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Influence of invasive shrubs and deer browsing on regeneration in temperate deciduous forests

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ABSTRACT

While both chronic white-tailed deer overbrowsing and invasive shrubs have been linked to native regeneration failure in temperate hardwood forests, little is known of their relative importance and possible synergistic effects. Therefore, we established three study areas in Connecticut to examine the interaction of three levels of invasive shrub control and absence/presence of deer herbivory on forest regeneration over nine years. Five observations suggest obtaining forest regeneration requires a comprehensive management strategy. First, competitive interference by invasive shrubs in intact thickets continued to impede forest regeneration, especially taller seedlings, after deer were excluded. Second, density of small seedlings increased following removal of the competitive interference by invasive shrubs. Third, deer browsing depressed growth of small seedlings into taller height classes. Fourth, preferential browsing reduced species richness, especially in taller seedling classes, by favoring growth of low palatability species such as beech. Lastly, if a disturbance (e.g., cutting) does not kill the root system of the invasive shrubs, the window of forest regeneration recruitment may be narrow because invasive shrubs can quickly recover. In stands with both established shrub thickets and high deer densities, invasive shrub control and multi-year reduction of deer densities are both recommended to obtain adequate forest regeneration.

Keywords: *Berberis thunbergii*, exclosure, non-native, *Odocoileus virginianus*, *Quercus*

44

45 **INTRODUCTION**

46 Among the myriad of factors that can depress establishment and growth of forest regeneration
47 are chronic damage caused by white-tailed deer (*Odocoileus virginianus* Zimmermann)
48 herbivory and the relatively recent stressor of competitive interference from invasive species.
49 White-tailed deer damage has long been recognized as potentially having a negative impact on
50 density and growth of forest regeneration (Behrend et al. 1970). Densities greater than 5-8 deer-
51 km⁻² have been reported to be detrimental for development of adequate tree regeneration
52 (Behrend et al. 1970; Tilghman 1989; deCalesta and Stout 1997, Horsley et al. 2003). White-
53 tailed deer have been reported to cause severe browse damage in eastern (Healy 1997; Saunders
54 and Puettmann 1999b; Katovich et al. 2004) and western United States (Anthony, 1982). Browse
55 damage by other cervid species have been observed in Europe (Bergquist and Örlander 1998;
56 Perrin et al. 2006, Kuijper et al. 2010) and Asia (Nomiya et al. 2002). High deer density in
57 natural areas and parks where hunting is prohibited can preclude adequate regeneration unless
58 seedlings are protected (Shuler et al. 2005; Brose et al. 2008; Abrams and Johnson 2012) or deer
59 densities are reduced (Behrend et al. 1970; Jenkins et al. 2015).

60 Because deer are selective browsers, they can function as biological filters favoring growth of
61 species with lower palatability (Arcese et al. 2014). Regeneration failure attributed to deer
62 browse damage has been reported for a diversity of desirable species including oaks (*Quercus*
63 spp.) (Rodewald 2003; Miller et al. 2016), eastern white pine (*Pinus strobus* L.) (Ziegler 1995),
64 sugar maple (*Acer saccharum* Marshall) (Gorchov and Trisel 2003), eastern hemlock (*Tsuga*
65 *canadensis* (L.) Carrière) (Anderson and Loucks 1979), and arborvitae (*Thuja occidentalis* L.)
66 (Cornett et al. 2000). In areas with moderate browse pressure, species with lower palatability or

those better able to tolerate browsing, such as American beech (*Fagus americana* Ehrh.) or black birch (*Betula lenta* L.), can predominate the regeneration strata (Smith and Ashton 1993; Long et al. 2007; Nuttle et al. 2013). Non-exclosure studies in forested landscapes have also linked increased proportion of invasive to native plants to higher deer densities (Eschtruth and Battles 2009a; Rooney et al. 2009).

Few native trees and shrubs are able to develop where chronic high browse pressure exists, which often results in a depauperate understory (Lorimer 1993). An understory without native woody trees and shrubs (Boulanger et al. 2015) creates an ecological vacuum that can be exploited by invasive species with low palatability (Eschtruth and Battles 2009b; Kalisz et al. 2014). In eastern North America, several such non-native shrub species have exploited this void to form local dense forest understory thickets including: Amur honeysuckle (*Lonicera maackii* Rupr.), glossy buckthorn (*Frangula alnus* Mill.), privets (*Ligustrum* L.), multiflora rose (*Rosa multiflora* Thunb.), and Japanese barberry (*Berberis thunbergii* DC).

