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Understory plant communities fail to recover species diversity after excluding deer for nearly 20 years

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Abstract

White-tailed deer (*Odocoileus virginianus*) have been overabundant in eastern North America for more than five decades, resulting in depauperate understories and ricocheting effects on higher trophic levels. Even after deer populations are reduced, understory plant communities may fail to recover for an unknown length of time due to persistent legacy effects. We surveyed understory plant communities in six deer exclosures and paired reference plots in northwestern Pennsylvania to determine the degree to which 19 years of deer exclusion was sufficient for recovery of species richness, diversity, percent cover, and understory structural complexity. We observed a 2.3-fold increase in tree cover and a 60% reduction in fern cover in the ground layer, as well as a 114-fold increase in foliage density between 80 and 200 cm above ground level, in exclosures compared to reference plots. However, the exclosures did not permanently support higher overall percent cover, species richness, or diversity in the ground layer, nor did we detect any meaningful divergence in community composition between exclosures and reference plots. We conclude that 19 years of release from chronic over-browsing are sufficient to restore understory structural complexity, but recovery of diversity in the ground layer will require more time or direct intervention.

Key words: white-tailed deer, exclosure, legacy effect, understory plant community, Allegheny National Forest

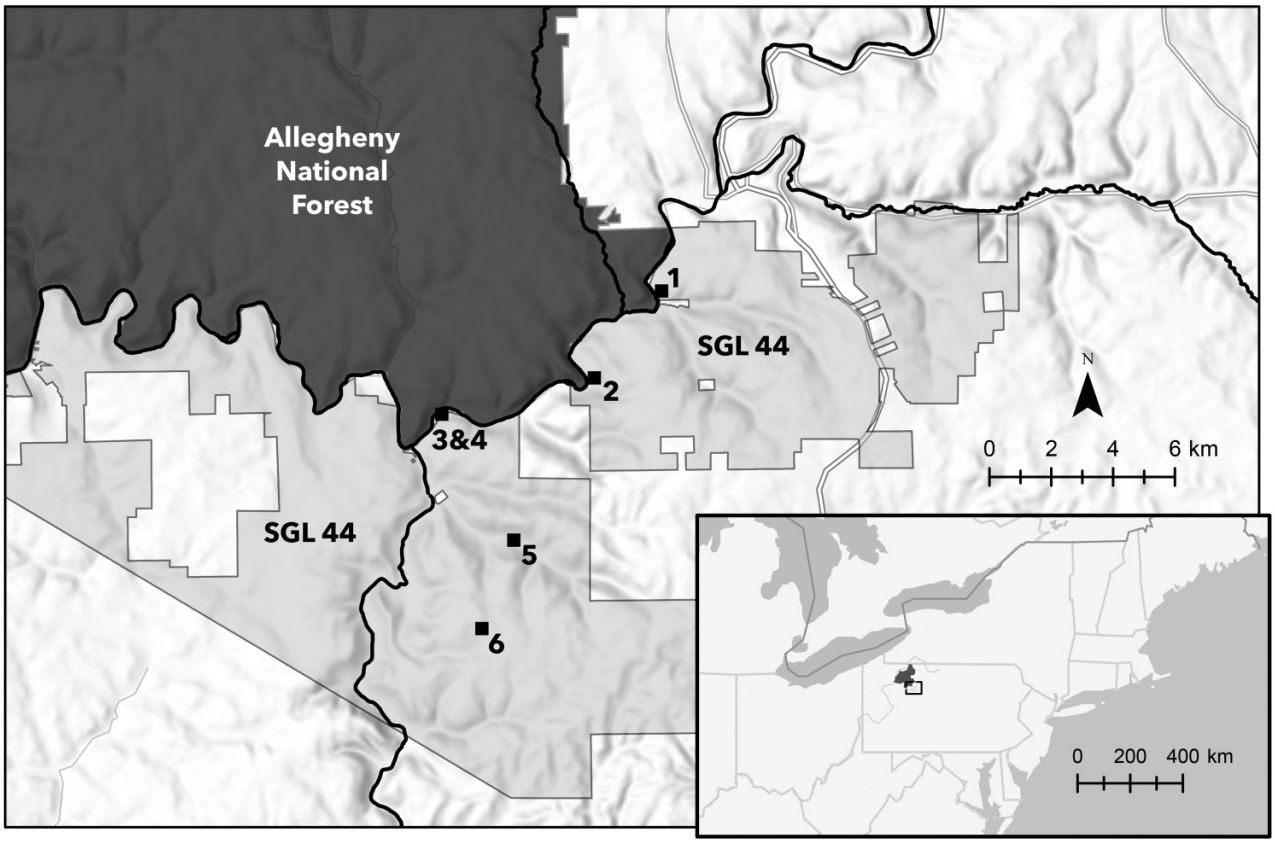
Introduction

In eastern North American forests, overabundant white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) are causing substantial declines in plant abundance, diversity, and reproduction, and are also altering plant species composition and simplifying understory vegetation structure (Rooney 2001; Russell et al. 2001; Côté et al. 2004; Russell et al. 2017). Heavy browse pressure that reduces palatable species abundance can also lead to the formation of dense recalcitrant understory layers composed of both non-native and native unpalatable and browse-resistant species (Horsley and Marquis 1983; Stromayer and Warren 1997; Royo and Carson 2006). Research throughout the Allegheny National Forest Region (ANFR) of northwestern Pennsylvania paints a bleak picture of the consequences of decades of over-browsing (e.g., Rooney and Dress 1997; Horsley et al. 2003; Kain et al. 2011; Carson et al. 2014; Royo and Carson 2022).

