



ARTICLE

Stasis in forest regeneration following deer exclusion and understory gap creation: A 10-year experiment

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Abstract

Chronically elevated ungulate browse pressure in temperate forests worldwide often generates ecological legacies characterized by low plant diversity and contributes to the formation of dense, nearly monodominant, and highly recalcitrant layers of understory vegetation. Once established, these recalcitrant layers combined with continued browsing may jointly constrain tree establishment and diversity so completely that understory recovery may be unattainable without mitigating browse pressure, the recalcitrant layer, or both. Here, we investigate the independent and synergistic effects of both white-tailed deer (*Odocoileus virginianus*) browsing and hay-scented fern (*Dennstaedtia punctilobula*) competition on tree regeneration in a 10-year experiment. Specifically, we examine how tree seedling establishment, growth, and composition are filtered by fern cover versus fern removal (gaps), browser presence versus absence (exclosures), and their combined effects during 10 years at three hardwood forest sites in Pennsylvania, USA. Fern gaps enhanced establishment for multiple tree species, increasing seedling density and diversity, particularly in the first 3 years post-treatment, and enhancing richness (≤ 1 species) over the course of the experiment. Excluding deer for a decade increased the height growth of other regeneration and altered species composition, but had no effect on diversity, richness, and density. Notably, we observed higher *Prunus serotina* seedling densities outside exclosures, possibly due to greater secondary dispersal. We argue that browsing legacies in second growth forests established at the turn of the last century created two conditions inimical to diverse forest regeneration: an overstory dominated by two species, *P. serotina* and *Acer rubrum* (86% of basal area), and a dense recalcitrant understory layer dominated by a native fern. The first condition limits propagule supply, the second strongly filters seedling establishment, and both create impoverished forest understories composed of few individuals and species. In undisturbed forest understories, the inertia toward impoverishment was sustained across the decade even where browsing was eliminated. Consequently, stand replacing disturbances (whether natural or anthropogenic) that disrupt the understory layer and reinitiate succession may be necessary to propel forests out of their current stasis and down a pathway leading to greater diversity.

KEYWORDS

advance regeneration, browse-tolerant species, deciduous forest, deer exclusion, *Dennstaedtia punctilobula*, herbivory, *Odocoileus virginianus*, plant diversity, recalcitrant understory layer, shade tolerant species

INTRODUCTION

In temperate deciduous forests around the world, large ungulates often act as keystone herbivores by regulating species abundance, mediating biodiversity, altering habitat structure, and affecting nutrient cycling (Askins, 2014; Nuttle et al., 2014; Waller & Alverson, 1997). Throughout vast areas of the Eastern Deciduous Forest Biome of North America, deer populations have persisted above presettlement population estimates of 3–8 deer·km⁻² for nearly a century because of active management for large herds, reduction of predators, milder winter temperatures, and changes in land use (Côté et al., 2004; McCabe & McCabe, 1997; McWilliams et al., 2018; Rooney, 2001). Regardless of the reasons, chronically high browse pressure from these abundant herds has caused major declines in the abundance and diversity of palatable species, and over decades has shifted understory composition toward a subset of highly unpalatable or browse-tolerant species (Begley-Miller et al., 2014; Côté et al., 2004; Goetsch et al., 2011; Horsley et al., 2003; Rooney, 2001). In other cases, unpalatable species, particularly if they are clonal, can spread following a natural or anthropogenic forest canopy disturbance to form dense layers in forest understories over vast regions (Royo & Carson, 2006; Young & Pepper, 2010). Royo and Carson (2006) termed these vegetation layers recalcitrant because, once established, they could remain intact for decades even if browsers are reduced in abundance, extirpated, or excluded via exclosures. Thus, restoring biodiversity in landscapes with strong legacies of browsing might require more than an extended and major reduction in browsers but also the eradication or mitigation of these recalcitrant layers of vegetation.

Recalcitrant understory layers are now quite common in forests worldwide and are likely to cause alternative and depauperate pathways of forest regeneration because they cast deep shade, provide a critical refuge for seed predators, compete for below ground nutrients, and are potentially allelopathic (Beltrán et al., 2020; Engelman & Nyland, 2006; Horsley, 1993b; Royo & Carson, 2006, 2008). Recalcitrant layers in forests of the eastern United States can cover millions of hectares (citations above, also Monk et al., 1985). Although there has been extensive research on canopy gaps in forests worldwide (reviewed by Denslow, 1987, Runkle & Yetter, 1987,

McCarthy, 2001, Muscolo et al., 2014), far less research has focused on how gaps within dense understory layers may mediate key dynamics from seedling to sapling stages. These dynamics are likely to determine which species make it back to the canopy and, thus, these layers, and gaps within them, may be a key filter regulating forest regeneration (Landuyt et al., 2019).

Overall, chronic, intense browsing combined with canopy disturbance has precipitated the development of dense understory layers and these layers may delay or prevent forest recovery even if browsing is significantly reduced or prevented altogether (Royo et al., 2010; Tanentzap et al., 2012). To date, few experiments have simultaneously examined both deer herbivory and understory competition in forest ecosystems and the focus of most of these studies were on invasive species removals (Bourg et al., 2017; Haffey & Gorchoy, 2019; Waller & Maas, 2013) or managed forest ecosystems (Brousseau et al., 2017; Horsley & Marquis, 1983; Thyroff et al., 2019). Moreover, nearly all of these studies are relatively short term (≤ 5 years). Thus, it remains unclear if their findings extend to mature forest understories dominated by native species over the long term.

Here, we evaluated the degree to which deer activity and a dense understory layer (fern), alone and together, regulate forest regeneration and diversity in northern hardwood forests. We tested three hypotheses: (1) Excluding browsers will cause an increase in tree seedling densities, diversity and height growth, and shift species composition toward less browse-tolerant or more palatable species. (2) The removal of a dense fern layer (creating an understory gap) will cause an increase in seedling densities, diversity and height growth and shift species composition toward less shade tolerant species. (3) Both excluding browsers and creating an understory gap will cause large increases in seedling density, diversity and height growth and shift species composition toward species that are both less browse resistant and less shade tolerant. Thus, for this last hypothesis, we predicted that the effect of excluding browsers and creating an understory canopy gap will be non-additive (i.e., significant interactions for multiple response variables). Additionally, predicted effects should accrue differentially over time with fern effect manifested early as this recalcitrant layer is known to limit seedling germination, establishment, and growth, whereas the browsing effect would occur later given deer often browse

on seedlings taller than 20 cm (Frerker et al., 2013; George & Bazzaz, 1999a, 1999b; Rooney et al., 2000). We tested these hypotheses using a factorial experiment where we created understory gaps, excluded deer, and then monitored tree species regeneration over a decade in three forest stands widely scattered across the Allegheny Plateau Forest region of Pennsylvania, USA.

METHODS

Study system and background

We conducted this study within the Allegheny High Plateau Region of northwestern Pennsylvania, USA in three mature second growth forests sites (>75 years) dispersed across three counties: Marienville (Forest County), Long Run (Elk County), and Clermont (McKean County). Forests within the region originated from extensive clear-cutting at the turn of the 20th century (Whitney, 1990) and the three stands chosen for this study had no history of recent logging since their establishment. Forest composition at all sites was representative of the Allegheny Hardwoods forest subtype of the hemlock northern hardwoods association (Eyre, 1980). The region has a cool and humid climate with an average summer temperature of 18.9°C and annual precipitation of 109 cm (Whitney, 1990). These forests are currently dominated by red maple (*Acer rubrum* L.) and black cherry (*Prunus serotina* Ehrh.), but American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marshall.), white ash (*Fraxinus americana* L.), cucumber magnolia (*Magnolia acuminata* L.), pin cherry (*Prunus pensylvanica* L.f.) and birch (*Betula* L.) occur but comprise little basal area. Average basal area for the sites was 31.4, 36.4 and 43.4 m²·ha⁻¹ for Clermont, Long Run, and Marienville, respectively. Relative density (%), a measure of overstory crowding that integrates both tree size and species identity was calculated as 76%, 82%, and 78% for Clermont, Long Run, and Marienville, respectively, values that correspond to the average maximum stocking expected in undisturbed stands in the region (Stout et al., 1987; see Table 1 for tree species composition and abundance).