The recalcitrant understory thickets formed by these invasive shrubs can competitively exclude native shrubs and forest regeneration (Woods 1993; Gorchov and Trisel 2003; Hanula et al. 2009). Competition from a shade-tolerant understory is perhaps the principal bottleneck to successful regeneration of oak (Lorimer 1993) and other tree species (Saunders and Puettmann 1999a; Katovich et al. 2004). Invasive shrubs have been linked to depauperate native herbaceous and shrub strata (Woods 1993; Kourtev et al. 1998; Collier et al. 2002; Harrington et al. 2003; Ward et al. 2017). While seeds of most native species can germinate under invasive thickets, the thickets can severely depress seedling growth and survival by limiting available photosynthetically active radiation (Brand and Janas 1988; Gorchov and Trisel 2003). For instance, controlling glossy buckthorn increased regeneration densities (Frappier et al. 2004) and

growth of maple, oak, and white ash (*Fraxinus americana* L.) seedlings (Fagan and Peart 2004; Hamelin et al. 2016). Similarly, survival of six species of planted hardwood seedlings was higher where Amur honeysuckle had been nearly eradicated compared to an intact stand (Hartman and McCarthy 2004).

Herbivory/invasive interactions

In contrast to the rich literature on the separate effects of herbivory and invasive species on tree seedling establishment and growth, few studies have examined their interactive effects. These reports differ on the relative importance of these stressors on native plants and whether their effects were synergistic (Dávalos et al. 2014). Both deer browse and native shrubs reduced tree seedling growth and survival (Kern et al. 2012). Control of invasive Amur honeysuckle but not protection from deer browse increased survival of planted chinquapin oak (*Quercus muehlenbergii* Engelm.) and black cherry (*Prunus serotina* Ehrh.) seedlings (Hartman and McCarthy 2004). In contrast, cutting Amur honeysuckle increased growth of sugar maple seedlings protected from deer browse, but decreased growth of unprotected sugar maple and northern red oak (*Quercus rubra* L.) seedlings because it left them more exposed to deer browse (Gorchov and Trisel 2003). Similarly, decreased native shrub cover following control of the invasive shrub Morrow's honeysuckle (*Lonicera morrowii* A. Gray) was linked, in part, to increased exposure of native shrubs to deer browsing (Love and Anderson 2008). Vegetation taller than tree seedlings can offer some protection from browse damage (Saunders and Puettmann 1999).

Objectives

In an earlier paper, we examined the influence of two stressors, deer browse and invasive shrubs, on native forb and shrub population dynamics over a seven-year period and found that controlling both stressors is required for ecological restoration (Ward et al. 2017). The objective of the current research was to examine whether forest regeneration population dynamics over a nine-year period was independent of deer browse and invasive shrub interference. We hypothesized that: (1) chronic levels of high deer browsing act as a filter that excludes woody species with high palatability and favors unpalatable and invasive species and (2) where invasive shrubs have exploited this situation to form recalcitrant thickets, they function as bottlenecks to adequate forest regeneration via competitive interference (*sensu* Lorimer 1993). Therefore, we examined the separate and interactive effects of invasive shrubs and deer herbivory on forest regeneration to determine if their effects were synergistic, additive, or antagonistic. Hopefully, our results will help forest managers design treatment prescriptions to obtain adequate forest regeneration in areas beset with chronic deer herbivory and invasive shrub infestations.

METHODS

Study Areas

In January 2007, we established three study areas in western, central, and eastern Connecticut: Egypt in Redding on the Centennial Watershed State Forest (41°17'02" N, 73°22'01" W); Tommy's Path in North Branford on a South Central Connecticut Regional Water Authority property (41°22'10" N, 72°46'19" W); Storrs on the University of Connecticut Forest in Mansfield (41°49'24" N, 72°15'07"). All study areas had remnant stone walls indicating the

133 forests had developed in abandoned agricultural fields or pastures. Storrs and Tommy's Path
134 were abandoned in the early 1900s and Egypt in the 1940s.

135 Except at Tommy's Path where ~70% of the upper canopy was removed during a salvage harvest
136 of eastern hemlock in the early 1990s, forest management has been negligible (small fuelwood
137 harvests of declining and subcanopy trees). Upper canopies at Storrs and Egypt were primarily
138 white ash, red maple (*Acer rubrum* L.), mixed oak, yellow-poplar (*Liriodendron tulipifera* L.),
139 and some black cherry. The remaining upper canopy of Tommy's Path was sugar maple with
140 mixed oak, American beech, and scattered yellow-poplar.

141 Medium to dense infestations of non-native woody species dominated the study site understories.
142 Species included Japanese barberry, multiflora rose, Oriental bittersweet (*Celastrus orbiculatus*
143 Thunb.), burningbush (*Euonymus alatus* (Thunb.), Siebold), and wine raspberry (*Rubus*
144 *phoenicolasius* Maxim.). The few native shrubs were primarily northern spicebush (*Lindera*
145 *benzoin* L.) and American witchhazel (*Hamamelis virginiana* L.). Estimated deer densities were
146 10 deer/km² at Storrs, 12 deer/km² at Egypt, and 16 deer/km² at Tommy's Path (Ward et al.
147 2017).