Although plant communities have been documented responding positively to the alleviation of browse pressure (Killmaster et al. 2007; Jenkins et al. 2015), recovery is often very slow and limited (Tanentzap et al. 2012). Long-term over-browsing may lead to persistent legacy effects, whereby reducing or eliminating browsing for a decade or more fails to restore diversity to what were once species-rich forest communities (e.g., Royo et al. 2010; Reed et al. 2021; Royo and Carson 2022). Exclosure studies across eastern North America have found that excluding deer for 8–20 years often does not lead to increases in species diversity; the understory communities remain depauperate (Webster et al. 2005; Habeck and Schultz 2015; Pendergast et al. 2016; Royo and Carson 2022). Nuttle et al. (2014) compared stands that had been experimentally exposed to varying deer densities (3.9–31.2 per km^2) during early succession. After 20 years of ambient deer density, the stands established at high deer density had lower forb and woody species cover, lower richness, and about five times greater fern cover compared to the low-density stands. In addition, Royo et al. (2010) found that reducing deer densities by 50% (about 12 to <6 per km^2) for four years across more than 30 000 ha of the Allegheny National Forest doubled forb cover and tripled shrub cover but did not lead to an increase in species richness.

The primary driver of legacy effects is that over-browsing has either extirpated or led to sparse distributions of browse-sensitive species both locally and regionally (Rooney and Dress 1997; Schumacher and Carson 2013). Browse-sensitive species frequently persist within isolated deer refugia such as the tops of large boulders and treefall tip-up mounds, and within dense piles of woody debris (Comisky et al. 2005;

Fig. 1. Regional location and site details of the exclosures in State Game Lands Number 44 (SGL 44) in northwestern Pennsylvania (PA), USA (extending from 41°24′1″N, 78°45′7″W to 41°19′36″N, 78°49′4″W; elevation approximately 410–650 m). The map was created using publicly available geospatial data from the Pennsylvania Game Commission, the US Forest Service, and the US Geological Survey in ArcGIS Pro (projection: Mercator Auxiliary Sphere; coordinate system: WGS 1984 Web Mercator; basemap from ArcGIS Pro).



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Krueger and Peterson 2006; van Ginkel et al. 2021). Once browsing has reduced vulnerable species to low and scattered abundance, it may take decades for these species to recover (Pendergast et al. 2016; Wilbur et al. 2017; Royo and Carson 2022) even if browsing intensity is reduced or eliminated. Forest plants that reproduce primarily vegetatively or have limited seed dispersal distances could be expected to spread and recolonize particularly slowly. Alternatively, vulnerable species may fail to recover from over-browsing because many forest understories, particularly in urban and urban-fringe forests, are infested with both non-native plant species, particularly shrubs, and invasive earthworms (Gaertner et al. 2017; Morrison 2017; Toth et al. 2020; Gorchov et al. 2021). It is likely that active management would be necessary to reintroduce many of these species, but the degree of management intensity remains unclear and likely varies according to local conditions and extirpated species.

In contrast to measures of species diversity, existing woody species often experience a period of rapid growth immediately following an alleviation of browse pressure (Jenkins et al. 2015; Wilbur et al. 2017). This results in an increase in vegetation density in the shrub and sapling layer and therefore a faster recovery of understory structural complexity (Rohleder 2013), an important habitat component that is positively associated with abundance of understory songbirds and arthropods (Bressette et al. 2012; Rushing et al. 2020).

Here we test the predictions that excluding deer for 19 years will (1) increase plant species richness, diversity, and overall percent cover (hereafter, "total cover"), (2) increase percent cover of trees, shrubs, forbs, and browse-sensitive plant species, (3) decrease percent cover of ferns, (4) create communities distinct from adjacent reference plots, and (5) increase understory structural complexity. Because of the long history of over-browsing in this region of Pennsylvania and elsewhere in eastern North America, it remains an open question whether nearly two decades of exclusion would lead to even partial recovery. Finally, we compare our 19-year experimental approach with two regional case studies that extend the temporal scale of legacy effects; namely, a single 60-year deer exclosure (Goetsch et al. 2011) and boulder-top refugia (Banta et al. 2005).

Methods

Study area

We conducted our study on Pennsylvania State Game Lands Number 44 (16 000 ha) which lies adjacent to the Allegheny

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Table 1. Example references for classification of plant species as browse-sensitive (criteria in "Methods" section). Nomenclature follows Rhoads and Block (2007).