The understory at all three sites was dominated by hay-scented fern (*Dennstaedtia punctilobula* [Michx] T.Moore). Hay-scented fern is unpalatable to white-tailed deer and exhibits aggressive vegetative growth as understory light increases (Cody et al., 1977; Nuttle et al., 2014). In the Allegheny region, hay-scented fern occupied less than 4% of the understory in old-growth stands; however, its abundance dramatically increased following the turn of the century harvests and regionally intense browse pressure (Horsley, 1993a; Lutz, 1930). At this time, hay-scented fern forms dense stands at or greater (multilayered) than 100%

cover throughout approximately one-third of the forests in the region (Royo et al., 2010). However, even within heavily fern-dominated areas, gaps in coverage exist. For example, Hill and Silander (2001) found fern-free areas in ~12% of an otherwise fern-dominated understory (see Horsley & Marquis, 1983 for values). Such gaps in the hay-scented fern canopy may occur from variation in the light availability, centrifugal growth arising from its forking rhizome architecture (Hill & Silander, 2001) or from disturbances including deer bedding areas, frost damage, or slash piles from overstory disturbance (A. A. Royo, personal observation). Hay-scented fern is considered a native invasive throughout large portions of the Eastern United States and Canada (de la Cretaz & Kelty, 1999; Engelman & Nyland, 2006; Ouimet et al., 2016), and is a well documented case of a native species forming dense, recalcitrant vegetation across broad regions (Royo & Stanovick, 2019). Hay-scented fern strongly limits tree seedling recruitment by inhibiting germination through litter accumulation and lowering light availability, altering red: far-red ratios, and intensifying seedling predation rates under its canopy (de la Cretaz & Kelty, 1999; Royo & Carson, 2008). Allelopathic inhibition is not strongly supported for this species (Horsley, 1993a).

White-tailed deer populations in the region increased dramatically during the 20th century following their near extirpation and subsequent reintroduction in 1905 (Frye, 2006). In mid-1970s, deer densities on the Allegheny National Forest had reached 15.6–22.6 deer·km⁻² (Redding, 1995). During the period of this study, deer densities in the region ranged from 11.2 to 4.5 deer·km⁻², with densities dropping by approximately half beginning in 2005 following the allocation of additional antlerless deer harvest permits (Royo & Stout, 2019).

Experimental design

We used a randomized, complete block, split-plot design with the exclusion of deer as the main-plot factor and the creation of understory gaps (fern removal) as the within-plot factor (Appendix S1: Figure S1). At each of the three stands, we established six paired (14 × 20 m) main plots in areas where the forest floor was entirely covered by hay-scented fern and largely devoid of taller advance regeneration (e.g., individuals ≥2.54 cm; see Appendix S1: Figure S1; Table 1). In October 2000, one plot from each pair was randomly selected as a fence treatment and the other served as an unfenced control. Fences were made of black polypropylene (4.45 × 5.1 cm mesh size) and were 2.1 m tall. In addition, we established four, 2.5 m × 2.5 m (6.25 m²) subplots within each fence and adjacent control plot in August 2000. In two of these four

TABLE 1 Overstory species composition in 2004 at three research sites used in this study

	Clermont		Long run		Marienville	
	Control	Fence	Control	Fence	Control	Fence
<i>Prunus serotina</i>	14.48	17.66	24.78	26.98	23.31	31.91
<i>Acer rubrum</i>	8.08	7.34	8.49	7.27	15.03	15.05
<i>Acer pensylvanicum</i>	0.02	0.18		0.01	0.01	
<i>Acer saccharum</i>	5.74	7.52	2.55	2.09	0.14	0.16
<i>Amelanchier</i> spp.						0.02
<i>Betula</i> spp.	0.02	0.02	0.18	0.02		0.05
<i>Fagus grandifolia</i>	0.71	1.06	0.25	0.16		
<i>Fraxinus americana</i>					0.18	0.11
<i>Hamamelis virginiana</i>			0.01			
<i>Ilex montana</i>						0.11
<i>Magnolia acuminata</i>					0.05	0.57
Total	29.04	33.77	36.25	36.52	38.70	47.99

Note: The sites are representative of the Allegheny hardwood forest type and are located in northwestern Pennsylvania, USA. Basal area ($\text{m}^2 \text{ha}^{-1}$) of individuals ≥ 2.54 cm diameter at breast height (dbh) at each of the three sites, by treatment.

subplots (randomly selected), we created gaps within the fern layer with herbicide in September 2000 using the rate recommended for this specific forest type (1.15 kg of glyphosate per hectare using Accord[®] and X-77[®] surfactant, Horsley, 1981). Glyphosate, the active ingredient in the herbicide, has little soil residual activity and, thus, does not depress seedling germination in the growing season post-application (Horsley, 1994). Thus, we had four subplots (two with understory gaps and two serving as controls) nested within 12 main plots (six fences paired with six control plots) \times three different forest stands for a total of 144 sampling units total. All subplots were separated from each other and from the main-plot perimeter by at least 3.0 m. To avoid edge effects, we sampled vegetation within 1-m² sampling plots placed in the center of each understory gap and control subplot. In a manner similar to studying large tree-fall gaps (Nuttle et al., 2013; Royo, Collins, et al., 2010), the understory gaps we created were allowed to fill in over the course of our study (See Appendix S1: Figure S1 for site conditions and treatments).

Sampling regime

We monitored seedling diversity, abundance, height, and establishment in the summers of 2001 through 2010 (2001, 2002, 2003, 2004, 2007, 2008, and 2010). In the first 4 years of the study, individual seedlings were marked with uniquely numbered plastic binder rings to identify the specific individual and cohort. New seedlings

(i.e., germinants) were differentiated from established seedlings by the presence of cotyledons and the lack of stem lignification. In subsequent years, new seedling cohorts were tallied, but not individually marked, and the height of the tallest stem, by species, was recorded. Thus, for any year, we could report both overall seedling densities and the fraction comprised of new germinants. We note that our analyses focused exclusively on individuals germinating beginning in 2001 as the herbicide application effectively killed the existing seedling layer. In the 2001 survey, prior year seedlings comprised 63% versus 3% of the seedlings in the untreated and treated plots, respectively (A. A. Royo, unpublished data), and these seedlings likely did not persist long, as seedling mortality under dense hay-scented fern can reach 100% in the 2 years post-establishment (Horsley, 1993a). Thus, for the purposes of this study we use the term “seedling” to refer to any of the individuals germinating beginning in 2001, regardless of height.

We measured percentage light attenuation at each subplot using an ACCUPAR linear photosynthetically active radiation (PAR) ceptometer (Decagon, Pullman, WA, USA). An additional sensor simultaneously measured full sunlight in nearby openings. Light readings were taken during the growing season (July and August) at dawn and dusk to obtain diffuse light measurements in 2002 and 2004. We averaged two measurements taken in cardinal number directions at each of two heights: 1 m (above fern) and 10 cm (below fern) and calculated total light attenuation as PAR below fern/PAR above overstory canopy.

