubs and herbaceous species with high palatability, but would benefit graminoids and ferns that had both low palatability and a growing point at or near ground level, and also benefit invasive species such as barberry that have low palatability because of high alkaloid concentrations [66].

4.2.1. Outside Exclosures

A distinct plant community was observed outside exclosures where invasive shrubs were controlled (I_1, I_3). Recovery of native shrubs remained severely depressed seven growing seasons after treatment. These areas were characterized by discrete clumps of invasive shrubs surrounded by a matrix of closely cropped, low-growing mat of graminoids, forbs, and especially vines. A Pennsylvania study attributed the minimal response of native shrubs and herbaceous plants after control of invasive bush honeysuckle to locally high deer densities [35]. With negligible interference from native shrubs and with herbivory precluding establishment of native woody vegetation [22], invasive shrubs may slowly increase and eventually dominate the site again; albeit much more slowly where invasive shrubs were intensively treated (I_3).

Outside the exclosures (U), graminoids exploited the available growing space where invasive shrubs were treated and deer herbivory severely suppressed growth of guilds with the potential to overtop and shade-out graminoids (e.g., native shrubs, tall perennial forbs). Graminoid cover was 10-fold greater outside the exclosures following partial invasive shrub control (I_1U) and accounted for nearly 60% of herbaceous cover on I_3U plots after seven growing seasons. The link between increasing relative dominance of graminoids with increasing herbivory is not unique to this study and has been reported in other studies using deer exclosures [14,16], deer enclosures [12], and landscape gradients of deer densities [13,65]. Disconcertingly, we also observed an aggressive invasive grass, Japanese stiltgrass (*Microstegium vimineum* (Trin.) A. Camus), appearing only outside of exclosures, as previously reported in Pennsylvania [10,18].

4.2.2. Inside Exclosures

Plant communities with a larger native shrub component were found where deer herbivory was excluded and invasive shrubs treated (I_1F and I_3F), especially where invasive shrubs were intensively treated (I_3F). However, it should be noted that native shrub cover remained below 25% and that *Rubus* species accounted for most of the native shrub cover. The minimal recovery of native shrubs within exclosures may be due, in part, to chronically high deer herbivory over several decades that stunted or killed native shrubs and likely precluded seed production necessary for new recruitment. Deer density at Tommy's Path was estimated at 17 deer-km^{-2} in 1991 [67], similar to current estimates (16 deer-km^{-2}) that still exceed levels (8 deer-km^{-2}) detrimental for many herbaceous species, excepting graminoids and ferns [6,7], and much higher than levels (5 deer/km^2) that suppress woody regeneration [6,68]. Estimated density at Egypt in 1991 was also similar to the 2008 estimate, 15 and 12 deer/km^2, respectively (S. Stamos, Aquarion Water Company, pers. comm. Redding, CT, USA), indicating a prolonged period of intense herbivory.

Vines accounted for fully 38% of vegetation cover seven growing seasons after intensive invasive shrub control treated in the absence of deer herbivory (I_3F). The doubling invasive vine cover and nearly 20-fold increase of native vine cover with this treatment combination relative to the control (i.e., I_0U, untreated invasives outside exclosures) was not anticipated. However, the literature does indicate that both invasive vines found in this study, Japanese honeysuckle and Oriental bittersweet, are preferred browse species [21,69,70]. This highlights that excluding all deer herbivory can have the deleterious, secondary effect of increasing growth of invasive vines. Further research could determine whether there is an intermediate level of herbivory that would simultaneously allow for development of native herbaceous species and limit growth of invasive vines.