Species	Common name	References
Acer rubrum L.	Red maple	Petrides 1941; Averill et al. 2017
Betula alleghaniensis Britton	Yellow birch	Banta et al. 2005
Cornus L. spp.	Dogwood	Petrides 1941; Alverson et al. 1988
Dryopteris intermedia (Muhl.) A. Gray	Wood fern	Banta et al. 2005
Erythronium americanum Ker Gawl.	Trout lily	Miller et al. 1992
Hamamelis virginiana L.	Witch hazel	Petrides 1941; Bressette et al. 2012
Maianthemum canadense Desf.	Canada mayflower	Rooney and Dress 1997; Royo et al. 2010
Maianthemum racemosum Link.	Solomon's plume	Averill et al. 2017
Medeola virginiana L.	Indian cucumber root	Alverson et al. 1988
Mitchella repens L.	Partridgeberry	Rooney and Dress 1997; Banta et al. 2005
Quercus alba L.	White oak	Alverson et al. 1988
Quercus montana Willd.	Chestnut oak	Bressette et al. 2012
Quercus rubra L.	Red oak	Averill et al. 2017
Rhus L. spp.	Sumac	Petrides 1941
Rubus L. spp.	Bramble	Horsley and Marquis 1983; Averill et al. 2017
Sassafras albidum (Nutt.) Nees	Sassafras	Averill et al. 2017
Trillium L. spp.	Wake-robin	Royo et al. 2010
Uvularia L. spp.	Bellwort	Miller et al. 1992
Viburnum acerifolium L.	Mapleleaf viburnum	Petrides 1941; Averill et al. 2017
Viola L. spp.	Violet	Rooney and Dress 1997; Banta et al. 2005

National Forest (207 600 ha; Fig. 1). The majority of the region is composed of closed-canopy, even-aged forest originating from exploitative lumber harvests around the turn of the 20th century. Our study site overstories were dominated by red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.), and also included black cherry (*Prunus serotina* Ehrh.), chestnut oak (*Quercus montana* Willd.), and white oak (*Quercus alba* L.; Table A1). The region has a cool, moist climate with a growing season of 100–130 days, average annual temperature of 7.8 °C, and average annual precipitation of 107 cm (Whitney 1990; Kain et al. 2011). White-tailed deer density surpassed 8 per km^2 in the ANFR by 1930 and largely remained high (9.7–17.4 per km^2) until herd reduction efforts brought it under 8 per km^2 in 2005, where it has remained since then (Whitney 1990; Royo et al. 2010; Royo and Stout 2019).

Field sampling

Six deer exclosures of varying sizes and shapes were erected by the Pennsylvania Game Commission on State Game Lands Number 44 in the year 2000 (2 m tall, 10 cm mesh wire fencing, ranging from 650 to 3000 m^2; Fig. 1). They were designed to exclude deer while allowing other smaller herbivores access (e.g., rabbits, squirrels, etc.). No data are available from the time of exclosure establishment. In May 2013, we established one 400 m^2 plot in the center of each of the six exclosures. One exclosure contained a small canopy gap, which was avoided by forming an L-shaped plot of the same size. We paired each exclosure with a 400 m^2 unfenced reference plot, about 3 m from the exclosure fence in the direction that appeared most comparable to the exclosure. We estimated percent cover of all vascular understory plant species below 1 m height in eight randomly placed 1 m × 1 m square subplots within each 400 m^2 plot. We conducted 20 min timed meander surveys throughout each 400 m^2 plot to identify any species that were missed by the 1 m^2 subplots. We repeated the survey in May 2019 with identical methods but sampled only five plot pairs because a treefall had badly damaged one of the exclosures. Sampling in both years occurred at a time when most plant species had already leafed out, but others, notably ferns, were still in the process of flushing out.

In May 2015, we conducted a three-dimensional foliage density survey in the lower shrub/sapling layer (≤2 m above ground; following Rohleder 2013) in four of the plot pairs. We randomly selected four or five points within each plot as nodes. The first plot pair sampled contained five nodes per plot; subsequent plots were reduced to four nodes to maximize time efficiency. We estimated the percentage of vegetation that occluded a 20 cm × 20 cm white card 2 m away from the node in all four cardinal directions (north, south, east, and west) at 20 cm height intervals beginning at ground level and extending up to 200 cm height.

To verify that forest stands were similar across all sites, we identified and recorded diameter at breast height (DBH) of all trees >13 cm DBH in the immediate vicinity of each plot. Because of variation in the shapes and sizes of the exclosures, area sampled varied from 650 to 1430 m^2 but always included the full 400 m^2 plot sampled for understory cover and diversity.

Data analysis

We quantified mean species richness at the plot level (400 m^2, $n = 6$ in 2013, $n = 5$ in 2019), including data from the meander surveys. We used R package "vegan" (Oksanen