148 **Design and Treatments**

149 This research originated as part of a project investigating the effectiveness of different
150 management techniques to control Japanese barberry (Ward et al. 2013). At each of the study
151 areas, three 30 x 30 m plots were established where all non-native woody species were not
152 treated (I_0 , dense invasive shrubs), treated once (I_1 , single mechanical cutting in March) (partial
153 control), or were treated three times (I_3 , initial mechanical cutting in March followed by directed
154 heating of survivors with propane torches in July and again in October) (intensive control)
155 (details below). Half of each treatment area was protected from deer herbivory with a 2.3 m-tall

fence (F-fenced exclosure) or was left unprotected (U-unprotected) (details below). This resulted in six treatment combinations I₃F, I₃U, I₁F, I₁U, I₀F, and I₀U. Treatments were randomly assigned.

The initial mechanical cutting was accomplished using a hydraulically driven, rotary wood shredder (Model# BH74FM, Bull Hog®, Fecon Inc., Lebanon, OH, USA) mounted to a tracked compact loader (Model# T300, Bobcat®, West Fargo, ND, USA). Brush saws (Model# FS450, Stihl®, Virginia Beach, VA, USA) were used to cut stems of non-native species missed by the rotary wood shredder (e.g., adjacent to trees, stone walls, or large rocks). Treatments were completed before leafout in April 2007.

After completing the mechanical cutting treatments, we installed a 2.3 m-tall polypropylene fence (Cintoflex® Type C, Tenax Corporation, Baltimore, MD, USA) surrounding each subplot designated to be protected from herbivory. Fences were fixed with pressure-treated wooden posts at corners with steel supporting posts between wooden posts. PVC-coated aluminum strand wire was affixed to the top of all posts and used to brace corner posts. Fencing was stretched between posts, attached to strand wires with hog rings, and staked to the ground. Access into exclosures was via a reinforced screen door. Vegetation was removed along fence-lines in untreated areas to allow fencing to reach the ground. Fences were periodically checked for damage and repaired as needed.

After initial cutting, the rootstocks of nearly all invasives produced new ramets (sprouts) several weeks into the growing season. Two of the study areas were on watersheds of water supply reservoirs. Public concerns of possible drinking water contamination on one watershed precluded use of herbicides to eradicate invasive species. Therefore, new ramets were heat treated in July 2007 using directed flame from a 100,000 BTU backpack propane torch (Model# BP 223 C

179 Weed Dragon, Flame Engineering, Inc., LaCrosse, KS, USA) on intensive treatment subplots.
180 Flame treatment was applied until individual stems became carbonized and glowed. The majority
181 of invasive shrubs that were taller than 150 cm survived both the initial cutting and the first
182 directed heat treatment. Their rootstocks produced a second set of ramets, albeit one-fifth the
183 original size by end of the first growing season (Ward et al. 2009). Therefore, any rootstocks of
184 non-native species that developed new ramets after the first heat treatment were treated with
185 directed heat for a second time in early October for the intensive treatment.

186 **Woody Vegetation Sampling**

187 Prior to treatments, cover of all non-native species, but not native species, was estimated using
188 methodology described in Ward et al. (2013). After initial cutting and installation of exclosures,
189 two transects of five vegetation sampling points were established in May 2007 within each of the
190 six treatment subplots at each study area. Sampling points were permanently demarcated with
191 plastic pipes. Points were spaced at 5-m intervals and were 5 m from subplot edges. Native and
192 non-native shrub cover was estimated within a 4 m² circular plot centered on permanent points.
193 Each 4 m² circular plot was divided into four 1 m² quadrants. Within each quadrant, cover of
194 individual species was nominally estimated to be 0% (not present), <2% (present), 10%, 25%,
195 75%, or 100%. Quadrant values for individual species were averaged to obtain the sample point
196 estimate. Estimated average height class across the quadrat was recorded during each sample
197 year for non-native shrubs and during final three sample years for native shrubs. Height classes
198 were <15 cm, 15-30 cm, 30-60 cm, 60-90 cm, 90-120 cm, 120-150 cm, 150-180 cm, > 180 cm.
199 Data from the ten sample points within each treatment subplot were averaged to avoid potential
200 pseudo-replication. Measurements were repeated in 2008, 2009, 2010, 2012, 2013, and 2015 to
201 cover the first nine growing seasons after initial treatments.

Stems of woody regeneration were also tallied during each survey within each 4 m² circular plots. For tree species capable of forming part of the upper canopy in a mature forest, we recorded the species and height class for all stems with a diameter < 2.5 cm at 1.4 m aboveground. Seedling height class was defined as the highest live bud and measured with a height class pole.