Areas inside the exclosures where invasive shrubs were treated (I_1F, I_3F) were also notable for having the highest native perennial forb cover. The decrease of perennial forb cover in the last two years of the study was likely attributable to increasing competitive interference as woody shrubs became taller and smothering vines (invasive and native) increased in size. Similarly, growth and fecundity of planted native perennials protected from herbivory increased when Amur honeysuckle was removed [38]. In contrast, trillium growth was increased by herbivory exclusion, but not by control of Japanese honeysuckle, an invasive vine [40]. A study in the southern Appalachian Mountains observed that recovery of vegetation within exclosures was largely restricted to those species that were able to persist during a period of chronic, intense herbivory due to a deer population eruption [71]. The authors suggested that because of the legacy effects of chronic herbivory, active management may be needed to restore some native herbaceous species.

5. Conclusions

While we found minimal evidence of synergistic or antagonistic interactions between invasive shrub control treatments and deer herbivory on cover metrics (extent, dynamics) for individual guilds, their separate effects on individual guilds resulted in distinct plant community assemblages. These findings have several practicable implications for natural resource managers whose goal is the conversion of invasive shrub thickets to communities dominated by native species.

(1) Neither invasive shrub control nor deer exclusion by themselves will restore native plant communities; restoration will require both stressors to be addressed.

(2) Plant community composition remained largely stable for a seven year period where recalcitrant invasive shrubs were not treated, even where deer were excluded. As none of the guilds showed evidence of directional change over the course of the study without controlling invasive shrubs, we believe it is likely these communities will persist for at least another decade, if not longer.

(3) Both mowing (I_1) and intensive control (I_3) of well-established invasive shrub thickets will not lead to reestablishment of native shrubs if they are not already present or can be recruited from the seedbank, as was the case with *Rubus* in the current study.

(4) Recovery of both native shrubs and native forbs increases with intensity of invasive shrub control treatments provided plants are protected from deer herbivory. Without controlling deer herbivory, recovery of native graminoids, and probably ferns, will increase with intensity of invasive shrub control treatments.

(5) Because both invasive vines and an invasive grass also increased following invasive shrub control where deer herbivory was excluded, managers will need to plan for this possibility.

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Appendix A

Table A1. List of species found on study areas including the number of times each species was observed on a sample point (1080 total potential observations) and the mean (standard error) species cover when species was observed at least once during study. Species with a * were considered invasive. Some species with few occurrences were locally dense when observed (e.g., *Berberis vulgaris*).

Latin	Species	Occurrence	Cover
	Non-native species		
Shrub			
Berberis thunbergii DC.	Japanese barberry *	884	33.6% + 1.1%
Berberis vulgaris L.	Common barberry	4	30.9% + 8.8%
Rosa multiflora Thunb.	Multiflora rose *	434	17.6% + 1.2%
Rubus phoenicolasius Maxim.	Wine raspberry *	149	6.4% + 0.7%
Vine			
Celastrus orbiculatus Thunb.	Oriental bittersweet *	668	12.7% + 0.8%
Lonicera japonica Thunb.	Japanese honeysuckle *	251	21.7% + 1.3%
Graminoid			
Microstegium vimineum (Trin.) A. Camus	Japanese stilt grass *	15	10.9% + 3.8%
Tall perennial forb			
Coronilla varia L.	Crown vetch	2	t
Cynanchum louiseae Kartesz & Gandhi	Louise's (black) swallow-wort *	1	t
Solanum dulcamara L.	Climbing nightshade	1	t
Trifolium pratense L.	Red clover	1	t
Short perennial forb			
Allium canadense L.	Meadow garlic	1	2.0% + %
Commelina communis L.	Asiatic dayflower	1	t
Plantago major L.	Common plantain	4	2.8% + 1.4%
Prunella vulgaris L.	Common selfheal	1	3.0% + %
Taraxacum officinale F.H. Wigg	Common dandelion	40	1.1% + 0.2%
Veronica officinalis L.	Common speedwell	82	2.5% + 0.3%
Annual/biennial			
Alliaria petiolata (M. Bieb.) C&G	Garlic mustard *	40	3.4% + 0.7%
Polygonum caespitosum Blume, nom. inq.	Oriental lady's thumb	75	3.3% + 0.6%
Verbascum thapsus L.	Common mullein	17	1.9% + 0.5%
	Origin uncertain		
Tall perennial forb			
Mentha spp. L.	Unknown mint	23	2.6% + 1.3%
Short perennial forb			
Polygonum spp. L.	Smartweed	2	1.0% + 0.5%
Unknown	Unknown forb	3	5.3% + 0.3%
Annual/biennial			
Galium spp. L.	Bedstraw	279	3.8% + 0.3%
	Native species		
Shrub			
Rubus allegheniensis Porter	Allegheny blackberry	7	4.3% + 2.1%
Rubus spp. L.	Blackberry/raspberry	293	12.0% + 1.0%
Vine			
Mitchella repens L.	Partidgeberry	162	2.8% + 0.2%
Parthenocissus quinquefolia (L.) Planch.	Virginia creeper	719	6.1% + 0.3%
Potentilla spp. L.	Cinquefoil	122	4.4% + 0.6%
Rubus hispidus L.	Bristly dewberry	206	7.0% + 0.6%
Smilax rotundifolia L.	Common greenbrier	42	3.3% + 0.6%
Toxicodendron radicans (L.) Kuntze	Eastern poison ivy	452	3.3% + 0.3%
Vitis spp. L.	Grape	406	3.9% + 0.4%