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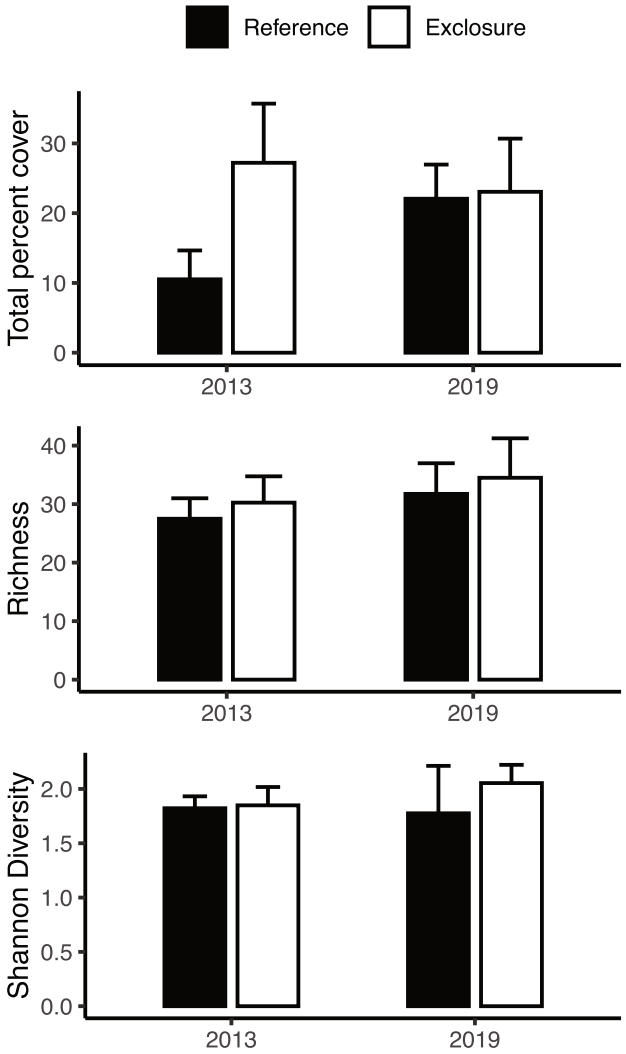
Fig. 2. Excluding deer did not cause significant increases in mean species richness or Shannon diversity (shown with bootstrap 95% confidence intervals). Total percent cover in the reference plots in 2013 was 62% lower than the exclosures in 2013 and 52% lower than the reference plots in 2019 (*post hoc* tests, $p = 0.008$ and 0.008, respectively; Table 2).



et al. 2020) to calculate the Shannon–Wiener diversity index in the combined eight 1 m^2 subplots surveyed in each 400 m^2 plot. Individual species browse sensitivity was determined by a brief literature survey. Species were included in our "browse-sensitive" category if the majority (at least two) of peer-reviewed articles stated or implied a browse-sensitive status (Table 1). "Browse-sensitive" was defined as (1) preferred forage by white-tailed deer, (2) intolerant of browsing, or (3) shown to suffer greater-than-expected negative effects from deer browsing.

To test our first three predictions (i.e., (1) species richness, diversity, and total cover will increase, (2) percent cover of trees, shrubs, forbs, and browse-sensitive plant species will increase, and (3) percent cover of ferns will decrease in exclosures compared to reference plots), we performed a series of eight two-way repeated measures analyses of variance (ANOVAs) (R package "MANOVA.RM"; Friedrich et al. 2022). The eight response variables were richness, diversity, total cover, tree species cover, shrub cover, forb cover, fern cover, and cover of browse-sensitive plant species. Graminoids were excluded from this analysis because they were at very low abundance, and the data remained non-normally distributed even after transformation. Each of the functional group cover variables was *log*-transformed for normality. There were two within-subject factors, exclosure treatment (fenced versus unfenced) and study year, and no between-subject factors. Each plot pair was considered an individual subject. We used the Benjamini–Hochberg method to generate adjusted *p*-values controlling the false discovery rate, which was set at 0.05. This procedure is valid under positive regression dependency (11 of the 28 variable pairings were correlated, $r \geq 0.50$; Benjamini and Yekutieli 2001). We tested the assumption of normality for the repeated measures ANOVA using the Shapiro–Wilk test and the assumption of homogeneity of variance across groups using Levene's test (R package "car"; Fox et al. 2022). Because of the paired design across study years, the compromised plot pair had to be excluded from this analysis. As a result of significant interaction terms in two of the ANOVAs, we conducted four *post hoc* paired *t* tests with Benjamini–Hochberg-corrected *p*-values for each ANOVA. We limited these comparisons to biologically meaningful group pairs, namely (1) 2013 exclosure versus 2013 reference, (2) 2019 exclosure versus 2019 reference, (3) 2013 exclosure versus 2019 exclosure, and (4) 2013 reference versus 2019 reference.

To test for possible divergence of community composition between exclosure and reference plots, we performed a two-way repeated measures permutational multivariate ANOVA test (PERMANOVA) using R package "vegan" (Oksanen et al. 2020). The two within-subject factors were exclosure treatment and study year. We used the Bray–Curtis index to generate the underlying distance matrix from our abundance data. We also calculated Sørensen's coefficient of similarity, which uses presence/absence data, including meanders, for each of the two surveys. Furthermore, we used R package "labdsv" (Roberts 2019) to perform an indicator species analysis (*sensu*Dufrêne and Legendre 1997) on our abundance data and determine if any individual species characterized either exclosure or reference plots. The indicator value for each species is calculated as the product of its relative frequency and its relative average abundance. *p*-Values are the results of 1000 iterations of randomized resampling.