Statistical Analyses

We calculated the volume of both non-native and native shrubs (m³/ha) for each sample year as follows:

$$\text{Volume (m}^3\text{/ha)} = \sum_i [\text{Cover}_{ij} (\%) * (\text{Height}_i(\text{cm}) * (1\text{m})/(100\text{cm})) * (10,000\text{m}^2/4\text{m}^2)]$$

for all *i* individual species. Volume estimates (*x*) were highly skewed and therefore not normally distributed. The data were subsequently natural log transformed ($\ln(x+1)$) prior to analysis (Zar 2010). To examine the separate and interactive effects of invasive control and herbivory exclusion, repeated measures analysis of variance (ANOVA) was conducted on the transformed volumes separately for both non-native and native shrubs. Years since initial treatment was the within subjects factor, and invasive control treatment (*I*₀, *I*₁, *I*₃), deer exclusion (*F*, *U*), and their interactions were utilized as the between subject factors with study areas as replicates. Reported *P*-values are those after applying the conservative Greenhouse-Geisser Epsilon correction for deviations from compound symmetry, i.e., non-sphericity (Hand and Crowder 1996).

Log transformed volumes at the end of nine growing seasons were analyzed using a full ANOVA model (SYSTAT 13, San Jose, CA, USA) with invasive control treatment and herbivory exclusion as factors, and study area as replicates. Models were examined without factors and interactions found non-significant in full model, and if the revised model had a lower

AIC_c estimate, then those factors/interactions were excluded in the final analysis reported here (Burnham and Anderson 2002). When appropriate, Tukey's HSD test was used to test for significant differences of non-native and native shrubs volumes among treatment or treatment combinations at $P \leq 0.05$.

Because of low stem counts of woody regeneration in the larger height classes, stems were assigned to one of three height classes: <30cm tall, 30-90cm tall, and >90 cm tall. It should be noted that analysis was of all tree seedlings and not by individual species. Height class counts (x) were highly skewed and not normally distributed; therefore, they were natural log transformed ($\ln(x+1)$) prior to analysis (Zar 2010). To examine the separate and interactive effects of invasive control and herbivory exclusion, repeated measures analysis of variance of stem count (transformed) was utilized. Years since initial treatment was the within subjects factor, and height class, invasive control treatment (I_0, I_1, I_3), deer exclusion (F, U), and their interactions were between subject factors with study areas as replicates. Reported P -values are those after applying the conservative Greenhouse-Geisser Epsilon correction for deviations from compound symmetry, i.e., non-sphericity (Hand and Crowder 1996). A three-factor (height class, herbivory protection, invasive treatment) ANOVA was used to compare the influence of herbivory protection and invasive treatments on seedling density in 2015 after nine growing seasons. Models were examined without factors and interactions found non-significant in full model, and if the revised model had a lower AIC_c estimate, then the factors/interactions were excluded in the final analysis reported here (Burnham and Anderson 2002).

RESULTS

Non-native shrubs

Pretreatment non-native shrub cover estimates did not differ among treatments and were 53% at Egypt, 60% at Storrs, and 82% at Tommy's Path (Ward et al. 2017). Japanese barberry was the most prevalent non-native shrub and accounted for 60% of all shrub cover over the course of the study (Table 1). Multiflora rose and burningbush were also observed on all study areas.

Non-native shrub volumes increased over time for all treatments ($F_{6, 72} = 15.07$, $P_{GG} < 0.001$, where P_{GG} is P -value after Greenhouse-Geisser Epsilon correction), but increases over time differed among invasive control treatments ($F_{12, 72} = 3.57$, $P_{GG} = 0.023$). The intensive treatment (mowing followed by directed heating) provided effective control for at least nine years (Fig. 1). Partial treatment (mowing only) provided moderate control as survivors expanded both horizontally and vertically. The rate of volume increase on more fully occupied untreated plots was lower than on treated plots. Changes in non-native shrub volumes over time did not differ by browse control ($F_{6, 72} = 0.91$, $P_{GG} = 0.697$) or invasive control $\times$ browse exclusion interactions ($F_{12, 72} = 0.16$, $P_{GG} = 0.952$).

After nine growing seasons, full model ANOVA indicated that non-native shrub volume did not differ between inside and outside exclosures ($F_{1, 12} = 0.55$, $P = 0.473$) or by invasive control $\times$ browse exclusion ($F_{2, 12} = 0.07$, $P = 0.937$). A parsimonious model with only invasive control had the lowest AIC_c and indicated that volumes differed among treatments ($F_{2, 15} = 5.11$, $P = 0.020$), with highest volumes on untreated plots and lowest volumes on plots cut and then treated twice with propane torches.