Finally, we assessed overstory tree composition in 2004 to characterize the canopy at each site following a windstorm that affected the overall Allegheny region in July 2003 (Evans et al., 2007). All trees ≥ 2.54 cm diameter at breast height (dbh) were identified and measured within each 14×20 m main plot and extending out to include individuals 10 m from the perimeter of the main plot.

Statistical analyses

The analyses proceeded as a multilocation (three different stands), repeated measures, and split-plot design using PROC GLIMMIX (SAS Institute Inc., 2013). For the analyses, fence, gap, year, and the associated interactions were fixed effects in the model. Blocks nested in site were modeled as a random variable to account for the multilocation portion of the study and fence \times gap \times block (site) was further added as a random variable to account for the split-plot nature of the design. The analysis of variance (ANOVA) approach tested changes in response to treatments and their interactions over time. Response variables included species richness (S), Shannon diversity (Magurran, 1988), and seedling densities and height of black cherry and red maple. The scarcity of all other species made it impossible to robustly examine their individual responses. Thus, we examined changes in density and height of all other tree species combined. This group included striped maple (*Acer pensylvanicum* L.), sugar maple, serviceberry (*Amelanchier arborea* [Michx. f.]), birch (*Betula* L.), American beech (*F. grandifolia* Ehrh.), white ash, cucumber magnolia (*Magnolia acuminata* L.), hop-hornbeam (*Ostrya virginiana* [Mill.] K.Koch), and pin cherry. For all analyses, we averaged the two replicates (i.e., subplots) of each gap treatment within each main plot prior to analyses, giving us a total N of 72 samples per year. Given the sampling scheme changed from measuring all seedlings to measuring the tallest seedlings, by species, average maximum height was calculated. Finally, we assessed the effects of experimental treatments on overstory canopy light attenuation (1 m above soil surface) and total light attenuation (10 cm above soil surface) in 2002 and 2004.

Species richness, diversity, and light were modeled using a normal distribution. Average seedling densities were modeled with a gamma distribution using the log link function after adding a small constant and seedling heights were modeled with a lognormal distribution with the identity link function. Correlations between years were initially modeled using an autoregressive first-order covariance structure, and amended to the heterogeneous extension of the autoregressive first-order structure in

order to adjust for heterogeneous residuals among years. We used the Kenward–Rogers denominator degrees of freedom adjustment method for each model. In addition, normality was statistically tested using the Shapiro–Wilk test, and homogeneity of variance was tested with Levene’s test. For significant treatment \times year effects, we compared treatments within years using the SLICE option of the LSMEANS statement. We used a critical value of $p = 0.05$ as significant and employed a sequential Bonferroni correction (i.e., Holm) when examining multiple comparisons.

To determine whether deer browsing and gaps in the fern canopy had an impact on community composition, we analyzed the mean abundance data using *vegan* and *indicspecies* packages in R (Oksanen et al., 2019; R Core Team, 2017). Because rare species can exert large effects on multivariate analyses, we removed species present in less than 5% of plots from the community matrix (McCune & Grace, 2002). As with the linear models, we averaged both species density values to a single plot-treatment value to avoid pseudoreplication. After these steps, we calculated multivariate distances between plots using the Bray–Curtis method. To test whether fern gaps, deer browsing, or both shifted the overall tree seedling composition, we ran a permutational multivariate analysis of variance (PerMANOVA) at three time periods (2001, 2004, 2010) (Oksanen et al., 2019).

RESULTS

Light attenuation

Understory light levels above the fern layer in these stands (1 m) averaged $7.3 \pm 0.3\%$ (SE) and $9.6 \pm 0.9\%$ (SE) of full sunlight in 2002 and 2004, respectively, and did not differ between gap and control plots. Creating gaps in the fern canopy increased light reaching the forest floor (10 cm) by 65%–129% in 2002 and 2004, respectively (Appendix S1: Figure S2; 2002: $F_{1,34} = 40.1$, $p < 0.0001$ and 2004: $F_{1,51} = 21.9$, $p < 0.0001$). Thus, creating understory gaps substantially increased light levels at the soil surface 4 years after we created them. We did not detect any effects of deer exclusion or interactions between treatments or stands for light availability.

Impacts of treatments on density, richness, and diversity

Excluding deer did not cause significant changes in the total tree regeneration density, richness, or diversity, and there were no significant interactions with year or fern

gaps. The creation of understory fern gaps significantly increased overall seedling density, species richness, and diversity (Table 2). Increases in seedling densities under fern gaps waned over time and disappeared entirely by 2010 (significant gap \times year interaction; Table 2 and Figure 1a). Creating fern gaps did increase species richness throughout the study, and this varied among years (significant gap \times year interaction; Table 2 and Figure 1b); however, the magnitude of the increase was never more than one additional species and less than that by the end of the study. Gaps significantly increased species diversity when averaged over the course of the experiment (i.e., significant main effect). Additionally, diversity increased during the first 3 years of the study regardless of treatments, and then leveled off for the duration of the experiment (Table 2 and Figure 1c).

Impact of treatments on focal tree species

Excluding deer led to a significant decrease in the seedling density of black cherry early in the study, but this disappeared by the end of the study. We documented significant year-to-year variation in overall densities of the two most common tree species and the combined densities of all other tree species (significant year effects; Table 3a and Figure 2). Gaps increased total seedling densities of black cherry, red maple, and all other tree species combined, early in the study, but these differences disappeared by the end of the study (significant gap \times year interaction; Figure 2a–c). Seedling densities for the two dominant species were often greater in areas open to deer. Over the course of the 10-year experiment, black cherry densities were 54% greater in unfenced areas ($\bar{X}_{\text{Control}} = 19.0 \pm 2.6$ seedlings $\cdot \text{m}^{-2}$ vs. $\bar{X}_{\text{Fence}} = 12.3 \pm 1.7$ seedlings $\cdot \text{m}^{-2}$; Table 2, Figure 3a). Additionally,

although deer alone did not affect red maple seedling densities (Figure 3b), in some years, fern gaps in unfenced areas had the greatest red maple seedling densities (significant fence \times gap \times year interaction; Table 3; Appendix S1: Figure S3). Seedling densities of all other tree species combined varied over time in response to deer exclusion (significant fence \times year interaction; Table 2), but the pattern was erratic across time and non-significant within years (Figure 3c).

Treatment effects on seedling establishment rates largely paralleled treatment effects on overall seedling density with two notable exceptions (Appendix S1: Table S1, Figure S4). First, although fern gaps increased total black cherry seedling densities, black cherry establishment rates were unaffected by gaps (Appendix S1: Table S1, Figure S4a). Second, when averaged over the course of the experiment, establishment rates of all other woody species combined were greater with deer present ($\bar{X}_{\text{Control}} = 1.5 \pm 0.4$ germinants $\cdot \text{m}^{-2}$ vs. $\bar{X}_{\text{Fence}} = 0.9 \pm 0.2$ germinants $\cdot \text{m}^{-2}$; Appendix S1: Table S1, Figure S4f), whereas overall seedling density was unaffected by deer.