We analyzed the results of the 3D structure survey with a two-way repeated measures ANOVA using the R package "MANOVA.RM" (Friedrich et al. 2022). Each plot pair was considered an individual subject, and the within-subject factors were exclosure treatment and height interval. The visual occlusion data had to be averaged across azimuths and nodes to generate a single plot-level value for each height interval. The response variable, % visibility occluded, was *log* transformed for normality. Despite the transformation, normality was rejected by the Shapiro–Wilk test. We used a permuted Wald-type statistic that is appropriate for non-normal distributions (Friedrich et al. 2022). As a result of a significant interaction

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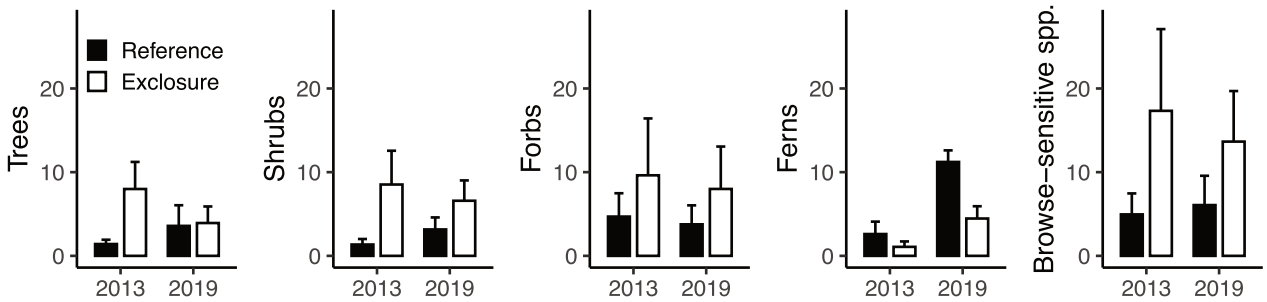
Table 2. Results of the main statistical analysis, a series of eight two-way repeated measures ANOVAs with exclosure treatment and study year as within-subject factors (mean ± SD). Statistically significant Benjamini–Hochberg-adjusted *p*-values are in bold (<0.05).

	Exclosure treatment			Study year			Exclosure × Year
Variable	Reference	Exclosure	*p*	2013	2019	*p*	Interaction
Richness	18.80 ± 5.41	17.70 ± 2.98	0.746	16.8 ± 3.16	19.70 ± 4.92	0.136	0.053
Diversity	1.80 ± 0.38	1.95 ± 0.23	0.483	1.84 ± 0.18	1.91 ± 0.42	0.689	0.483
Total cover	16.29 ± 8.34	25.14 ± 10.34	0.136	18.87 ± 11.97	22.57 ± 8.31	0.298	**0.050**
Tree cover	**2.49 ± 3.35**	**5.96 ± 3.96**	**0.019**	4.71 ± 4.48	3.75 ± 3.60	0.483	0.053
Shrub cover	**2.25 ± 1.72**	**7.55 ± 5.10**	**0.019**	4.94 ± 5.89	4.87 ± 3.14	0.483	**<0.001**
Forb cover	4.22 ± 3.49	8.81 ± 7.53	0.483	7.16 ± 6.97	5.88 ± 5.56	0.738	0.833
Fern cover	**6.91 ± 4.92**	**2.77 ± 2.33**	**<0.001**	**1.84 ± 1.79**	**7.84 ± 4.00**	**<0.001**	0.402
Browse-sensitive cover	**5.84 ± 3.92**	**15.24 ± 9.87**	**0.003**	10.89 ± 10.96	10.19 ± 6.86	0.833	0.689

Fig. 3. Mean percent covers of each functional group (with bootstrap 95% confidence intervals). Note that "Browse-sensitive spp." includes species found in other groups (Table 1 and Table 3). Trees, ferns, and browse-sensitive species showed a significant effect of exclosure treatment. Ferns also showed a significant effect of study year. Only shrub cover showed a significant Exclosure treatment × Year interaction (Table 2). In 2013, shrub cover was 6.3 times higher inside exclosures than outside (*post hoc*, $p = 0.031$).



term ($p < 0.001$), we conducted a series of *post hoc* paired *t* tests and used the Benjamini–Hochberg method to control the false discovery rate at 0.05. Because our research question concerned only differences between fenced and unfenced forest, and not between height intervals, we limited our *post hoc* tests to the 10 height interval pairs. The parametric *t* test is adequate because the deviation from normality was the result of reference plot data "piling up" at zero in the upper height intervals.

To test for possible canopy tree community differences between exclosure and reference plots, we calculated total richness and basal area (BA) for each plot using our canopy tree DBH data. We then performed an ANOVA on both richness and BA data with exclosure treatment as the main factor and a random effect term for site (exclosure/reference plot pair). We also tested for possible divergence of overstory species composition using a PERMANOVA on the species-BA matrix with a random effect term for site.

Results

Excluding deer for 19 years did not cause a significant increase in species richness or diversity compared to the reference plots ($p = 0.746$ and 0.483, respectively), and there was no significant change in these response variables between 2013 and 2019 ($p = 0.136$ and 0.689, respectively; Fig. 2 and Table 2). Tree species cover and browse-sensitive species cover within exclosures were respectively 2.3 times and 2.6 times that of the reference plots ($p = 0.019$ and 0.003, respectively). In contrast, fern cover was 2.5 times higher in reference plots ($p < 0.001$) and 4.3 times higher in 2019 versus 2013 ($p < 0.001$; Fig. 3 and Table 2). Both total cover and shrub cover had significant Exclosure treatment × Year interaction terms ($p < 0.001$ and $p = 0.050$, respectively). In 2013, shrub cover was 6.3 times higher inside exclosures than outside (*post hoc*, $p = 0.031$; Fig. 3) and total cover was 2.6 times as high in the exclosures (*post hoc*, $p = 0.008$). Total cover in reference plots subsequently increased 2.1-fold from 2013 to 2019 (*post hoc*, $p = 0.008$; Fig. 2 and Table 2).