Native shrubs

Native shrub cover outside of exclosures where invasive shrubs were not treated was likely similar to pretreatment levels. On those areas, native shrub cover averaged 0.3% and never rose above 0.5% (Ward et al. 2017). Blackberries and viburnums, primarily mapleleaf viburnum (*Viburnum acerifolium* L.) were the most commonly observed native shrubs (Table 1). Repeated measures ANOVA indicated neither treatment (P_{GG} ranged from 0.478-0.540) nor their interaction ($F_{4, 24} = 0.15$, $P_{GG} = 0.887$) had an effect on changes of native shrub volumes over time. However, native shrub volumes did differ among invasive control treatments ($F_{2, 14} = 9.74$, $P = 0.002$) and between inside and outside exclosures ($F_{1, 14} = 8.51$, $P = 0.011$). Native shrub volume was substantially higher inside exclosures where invasives were treated (361 ± 181 m³/ha) than inside exclosures where invasives were not treated (24 ± 16 m³/ha) or outside exclosures regardless of treatment (9 ± 4 m³/ha). It should be noted that native shrub volumes were generally orders of magnitude lower than volumes of non-native shrubs (Fig. 1).

Native tree seedlings

Repeated measures ANOVA indicated that the population dynamics of the three seedling size classes differed over the nine years of this study (Fig. 3, $F_{12, 276} = 3.40$, $P_{GG} = 0.004$). In general, densities increased over time where invasive shrubs were at least partially controlled ($F_{12, 276} = 2.73$, $P_{GG} = 0.017$). Seedling densities differed between inside and outside exclosures ($F_{1, 46} = 5.76$, $P_{GG} = 0.020$) with weak evidence that the influence of browse on population dynamics (i.e., decreasing, peaking, or increasing) differed among seedling size classes ($F_{12, 276} = 1.88$, $P_{GG} = 0.091$). Changes in seedling densities over time were independent of invasive control $\times$ browse exclusion interactions ($F_{12, 216} = 1.467$, $P_{GG} = 0.567$). It is notable that the three seedling size classes were remarkably stable where conditions remained unchanged over the nine growing

seasons of the study (Fig. 3), i.e., where deer were not excluded and where invasive shrubs were not controlled.

Black cherry, white ash, and maple were predominant in the small seedling size class (< 30 cm tall), accounting for 83% of all small seedlings observed during the seven inventories (Table 2). Density of the smallest size class increased after invasive shrubs were treated (Figs. 3a,b), and then declined as some stems transitioned into a larger size class, or died because of competition from recovering invasive shrubs (Fig. 1) and increased density of taller seedlings (Figs. 3).

Repeated measures ANOVA indicated that neither browse exclusion nor invasive shrub treatments had an effect on the pattern of small seedling density changes over time ($P_{GG} = 0.105$ and 0.591, respectively). The reduced competitive interference from invasive shrubs on treated plots (Fig. 1) was likely the cause for the increase of small seedling densities (Fig. 4). Small seedling densities peaked 1-3 years after treatment inside the exclosures (Fig. 3b) and 4-7 years outside the exclosures (Fig. 3a).

Density of small seedlings in the final inventory taken at the end of the ninth growing season differed between deer exclusion ($F_{1, 14} = 20.82$, $P < 0.001$) and among invasive shrub treatments ($F_{2, 14} = 3.78$, $P = 0.048$). Densities were much higher outside than inside exclosures (Fig. 5) and increased with increasing intensity of invasive shrub control (Fig. 4). Composition also differed among invasive shrub control treatments with relative and absolute density of ash decreasing, and black cherry, maple, and oak/hickory increasing with increasing treatment intensity (Fig. 4).

Black cherry, white ash, and maple accounted for a 45% plurality of seedlings in the medium-size class (30-90 cm tall). Similar to the analysis of small seedling density dynamics, repeated measures ANOVA indicated no significant influence of either browse exclusion or invasive shrub treatments on changes in medium seedling densities over time ($P_{GG} = 0.363$ and 0.171,

respectively). However, medium seedling densities did differ between inside and outside exclosures ($F_{1, 12} = 5.29$, $P = 0.040$), but did not differ among invasive control treatments ($F_{2, 12} = 2.67$, $P = 0.110$). Inside exclosures, medium seedling densities peaked 4-7 years after invasive shrub control treatments (Fig. 3d). On plots outside exclosures that were open to deer browsing, there was a delay of several years or longer for medium seedlings to reach comparable densities (Fig. 3c).

The absolute densities of all species in the medium size class increased with increasing intensity of invasive shrub treatments (Fig 4). However, the proportion of maple and oak/hickory on areas where invasives were not treated (19% and 38% of all medium seedlings, respectively) was higher than where invasives were intensely treated (11% and 6%, respectively). Relative to untreated areas, intensive invasive shrub treatments increased the proportion of black cherry (19% to 42% of all medium seedlings, respectively) and black birch (<0% to 11%, respectively).