Seedling height

Gaps significantly increased black cherry seedling height; however, the magnitude of the difference, at most, was 3 cm. Moreover, maximum heights of black cherry, averaged across either fence or gap treatments in 2010, were no different than at the beginning of the study (Table 5, Figure 2d). Gaps significantly increased red maple maximum seedling height and this difference grew to ~ 10 cm by 2010 (Table 5, Figure 2e). Gaps did not cause an increase in seedling height for all other tree species combined; however, height of these species steadily increased over time (Table 5, Figure 2f). Browsing did not affect

TABLE 2 Effects of white-tailed deer (*Odocoileus virginianus*) exclusion (i.e., Fence) and the creation of fern gaps from 2001 to 2010 on total seedling densities, species richness, and species diversity (H')

Effect	Total density		Richness		Diversity (H')	
	F-value	p-value	F-value	p-value	F-value	p-value
Fence	$F_{1,38} = 3.16$	0.0832	$F_{1,22} = 0.13$	0.7270	$F_{1,50} = 0.01$	0.9176
Fern gap	$F_{1,82} = 27.62$	<0.0001	$F_{1,58} = 39.47$	<0.0001	$F_{1,74} = 13.98$	0.0004
Fence \times Fern gap	$F_{1,51} = 0.54$	0.4671	$F_{1,58} = 0.05$	0.4823	$F_{1,74} = 1.35$	0.2485
Year	$F_{6,213} = 60.32$	<0.0001	$F_{6,176} = 65.36$	<0.0001	$F_{6,179} = 110.72$	<0.0001
Fence \times Year	$F_{6,52} = 2.22$	0.0559	$F_{6,176} = 1.24$	0.2858	$F_{6,179} = 1.06$	0.3902
Fern gap \times Year	$F_{6,212} = 5.14$	<0.0001	$F_{6,176} = 3.01$	0.0080	$F_{6,179} = 1.36$	0.2347
Fence \times Fern gap \times Year	$F_{6,51} = 0.23$	0.9641	$F_{6,176} = 1.10$	0.3630	$F_{6,179} = 0.73$	0.7284

Note: Seedling densities were modeled using a gamma distribution with a log link function, whereas richness and diversity were both modeled using a normal distribution.

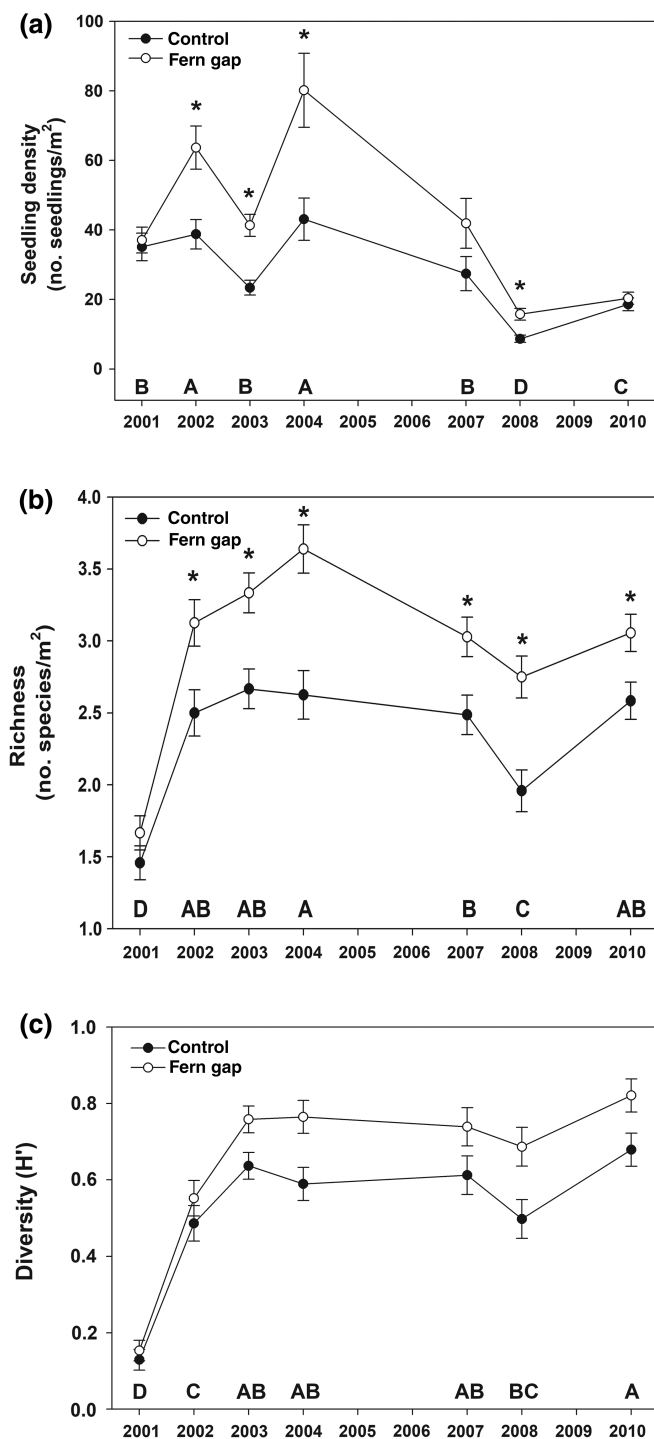


FIGURE 1 The effect of fern gaps from 2001 to 2010 on (a) overall seedling density, (b) seedling species richness, and (c) diversity (Shannon-Wiener index, H'). Back-transformed seedling density mean and standard error ($\pm 1SE$) are reported. Asterisks denote significant ($p < 0.05$) pairwise differences between treatments in a particular year following a significant treatment \times year effect. Different letters denote significant pairwise differences among years

heights of either black cherry or red maple (Table 5, Figure 3d,e). However, averaged across the study, browsing did reduce height of all other tree species combined with

seedlings within fences being $\sim 8\text{--}9$ cm taller than those exposed to browsing (significant browsing effect; Table 5, Figure 3f).

Species composition

Understory gap creation, but not browsing, led to the formation of contrasting communities in gaps versus the intact fern canopy in 2001 and 2004 (Table 4, Figure 4). In contrast, by 2010, deer exclusion, but not gap formation, created contrasting communities (Figure 3). Pin cherry was significantly associated ($p < 0.05$) with fern gaps in 2001 and 2004 ($\text{IndVal}_{01} = 0.57$, $\text{IndVal}_{04} = 0.68$) as were birch, white ash, and cucumber magnolia in 2004 ($\text{IndVal}_{01} = 0.64$, 0.58 , and 0.34 , respectively). In 2010, black cherry was significantly associated with unfenced, control areas ($\text{IndVal} = 0.78$).

DISCUSSION

Static and constrained forest regeneration

We excluded deer for a decade and created understory canopy gaps that substantially increased light availability for 4 years after gap creation and likely to persist for several years thereafter. Although the manipulation of these two major biological filters did affect tree regeneration in ways that were consistent with the predictions of our hypotheses, few differences persisted by the end of the 10-year study. Moreover, even when the analyses revealed lasting changes in community composition, these were not caused by understory gap creation or the manipulation of browsing, per se. Rather, we suspected that observed changes were largely due to variation in seed dispersal and a substantial decline in black cherry recruitment over the 10 years of the study. In the following paragraphs, we identify the importance of dispersal and the potential role legacy effects play in explaining these unexpected results.