The exclosure and reference communities were significantly different between years and between exclosure and reference plots (PERMANOVA, $p = 0.036$ and 0.024, respectively), but neither exclosure treatment nor year explained much variation ($r^2 = 0.11$ and 0.10, respectively). There was no Exclosure treatment × Year interaction ($p = 0.063$). Similarly, Sørensen's coefficient showed a high degree of community similarity between exclosures and reference plots in both 2013 (0.662) and 2019 (0.755). Red oak was the only species associated with exclosures (2013, indicator

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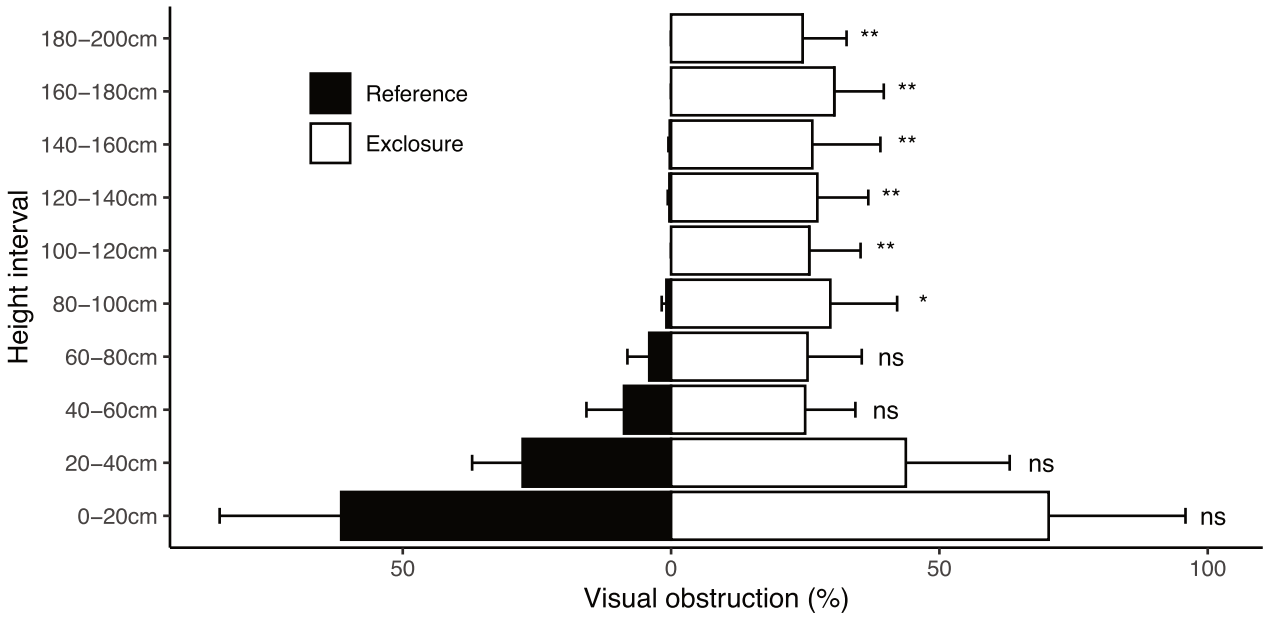
Table 3. Mean percent cover (±SD) of plant species in exclosure and reference plots, as well as *p*-values from the indicator species analysis (ISA). Species with an ISA *p*-value < 0.05 are in bold. Only positively identified species that occurred at ≥ 0.02 percent cover across the study are shown. Nomenclature follows Rhoads and Block (2007).