Species composition of the large seedling size class (> 90 cm tall) differed from small and medium size classes. Hophornbeam (*Ostrya virginiana* (Mill.) K. Koch), American beech, and black birch contributions were negligible in the small seedling size class (7%), but comprised over 63% of the large seedlings observed. Repeated measures ANOVA indicated browse exclusion ($F_{6, 72} = 1.78$, $P_{GG} = 0.183$) had no effect and only a weak effect of invasive shrub treatments ($F_{12, 72} = 2.13$, $P_{GG} = 0.096$) on how large seedling densities changed over time. Large seedling densities remained unchanged outside of the exclosures (Fig. 3e) and inside the exclosures where invasive shrubs were not treated, but increased where invasive shrubs were treated (Fig. 3f).

In the final inventory taken at the end of the ninth growing season, composition of large seedlings was markedly different between inside and outside exclosures (Fig. 5). Large seedling

density inside exclosures was much more diverse than outside. American beech and hophornbeam accounted for 89% of large seedlings outside exclosures compared with only 30% of large seedlings inside exclosures, where black birch was the most abundant species.

DISCUSSION

Several major conclusions can be drawn from this study. First, forest regeneration will remain sparse and relatively unchanged for at least a decade in forests with well-established invasive shrub thickets even if deer browsing is excluded. Second, controlling invasive shrubs will result in increased regeneration densities by removing the bottleneck of competitive interference from invasive shrubs. Third, white-tailed deer browsing is a functional bottleneck that reduces the rate at which seedlings are able to grow into progressively taller size classes. Fourth, compounding the effects of a white-tailed deer bottleneck that reduces seedling growth is their preferential browsing which acts as a filter that favors species with lower palatability and results in forest regeneration with lower species richness. Fifth, the window for establishment of new forest regeneration is brief because established invasive thickets are remarkably recalcitrant and are able to recover from a single cutting. Each of these are addressed in turn and then tied to practical management implications.

Our observation of low seedling recruitment in areas with intact invasive shrub thickets is not unique. Earlier research reported that clonal shrub patches in full sunlight were highly resistant to tree seedling recruitment and growth in Connecticut (Niering and Goodwin 1974), Quebec (Meilleur et al. 1994), and New York (Hill et al. 1995). Later research found that tree seedling densities were greatly reduced under Amur honeysuckle (Collier et al. 2002; Runkle et al. 2007), Tatarian honeysuckle (*Lonicera tatarica* L.) (Woods 1993), glossy buckthorn (Fagan and Peart

2004), and Chinese privet (*Ligustrum sinense* Lour.) (Hanula et al. 2009). In a literature review, Royo and Carson (2006) noted that recalcitrant understory shrub thickets are globally common, of increasing importance because of anthropogenic alterations of disturbance regimes, and can shift the dynamics of forest succession. There have been few experimental studies that directly partitioned the potential causal mechanisms of invasive shrub competitive interference on forest regeneration. Shrub thickets have been reported to directly impact smaller plants by reducing available light (Braithwaite et al. 1989; Hamelin et al. 2016) and soil moisture (Putz and Canham 1992; Gorchov and Trisel 2003), and indirectly by altering nutrient cycling (Kourtev et al. 1999; Ehrenfeld et al. 2001) and reducing leaf litter depth (Madritch and Lindroth 2009).

There was a striking response of increasing density of tree seedlings of all size classes as the intensity of invasive shrub control increased. This provided strong, albeit indirect, evidence that invasive shrub thickets are an inhibitory bottleneck to the establishment and development of native woody species. Surprisingly, few invasive control studies have examined the post-treatment response of native woody regeneration (Kettenring and Adams 2011). Native tree seedling densities increased following Amur honeysuckle control in Ohio (Boyce 2015) and glossy buckthorn control in New Hampshire (Frappier et al. 2004). Removal of an Amur honeysuckle understory improved three-year survival, but not growth, of six hardwood species planted in a southern Ohio forest (Hartman and McCarthy 2004). Two-year growth of planted oak and maple seedlings was greater where understory glossy buckthorn had been treated in Québec (Hamelin et al. 2016). In New Hampshire, height growth of native saplings was depressed when growing under glossy buckthorn (Fagan and Peart 2004).