Numerous studies have shown that chronic deer browsing can mediate forest regeneration and cause substantial declines in plant diversity (reviewed by Côté et al., 2004). In general, browse-induced changes to vegetation appear rapidly where light levels are high following overstory disturbance (e.g., Horsley et al., 2003; Nuttle et al., 2013) and more gradually (i.e., ≥ 10 years) in areas where light is limiting due to an intact overstory (e.g., Begley-Miller et al., 2014; Kain et al., 2011; Long et al., 2007). Here, we found that our manipulations of browsing across a decade failed to cause ecologically important changes of large magnitude in the regenerating tree community. Specifically, deer did not

TABLE 3 Effects of white-tailed deer (*Odocoileus virginianus*) exclusion (i.e., Fence) and the creation of fern gaps from 2001 to 2010 on total seedling densities of black cherry (*Prunus serotina*), red maple (*Acer rubrum*), and all other tree regeneration pooled

Effect	Black cherry		Red maple		Other regeneration	
	F-value	p-value	F-value	p-value	F-value	p-value
Fence	$F_{1,62} = 5.11$	0.0273	$F_{1,29} = 0.50$	0.4870	$F_{1,48} = 0.08$	0.7834
Fern gap	$F_{1,58} = 6.45$	0.0138	$F_{1,134} = 26.34$	<0.0001	$F_{1,79} = 12.75$	0.0006
Fence × Fern gap	$F_{1,58} = 0.47$	0.4954	$F_{1,134} = 0.66$	0.4193	$F_{1,79} = 0.79$	0.3774
Year	$F_{6,185} = 58.65$	<0.0001	$F_{6,163} = 92.24$	<0.0001	$F_{6,167} = 36.47$	<0.0001
Fence × Year	$F_{6,185} = 0.66$	0.6805	$F_{6,163} = 1.83$	0.0970	$F_{6,167} = 2.22$	0.0440
Fern gap × Year	$F_{6,185} = 5.97$	<0.0001	$F_{6,163} = 4.13$	0.0007	$F_{6,167} = 4.57$	0.0003
Fence × Fern gap × Year	$F_{6,185} = 0.22$	0.9703	$F_{6,163} = 2.21$	0.0446	$F_{6,167} = 1.08$	0.3735

Note: Seedling densities were rounded to nearest whole number and right skewed and overdispersed; hence, they were tested using a gamma distribution with a log link function.

affect overall community-level stem densities, richness, or diversity over the 10-year period, nor did their exclusion result in increased seedling densities of black cherry, red maple, or all other tree taxa combined for the duration of the study. As predicted, the elimination of browsing did cause an overall increase in height of tree species other than black cherry or red maple, a group containing several palatable species including sugar maple and white ash (Healy, 1971; Latham et al., 2005; Royo & Stanovick, 2019). Yet, even here, the magnitude of the response was at most 9 cm over the course of the decade.

Notably, although observed changes in composition in fenced areas in 2010 partially supported our expectations, the mechanism underlying the change is likely not browsing, as hypothesized, but rather other types of activity from deer and other mammals. Both establishment and overall seedling densities of the generally unpalatable species, black cherry, were greater outside fences, versus inside, which led to a slight shift (low R^2 for PERMANOVA) in species composition over time. If this compositional shift was caused by browsing, we would have expected a reduction in relatively more palatable species in control areas (Horsley et al., 2003; Nuttle et al., 2011); but this did not occur. Quite the opposite, in some years, red maple densities in fern gaps and establishment of all other tree species combined were both greater in unfenced, control areas. Although speculative, we suggest that the fences served as barriers to seed dispersal, thereby elevating seedling densities in unfenced areas, relative to within the exclosures (e.g., Pellerin et al., 2010). The fences excluded large mammals, known to consume black cherry drupes, including deer and other mammalian omnivores (e.g., bear, foxes), which then disperse these seeds via endozoochory (LoGiudice & Ostfeld, 2002; Marquis, 1990). The smaller mesh size of polypropylene fencing also accumulated heavy plant detritus along the base and thus were

likely to serve as a windbreak, and at the same time, reduce small mammal entry, thereby limiting secondary seed dispersal from wind and scatter-hoarding activities of small mammals into the exclosure (Matlack, 1989; Vander Wall et al., 2005). Additionally, trampling effects and other non-trophic disturbances caused by deer and other animals are known to enhance seedling emergence (e.g., Chips et al., 2014; Nomiya et al., 2003). It is unlikely that variation in seedfall explained the differences in seedling densities, because overstory tree basal area was either equivalent (red maple) or lower (black cherry) in control areas, relative to within the exclosures (Table 1).

The relatively minor browsing impacts on the seedling stratum may be due to a variety of factors. First, regional deer densities declined over the course of our experiment. Estimated deer densities in 2001 averaged 11.2 deer·km⁻², densities that are greater than pre-settlement values and higher than the threshold whereby browsing becomes inimical to forest regeneration. However, beginning in the fall of 2003, land managers implemented new regulations that intensified the culling efforts by hunters, which quickly halved deer densities regionally, and thus probably reduced browsing pressure (Royo & Stout, 2019). Second, the seedling layer in our study was overwhelmingly dominated by low to moderately palatable species (i.e., black cherry and red maple, respectively; Healy, 1971) for which seedling heights averaged at most <20 cm, thus making them smaller than the threshold sizes typically browsed by deer (0.2–1.8 m; Frerker et al., 2013). Additionally, these generally small individuals were largely overtopped by a hay-scented fern canopy (30–74 cm tall; Cody et al., 1977), probably making them far less apparent to deer.

In addition to the likely low browse pressure experienced by small seedlings, we suggest that excluding deer