	2013			2019		
	Reference	Exclosure	ISA *p*-value	Reference	Exclosure	ISA *p*-value
Trees						
Acer rubrum L.	0.4 ± 0.2	2.9 ± 2.5	0.120	0.5 ± 0.2	1.6 ± 1.9	0.345
Acer saccharum Marshall	0.0 ± 0.0	1.5 ± 3.1	0.179	0.0 ± 0.0	0.0 ± 0.0	1.000
Betula alleghaniensis Britton	0.1 ± 0.1	0.0 ± 0.0	1.000	0.7 ± 1.3	0.0 ± 0.0	0.453
Betula lenta L.	0.5 ± 0.4	0.6 ± 1.2	0.695	0.1 ± 0.2	0.1 ± 0.2	0.729
Carpinus caroliniana Walter	–	–	–	0.0 ± 0.0	0.1 ± 0.2	1.000
Cornus L. spp.	0.0 ± 0.0	0.1 ± 0.2	1.000	–	–	–
Magnolia acuminata (L.) L.	–	–	–	0.1 ± 0.2	0.2 ± 0.5	1.000
Nyssa sylvatica Marshall	0.0 ± 0.0	0.0 ± 0.0	0.451	0.1 ± 0.1	0.1 ± 0.2	1.000
Ostrya virginiana (Mill.) K.Koch	0.0 ± 0.0	0.1 ± 0.2	1.000	0.1 ± 0.2	0.2 ± 0.4	0.423
Prunus serotina Ehrh.	0.2 ± 0.4	1.2 ± 2.6	0.764	0.0 ± 0.0	0.3 ± 0.5	0.561
Quercus montana Willd.	0.0 ± 0.1	0.3 ± 0.5	0.439	0.9 ± 2.0	0.2 ± 0.3	1.000
***Quercus rubra* L.**	**0.3 ± 0.3**	**1.3 ± 0.7**	**0.008**	1.0 ± 1.0	1.1 ± 1.0	0.858
Shrubs, sub-shrubs, and lianas						
Amelanchier arborea (F.Michx.) Fernald	0.5 ± 0.3	1.0 ± 0.6	0.790	0.5 ± 0.4	1.0 ± 0.5	0.556
Gaultheria procumbens L.	0.2 ± 0.3	3.5 ± 6.6	0.303	0.6 ± 1.0	1.0 ± 1.0	0.636
Hamamelis virginiana L.	0.1 ± 0.2	0.2 ± 0.3	0.578	0.3 ± 0.4	0.3 ± 0.4	0.730
Ilex montana (Torr. and A.Gray) A.Gray	–	–	–	0.1 ± 0.2	0.3 ± 0.4	0.916
Rhododendron maximum L.	0.0 ± 0.0	0.1 ± 0.2	1.000	0.0 ± 0.1	1.1 ± 2.4	1.000
Rubus allegheniensis Porter	0.4 ± 0.8	2.8 ± 3.4	0.118	0.9 ± 1.1	2.3 ± 3.0	0.371
Rubus flagellaris Willd.	0.1 ± 0.1	0.5 ± 1.0	1.000	0.1 ± 0.3	0.0 ± 0.1	0.723
Rubus odoratus L.	–	–	–	0.0 ± 0.0	0.4 ± 0.6	0.441
Smilax rotundifolia L.	0.0 ± 0.0	0.0 ± 0.0	0.483	0.2 ± 0.5	0.0 ± 0.0	1.000
Vaccinium angustifolium Aiton	0.0 ± 0.1	0.5 ± 0.5	0.225	0.3 ± 0.5	0.2 ± 0.3	0.888
Forbs						
Eurybia divaricata (L.) Nesom	0.0 ± 0.1	0.0 ± 0.0	1.000	0.1 ± 0.1	0.1 ± 0.1	1.000
Lysimachia quadrifolia Sims	0.0 ± 0.1	0.0 ± 0.0	0.869	0.7 ± 1.4	0.0 ± 0.1	0.127
Maianthemum canadense Desf.	3.5 ± 2.8	7.0 ± 7.6	0.387	1.0 ± 0.7	4.0 ± 6.8	0.578
Medeola virginiana L.	0.0 ± 0.0	0.1 ± 0.1	1.000	0.1 ± 0.1	0.3 ± 0.7	1.000
Mitchella repens L.	0.0 ± 0.0	1.7 ± 2.4	0.448	0.0 ± 0.0	2.5 ± 3.6	0.444
Podophyllum peltatum L.	0.8 ± 1.7	0.0 ± 0.0	1.000	1.0 ± 2.3	0.0 ± 0.0	1.000
Ranunculus L. spp.	–	–	–	0.0 ± 0.1	0.0 ± 0.1	1.000
Trientalis borealis Raf.	0.2 ± 0.3	0.2 ± 0.5	0.787	0.2 ± 0.3	0.1 ± 0.2	0.787
Trillium undulatum Willd.	0.0 ± 0.0	0.2 ± 0.5	1.000	0.0 ± 0.0	0.3 ± 0.6	1.000
Uvularia sessilifolia L.	0.1 ± 0.2	0.3 ± 0.6	0.739	0.1 ± 0.3	0.1 ± 0.1	1.000
Viola L. spp.	0.0 ± 0.0	0.0 ± 0.0	1.000	0.4 ± 0.8	0.6 ± 1.1	0.721
Graminoids						
Brachyelytrum erectum (Schreb.) P. Beauv.	0.1 ± 0.2	0.0 ± 0.0	1.000	0.2 ± 0.4	0.0 ± 0.0	1.000
Carex L. spp.	0.3 ± 0.4	0.0 ± 0.0	0.193	0.1 ± 0.1	0.1 ± 0.2	0.858
Dichanthelium acuminatum (Sw.) Gould and C.A.Clark	–	–	–	0.1 ± 0.1	0.0 ± 0.0	0.324
Ferns and clubmosses						
***Dennstaedtia punctilobula* (Michx.) T. Moore**	1.6 ± 1.2	0.7 ± 0.7	0.294	**9.4 ± 3.3**	**3.7 ± 1.9**	**0.016**
Lycopodium obscurum L.	0.1 ± 0.2	0.0 ± 0.0	1.000	0.0 ± 0.0	0.0 ± 0.0	0.467
Thelypteris noveboracensis (L.) Nieuwl.	0.9 ± 2.1	0.1 ± 0.2	0.835	1.8 ± 2.7	0.6 ± 0.6	0.393

value = 0.83, $p = 0.006$), and hay-scented fern (*Dennstaedtia punctilobula* (Michx.) T. Moore) was the only species associated with reference plots (2019, indicator value = 0.72, $p = 0.012$; Table 3). Of the 114 species recorded, 27 were found only inside exclosures, while 17 were unique to the reference plots. Twenty species were found only in 2013 sampling, and 23 in 2019 only. All of these unique species were at very low abundance: the maximum cover for a single 1 m^2 subplot was 3.5%,

Fig. 4. Mean (with bootstrap 95% confidence intervals) % visual obstruction as measured in 20 cm height intervals, recorded by the 2015 three-dimensional structure survey. The *x*-axis is positive in both directions away from zero. (∗) indicates a *post hoc* height interval pair with statistical significance at a Benjamini–Hochberg-adjusted $0.05 > p > 0.01$. (∗∗) indicates statistical significance at $p < 0.01$. *p*-Values, in ascending order from 0–20 cm to 180–200 cm, are as follows: 0.415, 0.085, 0.146, 0.105, 0.035, 0.003, 0.007, 0.007, 0.003, and 0.003. Above 80 cm height, reference plots averaged 0.2% visual obstruction, compared to the exclosure plots' 27.3%.