Reducing invasive cover in forest understories, even temporarily, may provide native species a brief window for re-establishment (Gorchov and Trisel 2003). In our study, the increase in small

seedling (< 30 cm tall) density following invasive shrub control was temporary and actually declined nine growing seasons after invasive shrubs were cut. This reduction was likely due in part to the deleterious effect of slowly recovering invasives, but also to increasing medium (30-90 cm tall) and large (>90 cm tall) seedling densities, and increasing native shrub cover. Similar short-term increases soon after invasive shrub control, followed by declines, were reported for perennial and annual/biennial forbs (Ward et al. 2017). These short-term increases of forb populations were likely another contributing factor to the decline of small seedlings, especially within the exclosures where forb increases were greatest.

Medium and large seedling densities increased more rapidly and to higher absolute levels when protected from deer browse following invasive shrub control in our study. Deer browsing delayed, but did not stop, eventual movement of small seedlings into the medium seedling size class and medium seedlings into the large seedling size class, albeit with a reduced diversity of species (discussed below). The lag was at least five years for medium seedlings and potentially ten years or more for large seedlings. Deer browse reduced two-year growth of yellow birch (*Betula alleghaniensis* Britton), red maple, and black cherry seedlings, but not American beech in Pennsylvania (Krueger et al. 2009). Ten-year height growth of advanced northern red oak seedlings was increased by protection from deer browse in Pennsylvania (Miller et al. 2016). However, planted yellow birch and hemlock were only marginally taller when protected from deer browse for four years in northern Wisconsin (Kern et al. 2012). Similarly, herbivory reduced recruitment into sapling size classes in Poland (Kuijper et al. 2010).

Tall regeneration density was greater in areas protected from deer browse after 15 years (Trumbull et al. 1989) and 9-22 years in Pennsylvania (Marquis 1980), and five years in West Virginia (Nuttle et al. 2013). Eighteen years after deer exclusion fencing was installed, native

tree seedling density was five times higher inside than outside exclosures (Abrams and Johnson 2012). Seedling density declined over nine years outside of exclosures while increasing where protected from deer (Long et al. 2007). An intense hunting program on a 2100-ha forest in Wisconsin reduced deer densities from 11 to 5 deer-km⁻², which released browsed-suppressed seedlings and resulted in a 100-fold increase in seedlings > 1m tall (Behrend et al. 1970). Hunting also increasing density of 50-200 cm tall regeneration in Indiana (Jenkins et al. 2015). It is interesting that species richness of small and medium seedlings differed little between inside and outside exclosures; but deer browsing has had a profound influence on the composition of large seedling size class, those stems most likely to continue growing and eventually become part of a future upper canopy. Eighteen years after deer exclusion fencing was installed in Pennsylvania, native tree seedling richness was three times higher inside than outside exclosures (Abrams and Johnson 2012). Other Pennsylvania studies reported native tree seedling richness was higher where browsing was excluded for both five (Nuttall et al. 2013) and nine years (Long et al. 2007). Hunting increased species richness of tall woody regeneration over a 14-year period (Jenkins et al. 2015).

The effects of chronic deer herbivory can have long-term legacy effects as populations of browse intolerant (i.e., highly palatable) species may take a decade or longer to recover, if ever (Webster et al. 2005; Tanentzap et al. 2009; Jenkins et al. 2015). While mesophication of North American eastern deciduous forests in the absence of fire has created conditions more favorable for shade tolerant/fire intolerant species (Nowacki and Abrams 2008), it should also be recognized that species that are both shade and browse tolerant have a competitive advantage in areas with high deer density (Long et al. 2007; Krueger et al. 2009). An example of a fire intolerant/shade tolerant/browse tolerant species is American beech (Nuttall et al. 2013), which was the most

common tall seedling in our study outside of the exclosures. Beech was the least browsed species in 1-3 year-old clear-cuts in West Virginia (Miller et al. 2009) and in Pennsylvania forests (Krueger et al. 2009) where it was the only species whose height growth rate was independent of exposure to deer browse. Similarly, beech seedlings predominated, and beech saplings were the most common species outside exclosures in undisturbed forests after five years in West Virginia (Nuttle et al. 2013) and nine years in Pennsylvania (Long et al. 2007). A longer 9-22 year study reported that beech sapling densities were higher outside exclosures while preferred species were higher inside exclosures in northern Pennsylvania (Marquis 1980). Chronic deer browsing favored development of less palatable black birch in 20-year-old clear-cuts in Connecticut (Smith and Ashton 1993) and replacement of native woody species by invasives in the mid-Atlantic (Eschtruth and Battles 2009b).

Recovery of invasive shrubs following cutting was steady over nine years on both areas with and without exposure to deer browse, extending our earlier seven year observations (Ward et al. 2017). If invasive shrubs continue to grow at the same rate on cut-only plots, recovery to pre-treatment levels is likely within 20 years of initial treatment. The quick recovery of invasive shrubs suggests there is a relatively short window for tree seedlings to become established after initial invasive shrub control when herbicides are not used.