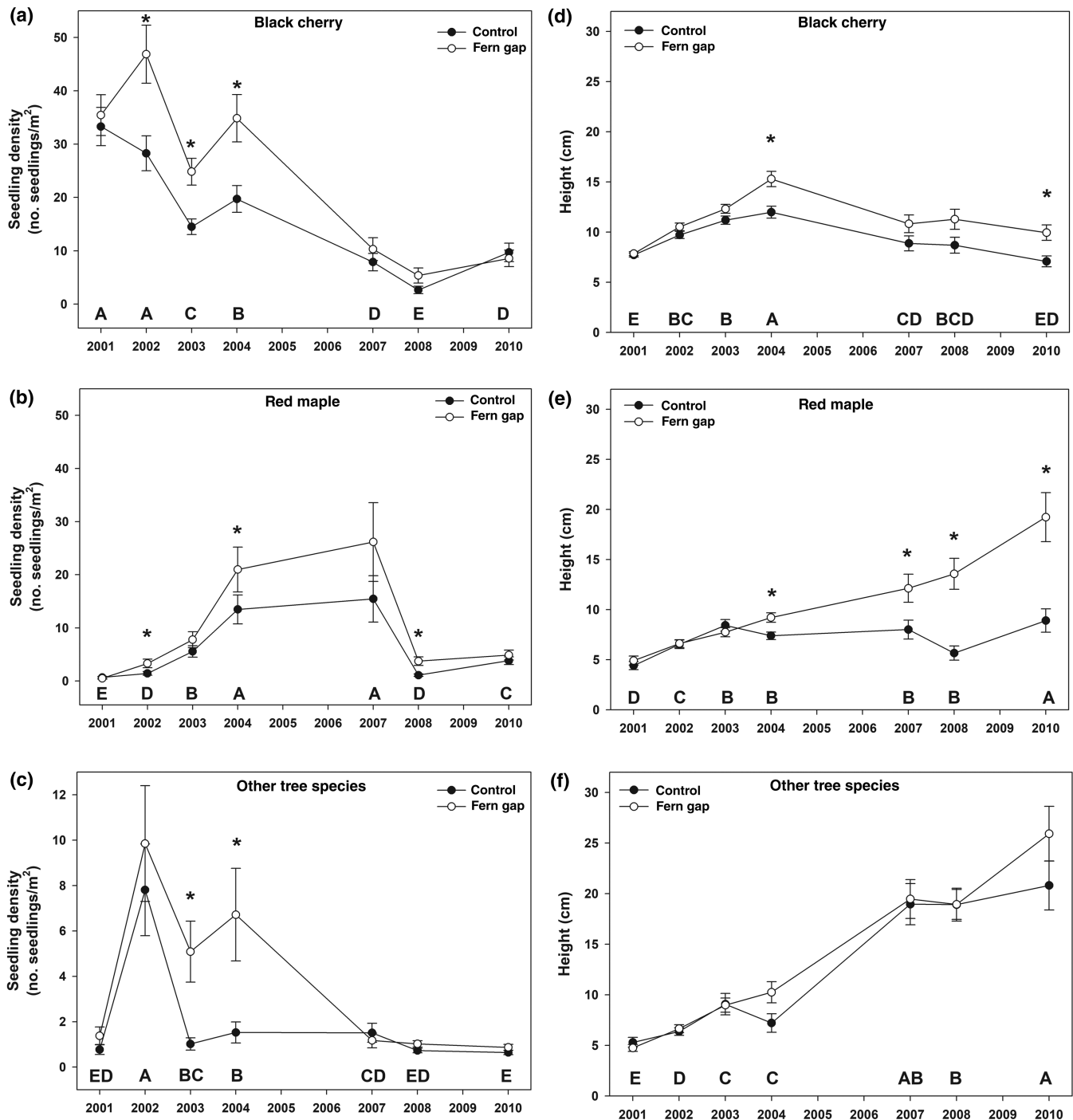


FIGURE 2 The effect of fern gaps from 2001 to 2010 on (a) black cherry (*Prunus serotina*), (b) red maple (*Acer rubrum*), (c) all other tree species seedling densities, (d) black cherry, (e) red maple, and (f) all other tree species stem heights. Seedling height is based on height of tallest stem, per species. Back-transformed means and standard errors (± 1 SE) are reported. Asterisks denote significant ($p < 0.05$) pairwise differences between treatments in a particular year following a significant treatment \times year effect. Different letters denote significant pairwise differences among years

for a decade, or even the low-moderate deer densities found outside the exclosures, failed to alter forest regeneration because of regional browse legacies that include an impoverished overstory and a dense fern layer, which had been present for decades. Nearly a century of

browsing by high density deer herds created a stasis, caused in part by a dense fern layer and an impoverished overstory community (e.g., Royo et al., 2010). Throughout the Allegheny Plateau region of the eastern United States, forest succession following the early 20th century clearcuts

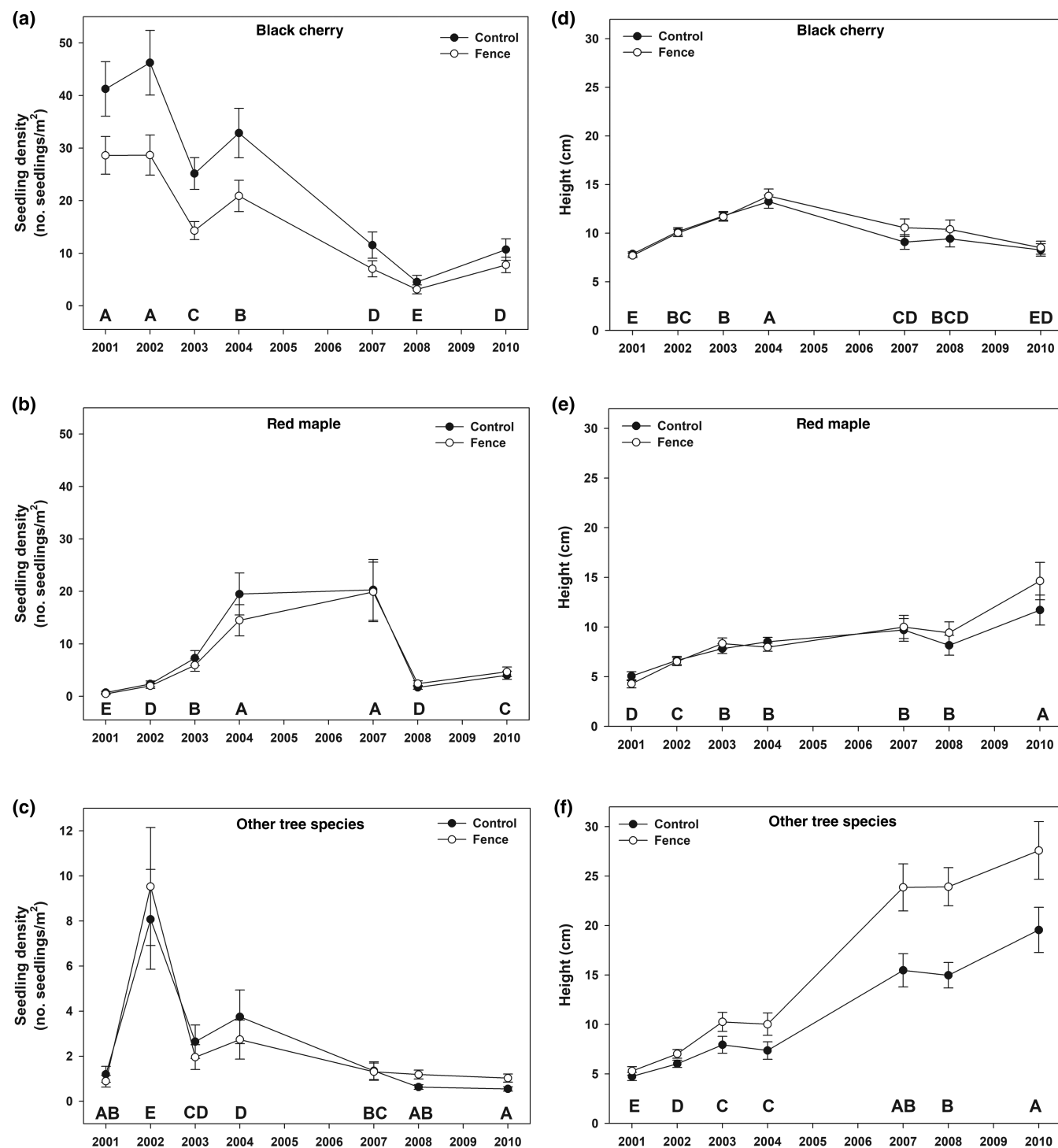


FIGURE 3 The effect of white-tailed deer (*Odocoileus virginianus*) exclusion from 2001 to 2010 on (a) black cherry (*Prunus serotina*), (b) red maple (*Acer rubrum*), (c) all other tree species seedling densities, and (d) black cherry, (e) red maple, and (f) all other tree species stem heights. Seedling height is based on height of tallest stem, per species. Back-transformed means and standard errors (± 1 SE) are reported. Different letters denote significant pairwise differences among years

coincided with and was shaped by chronically high levels of browsing (Hough & Forbes, 1943; Whitney, 1990), leading to the ascendancy of the shade-intolerant and relatively unpalatable black cherry (Royo et al., 2021).

Experimental documentation of the role that browsing plays in creating depauperate forests following harvests comes from a long-term controlled browsing experiment in the region (Horsley et al., 2003; Nuttle et al., 2011;

TABLE 4 Response of tree seedling composition to fern gap creation and white-tailed deer (*Odocoileus virginianus*) exclusion (i.e., Fence) treatments one (2001), four (2004), and 10 (2010) years post-treatment

Effect	2001			2004			2010		
	F-value	R ²	p-value	F-value	R ²	p-value	F-value	R ²	p-value
Fence	$F_{1,67} = 0.32$	0.004	0.7470	$F_{1,67} = 0.60$	0.008	0.5410	$F_{1,67} = 2.87$	0.039	0.0340
Fern gap	$F_{1,67} = 2.26$	0.032	0.0570	$F_{1,67} = 5.23$	0.071	0.0010	$F_{1,67} = 1.19$	0.016	0.2270
Fence × Fern gap	$F_{1,67} = 1.83$	0.026	0.1010	$F_{1,67} = 0.48$	0.006	0.6890	$F_{1,67} = 2.03$	0.027	0.0590

Note: Permutational analyses of variance analyses (PerMANOVA) were run using the *Adonis* function in the R package, *vegan* (Oksanen et al., 2019).