Table A1. *Cont.*

Latin	**Species**	**Occurrence**	**Cover**
Native species			
Graminoid			
Cyperaceae	Unknown sedge	784	12.4% + 0.7%
Poaceae	Unknown grass	13	11.6% + 4.7%
Tall perennial forb			
Actaea pachypoda Elliott	White baneberry	74	1.9% + 0.2%
Ageratina altissima (L.) R.M. King & H. Rob.	White snakeroot	2	t
Amphicarpaea bracteata (L.) Fernald	Hogpeanut	136	4.0% + 0.4%
Arisaema triphyllum (L.) Schott	Jack-in-the-pulpit	407	3.7% + 0.2%
Asclepias syriaca L.	Common milkweed	5	2.1% + 1.1%
Boehmeria cylindrica (L.) Sw.	False nettle	4	1.5% + 0.6%
Circaea lutetiana L.	Enchanter's nightshade	164	6.0% + 0.6%
Desmodium paniculatum (L.) DC.	Panicledleaf ticktrefoil	3	2.3% + 1.3%
Eupatorium dubium Willd. ex Poir.	Eastern joe-pye weed	1	3.0% + %
Euphorbia corollata L.	Flowering spurge	1	t
Eurybia divericata (L.) G.L. Nesom.	White wood aster	297	4.9% + 0.3%
Eurybia spp. (Cass.) Cass.	Unknown aster	24	4.3% + 1.1%
Euthamia tenuifolia (Pursh) Nutt.	Slender fragrant goldenrod	7	2.5% + 0.7%
Galium asprellum Michx.	Rough bedstraw	1	t
Galium circaezans Michx.	White wild licorice	1	t
Galium lanceolatum Torr.	Lance-leaved wild licorice	56	2.5% + 0.4%
Geranium maculatum L.	Wild geranium	9	1.7% + 0.4%
Geum canadense Jacq.	White avens	11	1.4% + 0.3%
Geum virginianum L.	Rough avens	14	1.6% + 0.4%
Hypericum ascyron L.	Great St. Johnswort	1	11.8% + %
Lysimachia quadrifolia Sims	Whorled loosestrife	6	t
Maianthemum racemosum (L.) Link	False Solomon's seal	90	1.7% + 0.2%
Medeola virginiana L.	Indian cucumber root	11	1.7% + 0.3%
Penstemon digitalis Nutt. ex Sims	Talus slope penstemon	1	t
Phryma leptostachya L.	American lopseed	15	1.4% + 0.4%
Phytolacca americana L.	Pokeweed	32	3.2% + 0.7%
Polygonatum biflorum (Walter) Elliott	Great Solomon's seal	16	4.8% + 1.4%
Polygonatum pubescens (Willd.) Pursh	Hairy Solomon's seal	58	2.7% + 0.4%
Polygonum scandens L.	Climbing false buckwheat	1	t
Polygonum virginianum L.	Virginia jumpseed	1	t
Prenanthes altissima L.	Tall white lettuce	33	2.5% + 0.6%
Prenanthes trifoliolata (Cass.) Fernald	Gall-of-the-earth	14	1.8% + 0.8%
Ranunculus recurvatus Poir.	Hooked crowfoot	10	2.0% + 0.5%
Smilax herbacea L.	Smooth carrionflower	4	1.5% + 0.6%
Solidago caesia L.	Bluestem goldenrod	218	3.9% + 0.2%
Solidago hispida Muhl. ex Willd.	Hairy goldenrod	1	t
Solidago rugosa Mill.	Rough-stemmed goldenrod	135	3.5% + 0.4%
Solidago spp. L.	Goldenrod	110	3.3% + 0.4%
Symphyotrichum lateriflorum (L.) Löve & Löve	Calico aster	16	1.7% + 0.4%
Symplocarpus foetidus (L.) Salisb. ex Barton	Skunk cabbage	2	t
Urtica dioica L.	Stinging nettle	1	1.0% + %