The lack of long-term control of invasives shrubs by cutting without follow-up treatments concurs with practical manuals recommending multiple treatments for comprehensive control (Loux et al. 2005; Miller et al. 2010). The need for multiple treatments is predicated on the ability of many invasives to vigorously resprout after aboveground stems are cut (Pergams and Norton 2006; Hanula et al. 2009; Loeb et al. 2010) and then continue to grow in the understory (Harrington et al. 2004; Knight et al. 2007). It should be noted that properly applied herbicides

can provide enhanced control by killing root systems of invasive shrubs (Miller et al. 2010, Ward et al. 2013).

Our study indicates that restoring forest regeneration in stands with both established invasive shrubs and high deer densities will require both controlling invasive shrubs and a multi-year program to reduce deer browsing intensity. While there are much more cost-effective methods of controlling competitive interference such as invasive shrubs (Brose et al. 2008; Ward et al. 2013), our cut/burn/burn method can provide effective control where herbicide use is restricted by regulations or by active public opposition. Equally important as controlling invasive shrubs is implementing a strategy to reduce browse intensity to the equivalent of 5-8 deer-km⁻² or lower to obtain adequate tree regeneration (Behrend et al. 1970; Tilghman 1989; deCalesta and Stout 1997, Horsley et al. 2003). Without reducing browsing intensity, some tree regeneration will become established, but it will take longer and will be comprised of species with both lower economic and ecosystem services values.

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Table 1. Mean cover (%) and volume (m³/ha) of shrub species observed nine growing seasons after treatment in a southern New England study of invasive shrub control and deer herbivory exclusion.

Origin	Scientific name	Common name	Cover	Volume
			(%)	(m ³ /ha)
Non-native	<i>Berberis thunbergii</i>	Japanese barberry	30.4%	2174
	<i>Rosa multiflora</i>	Multiflora rose	8.8%	1107
	<i>Euonymus alatus</i>	Burningbush	1.1%	95
	<i>Rubus phoenicolasius</i>	Wine raspberry	0.8%	52
	<i>Viburnum dilatatum</i>	Linden arrowwood	<0.1%	8
	<i>Ligustrum vulgare</i>	European privet	0.0%	6
Native	<i>Rubus</i> spp.	Blackberry/raspberry	5.9%	372
	<i>Viburnum</i> spp.	Viburnum	0.3%	12
	<i>Ilex verticillata</i>	Winterberry	<0.1%	2
	<i>Corylus cornuta</i>	Beaked hazelnut	<0.1%	0.2
Combined			47.6%	3828

Table 2. Total number of observed seedlings by species and height class in seven inventories over nine growing seasons in a southern New England study of invasive shrub control and deer herbivory exclusion.

Scientific name	Common name	Seedling height class (cm)			Total
		<30	30-90	>90	
<i>Prunus serotina</i>	Black cherry	7581	289	28	7898
<i>Fraxinus americana</i>	White ash	5202	113	11	5326
<i>Acer saccharum</i>	Sugar maple	2822	107	5	2934
<i>Acer rubrum</i>	Red maple	1530	31	1	1562
<i>Betula lenta</i>	Black birch	926	75	65	1066
<i>Carya</i> spp.	Hickory	805	69	2	876
<i>Quercus</i> spp.	Oaks	767	85	-	852
<i>Ostrya virginiana</i>	Hophornbeam	252	195	79	526
<i>Fagus grandifolia</i>	American beech	168	95	72	335
<i>Liriodendron tulipifera</i>	Tulip poplar	207	43	20	270
<i>Carpinus caroliniana</i>	American hornbeam	108	25	7	140
<i>Cornus florida</i>	Flowering dogwood	72	37	12	121
Other		169	33	39	241
Combined		20609	1197	341	22147

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Figure 1. Changes in non-native shrub volume by number of treatments to control invasive shrubs.

Figure 2. Volume (m^3/ha) of shrubs nine years after initial treatment I0-invasive shrubs not treated, I1-invasive shrubs cut, I3- invasive shrubs cut and new sprouts treated twice with directed flame using propane torches.

Figure 3. Changes in density (n/ha) of seedling size classes by browse protection (outside or inside exclosures) and invasive control treatments (I0-invasive shrubs not treated, I1-invasive shrubs cut, I3- invasive shrubs cut and new sprouts treated twice with directed flame using propane torches).

Figure 4. Distribution of species by invasive shrub control treatments and seedling size classes nine growing seasons after treatments: I0-invasive shrubs not treated, I1-invasive shrubs cut, I3-invasive shrubs cut and new sprouts treated twice with directed flame using propane torches. Values are least-square means across browse protection treatments.

Figure 5. Distribution of species by deer exclusion and seedling size classes nine growing seasons after erection of exclosures. Values are least-square means across invasive shrub control treatments.