Tilghman, 1989). Here, stands exposed to deer densities of 18 and 25 deer·km⁻² had up to five times greater fern cover and two times greater basal area of black cherry compared with stands where deer densities were fewer than 8 deer·km⁻². At our experimental sites, black cherry and red maple jointly dominate the overstory (74%–99%; mean = 89% of total basal area). In undisturbed forests, the extant overstory community directly shapes propagule supply and, thus, largely determines the composition of the germinating seedling layer (Fisichelli et al., 2013; McGarvey et al., 2013; Webster et al., 2018; Willis et al., 2016). The primacy of an impoverished propagule supply is clear at our study sites, because the combined relative abundance of red maple and black cherry in the seedling layer mirrored their dominance in the overstory (see Table 1 and Figure 4). This depauperate and static forest regeneration is common in the region and occurs across a range of deer densities and overstory management conditions (Horsley et al., 2003).

Fern as an ecological filter and germination phenology

The creation of gaps in the hay-scented fern canopy caused a recruitment burst for multiple species and increased total seedling density, species richness, diversity (Shannon–Wiener index, H'), and even altered species composition. However, the increase in seedling density and shifts in composition due to fern gaps waned during the experiment. This is likely to have occurred because many seedlings of the relatively shade-intolerant species were established when the fern gaps provided a temporary window of higher light at the forest floor, but these individuals were unable to persist at light levels found under the intact tree canopy. These understory light levels would have declined further with the inexorable clonal re-invasion of the gaps by hay-scented fern following 2004. The impact of fern cover on tree recruitment was contingent on how the timing of fern shading effects interacted with tree species' phenology, shade tolerance, and seed-banking ability. For example, fern cover

dampened red maple establishment, whereas creating fern gaps did not affect black cherry establishment. Black cherry germinates from early to mid April before maturing hay-scented-fern fronds cast deep shade (Hill, 1996). In contrast, red maple seeds disperse in the spring and continue to germinate into summer (Walters & Yawney, 1990), thus exposing a portion of the seed cohort to increasingly shaded conditions under the maturing fern stratum (George & Bazzaz, 1999a; Royo & Carson, 2008). Moreover, although black cherry and red maple were both taller in fern gaps, only the more shade tolerant red maple capitalized on the higher understory light conditions through greater growth over time, whereas the shade-intolerant black cherry stagnated (Horsley, 1993a). Fern gaps also initially enhanced the recruitment of other shade-intolerant and intermediately tolerant taxa, including pin cherry, birch, and white ash. The increase in light, and possibly soil temperature, under fern gaps probably triggered pin cherry germination, which also occurred following overstory gaps (Marks, 1974; Nuttle et al., 2013). In contrast, fern gaps decreased shading and fern frond litter cover, both factors known to limit birch recruitment (George & Bazzaz, 1999a). In summary, the hay-scented fern stratum is an archetypal example of a recalcitrant understory layer known to strongly filter tree emergence, survival, and growth through a variety of mechanisms in temperate forests globally (Royo & Carson, 2006; reviewed by De Lombaerde et al., 2021).

Recalcitrant understory layers exacerbated by browsing can persist long after the deer population have reduced (Nuttle et al., 2014). In Massachusetts, USA, de la Cretaz and Kelty (1999) evaluated the effects of 3 years of deer population culls on understory vegetation following decades of high deer densities. Lowering deer herds did little to alter hay-scented fern dominance and enhance tree recruitment. Slow vegetation recovery following deer herd reductions are common in forests that are experiencing strong legacies of browsing (reviewed by Tanentzap et al., 2012). Here, we experimentally demonstrated that recalcitrant hay-scented fern layers limit tree seedling recruitment, even following a decade of complete deer exclusion. The browse legacies manifested here