Table A1. *Cont.*

Latin	Species	Occurrence	Cover
Native species			
Short perennial forb			
Allium canadense L.	Wild garlic	7	2.3% + 0.8%
Allium tricoccum Aiton	Ramp (wild leeks)	5	2.4% + 0.6%
Anemone quinquefolia L.	Wood anemone	15	4.3% + 0.9%
Chimaphila maculata (L.) Pursh	Spotted wintergreen	1	t
Hepatica nobilis Schreb.	Round-lobed hepatica	9	t
Maianthemum canadense Desf.	Canada mayflower	663	7.6% + 0.4%
Monotropa uniflora L.	Indian pipe	5	t
Oxalis stricta L.	Wood sorrel	176	2.2% + 0.2%
Pyrola americana Sweet	Round-leaved pyrola	1	3.0% + %
Pyrola elliptica Nutt.	Shinleaf	3	2.0%+ 0.8%
Sanguinaria canadensis L.	Bloodroot	19	2.3% + 0.6%
Trillium erectum L.	Red trillium	37	2.3% + 0.4%
Uvularia spp. L.	Bellwort	1	t
Uvularia perfoliata L.	Perfoliate bellwort	14	2.3% + 0.8%
Uvularia sessilifolia L.	Sessileleaf bellwort	163	1.9% + 0.2%
Viola spp. L.	Violet spp.	114	1.8% + 0.2%
Viola triloba Schwein	3 lobed violet	2	1.5% + 1.0%
Unknown forb	Unknown forb	14	1.1% + 0.3%
Annual/biennial			
Bidens frondosa L.	Devil's beggartick	4	t
Epifagus virginiana (L.) W.P.C. Barton	Beechdrops	7	2.0% + 0.4%
Galium aparine L.	Cleavers bedstraw	9	2.6% + 1.2%
Lobelia inflata L.	Indian tobacco	12	1.3% + 0.4%
Prenanthes alba L.	White lettuce	1	t
Pseudognaphalium helleri (Britton) Anderb.	Heller's cudweed	2	t
Sanicula spp. L.	Snakeroot	6	t
Fern			
Athyrium filix-femina (L.) Roth	Lady fern	7	2.0% + 0.8%
Dennstaedtia punctilobula (Michx.) T. Moore	Hayscented fern	54	16.9% + 3.1%
Polystichum acrostichoides (Michx.) Schott	Christmas fern	104	10.0% + 0.7%
Thelypteris noveboracensis (L.) Nieuwl.	New York fern	10	26.9% + 8.3%
Pteridophyta	Unknown fern	2	t

t – less than 1%

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