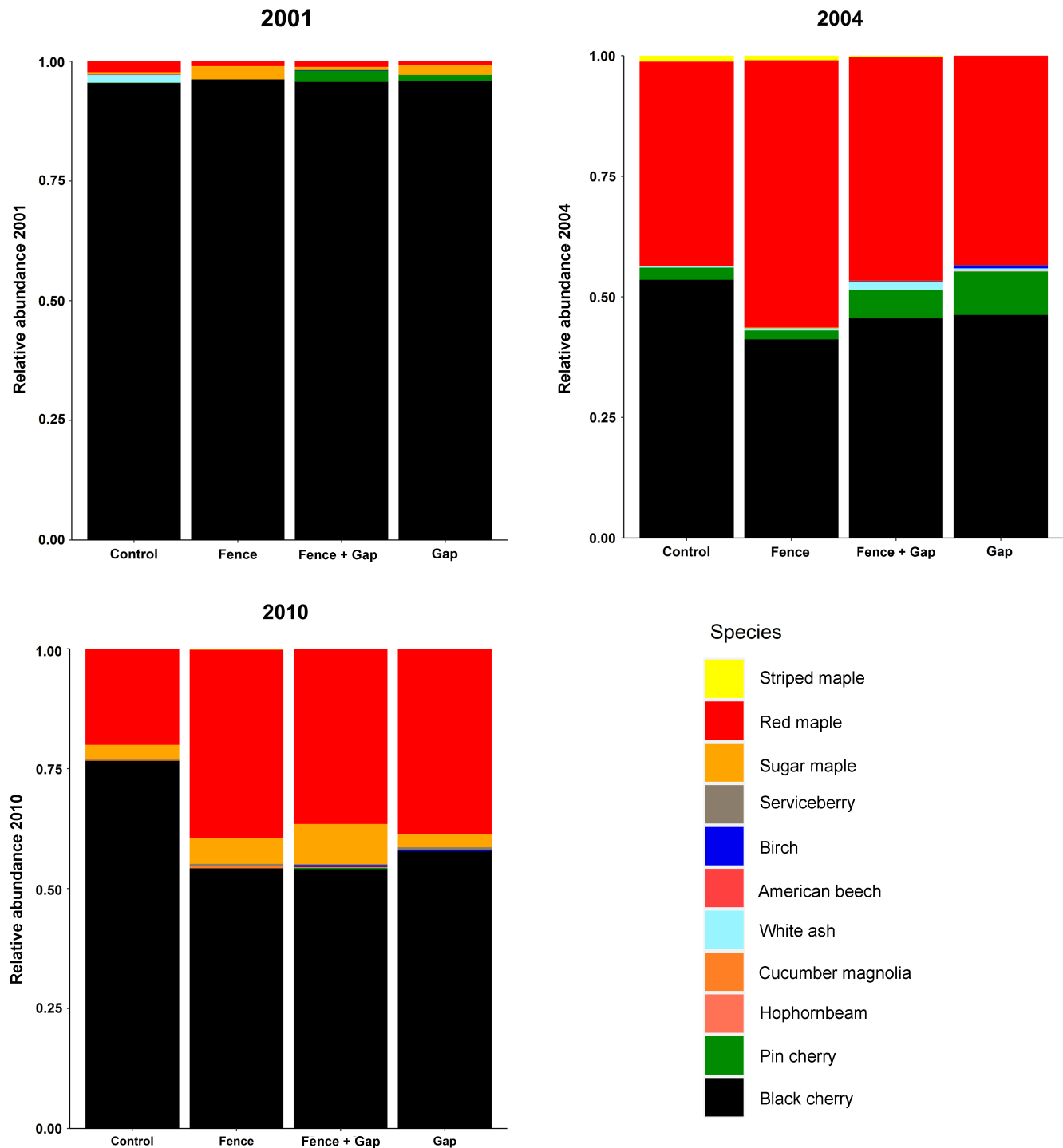


FIGURE 4 Relative abundance of woody species in understory, by treatment, in 2001, 2004, and 2010. Fern gaps altered species composition in 2001 (PerMANOVA_{GAP}: $F = 2.26$, $R^2 = 0.03$, $p = 0.04$) and 2004 (PerMANOVA_{GAP}: $F = 5.23$, $R^2 = 0.07$, $p = 0.0001$), whereas only browsing altered composition by 2010 (PerMANOVA_{FENCE}: $F = 2.87$, $R^2 = 0.04$, $p = 0.02$). Although the overwhelming dominance (>95% of seedlings) of black cherry (*Prunus serotina*) in 2001 or black cherry and red maple (*Acer rubrum*) combined in 2004 and 2010 hinders discernment of co-occurring species, fern gaps contained greater pin cherry (*Prunus pensylvanica*) in 2001 and 2004 (IndVal₀₁ = 0.57, IndVal₀₄ = 0.68; green color) and greater birch (*Betula* spp.), white ash (*Fraxinus americana*), and cucumber magnolia (*Magnolia acuminata*) in 2004 (IndVal₀₁ = 0.64, 0.58, and 0.34, respectively). In contrast, black cherry was associated with unfenced areas in 2010 (IndVal: 0.78). Additional species include striped maple (*Acer pensylvanicum*), sugar maple (*Acer saccharum*), serviceberry (*Amelanchier arborea*), American beech (*Fagus grandifolia*), and hop-hornbeam (*Ostrya virginiana*)

TABLE 5 Effects of white-tailed deer (*Odocoileus virginianus*) exclusion (i.e., Fence) and the creation of fern gaps from 2001 to 2010 on seedling heights of black cherry (*Prunus serotina*), red maple (*Acer rubrum*), and all other tree regeneration pooled

Effect	Black cherry		Red maple		Other regeneration	
	F-value	p-value	F-value	p-value	F-value	p-value
Fence	$F_{1,59} = 0.61$	0.4378	$F_{1,69} = 0.17$	0.6784	$F_{1,21} = 19.19$	0.0003
Fern gap	$F_{1,79} = 14.89$	0.0002	$F_{1,69} = 20.46$	<0.0001	$F_{1,67} = 1.49$	0.2267
Fence × Fern gap	$F_{1,79} = 0.74$	0.3910	$F_{1,69} = 0.02$	0.9004	$F_{1,67} = 0.08$	0.7789
Year	$F_{6,156} = 70.25$	<0.0001	$F_{6,122} = 21.31$	<0.0001	$F_{6,110} = 77.00$	<0.0001
Fence × Year	$F_{6,156} = 0.40$	0.8791	$F_{6,122} = 1.28$	0.2733	$F_{6,110} = 1.20$	0.3138
Fern gap × Year	$F_{6,156} = 2.96$	0.0092	$F_{6,122} = 6.27$	<0.0001	$F_{6,109} = 1.49$	0.1876
Fence × Fern gap × Year	$F_{6,156} = 0.56$	0.7596	$F_{6,122} = 0.24$	0.9614	$F_{6,109} = 0.26$	0.9531

Note: Seedling height values were based on average height of tallest stem, by species. Data distribution was continuous, right skewed and overdispersed and thus was tested using a lognormal distribution.

by a depauperate canopy and a recalcitrant fern layer will be difficult to reverse. Indeed, a complementary study at these sites demonstrated that even supplemental seeding of multiple species spanning a range of shade tolerance failed to enhance tree recruitment due to the intensified small mammal seed predation under the fern cover (Royo & Carson, 2008). Thus, in the absence of management interventions (e.g., herbicide application; Engelman & Nyland, 2006) these recalcitrant fern layers can suppress tree recruitment for decades.

Changes in black cherry dominance

Our long-term experiment coincidentally captured a window in time when black cherry regeneration dynamics, the dominant species regionally, fundamentally changed. When we began our study in 2001, anecdotal reports surfaced that the previously consistent and abundant black cherry establishment had grown erratic and had diminished (Royo et al., 2021). Our long-term monitoring over a decade documented average black cherry seedling densities decreased by an order of magnitude. The calculated average decline masks the severity of the deterioration given the most commonly observed density value for black cherry (i.e., mode) dropped from 48 seedlings·m⁻² in 2002 to just one (1) seedling·m⁻² by 2010. The lack of sustained effects for most of the treatments in this study provides the first documentation of these declines in an experimental context, thereby allowing us to exclude some potential underlying factors. Our findings demonstrate that seedling densities declined at the same rate in both the fenced and control plots over the decade (i.e., no fence × year interaction). Similarly, we note that, although fern cover did suppress black cherry seedling densities by 30%–40% in any given year, the declines over time were far more

pronounced. Thus, we suspect that the observed declines in black cherry regeneration were not due to variation in browse pressure or sustained fern suppression. Rather, Royo et al. (2021) hypothesized that increased pathogenicity by antagonistic microbes and sharp reductions in nitrate deposition may underlie the observed declines.

Conclusions

Nearly a century of deer overabundance in the decades following exploitative harvesting at the turn of the 20th century in the Allegheny region created a floristically impoverished forest characterized by a recalcitrant hay-scented fern stratum and an overstory dominated by only two tree species. Our results demonstrated that managing light availability at the forest floor is vital to initially augment seedling layer diversity. Within the first 4 years of mitigating the deeply shaded conditions caused by fern, we significantly increased seedling density by nearly two-fold and altered the advance regeneration layer composition to include several shade-intolerant or intermediately tolerant species. Nonetheless, these species remain shaded beneath an intact canopy, thus overstory removal treatments timed with herbicide treatments or mechanical removal to control the fern layer will likely be required to capitalize on the diversity gains made by controlling the recalcitrant fern layer (Ristau et al., 2011; Royo et al., 2019). Moreover, despite not detecting strong deer browsing impacts on the small seedlings censused in this study during an era of lower deer densities (i.e., <8 deer·km⁻²), a wealth of evidence demonstrated that diverse regeneration often hinges on managing deer impacts when densities are higher (Côté et al., 2004; Horsley et al., 2003; Nuttle et al., 2013; Russell et al., 2001). In regions where deer densities are higher than those

experienced during this study, this can be accomplished directly via fencing or culling the herd or indirectly through management actions that augment the abundance of forage-rich habitats (e.g., early successional forest), thereby diluting browse impact (Beguín et al., 2016; Royo et al., 2017).

Forests within the region confront an ever-escalating array of stressors including introduced pests and pathogens along with increasing climate-related disturbance regimes (Cohen et al., 2016; Herms & McCullough, 2014; Houston, 1994; Kizlinski et al., 2002). These stressors are increasing overstory tree mortality, thereby diminishing propagule supply and hastening canopy gap formation (Eschtruth et al., 2006; Herms & McCullough, 2014). Typically, canopy gap formation should stimulate diverse tree recruitment and growth (i.e., “gap-phase regeneration paradigm” sensu Whitmore, 1989). However, these dynamics are now occurring over depauperate understories dominated by a recalcitrant vegetation layer and experiencing continued browse pressure, factors known to strongly constrain regeneration responses (Kern et al., 2012; Walters et al., 2020). Consequently, the future forests of this region may inexorably march toward further impoverishment in the absence of stand replacement disturbances of sufficient size and severity that may disrupt the recalcitrant vegetation layer, lessen browse pressure, or both (e.g., Royo et al., 2016). Left unchecked, these threats and their ensuing impacts may compel ecologists and land managers to employ heroic efforts across broad portions of the landscape to sustain forest diversity. Active forest management that promotes the establishment and growth of diverse regeneration may not only be useful, but perhaps indispensable, to sustain diversity in these forests, particularly in the face of climate change.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Royo, 2021) are available in the USDA Forest Service Research Data Archive at <https://doi.org/10.2737/RDS-2021-0039>.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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