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and only two species occurred at ≥ 1 percent cover in two or more subplots (*Carex communis* Bailey in reference plots only and *Dryopteris intermedia* (Muhl.) A. Gray in exclosure plots only).

In the structural complexity analysis (two-way repeated measures ANOVA), the Exclosure treatment × Height interval interaction was significant ($p < 0.001$). In the *post hoc* tests, all height intervals above 80 cm were significant, and those below 80 cm were not (*p*-values in Fig. 4 caption). Across the significant height intervals, exclosures had 114 times greater foliage density than reference plots (Fig. 4). See Table A2 for plot-level structural complexity data.

We found no significant differences between exclosure and reference plot canopies in terms of BA or species richness (ANOVAs; $p = 0.383$ and 0.455, respectively). Our PERMANOVA also failed to detect any statistically significant difference in canopy composition ($r^2 = 0.03$, $p = 0.688$). See Table A1 for plot-level canopy details.

Discussion

Excluding deer for 19 years did not cause increases in forb cover, overall species richness, or species diversity, thereby demonstrating a legacy effect of over-browsing lasting nearly two decades. Total cover was about 2.6 times as high inside the exclosures in 2013, but this difference was eliminated by 2019 due to an increase in plant abundance outside exclosures (Fig. 2). Exclosure and reference communities had similar plant species composition, and excluding deer explained little variation in composition. Trees, shrubs, and known browse-sensitive species were more than twice as abundant inside the exclosures (2013 only for shrubs; Fig. 3), but only one individual species was associated with the exclosures (red oak, a deer-preferred tree species present in the overstories of all plots; Averill et al. 2017; Table A1). The one species associated with the reference plots was hay-scented fern, which forms dense recalcitrant understory layers in heavily browsed forests in the region of our study and elsewhere (Royo and Carson 2006, 2022). Ferns were 2.5 times as abundant in reference plots compared to exclosure plots. Fern cover also increased by a factor of 4.3 from 2013 to 2019 (Fig. 3), possibly due to phenological variation between years. Sampling in 2019 occurred about a week later than 2013 sampling, and leaf-out could have occurred earlier in 2019 because of favorable weather. The month prior to sampling in 2019 had twice as much precipitation and averaged 0.90 °C higher daily maximum temperature and 3.14 °C higher daily minimum compared to 2013 (Menne et al. 2012). Some of the variation in fern cover could also be attributed to the modest year-to-year variation characteristic of hay-scented fern, the most common fern in our plots (Hill and Silander 2001). Our findings represent a significant growth response of woody plants released from browse pressure and a corresponding decrease in fern abundance. However, neither traditional measures of plant diversity nor statistical comparisons of community composition provided any evidence for a biologically meaningful recovery of the plant community as a whole.

The lack of a difference in species richness and diversity between the exclosure plots and the reference plots could

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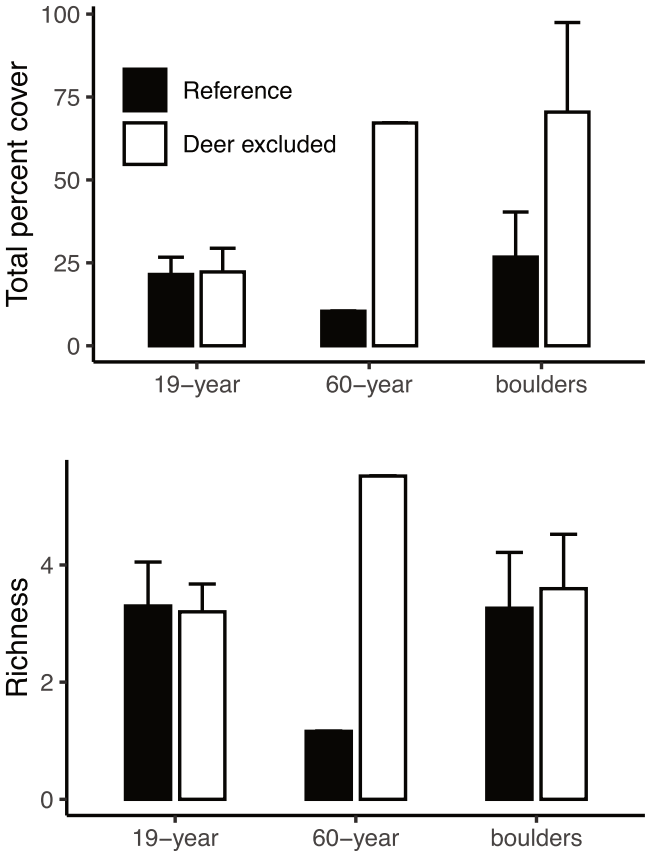
Fig. 5. Comparison of total percent cover and species richness at the 1 m^2 subplot scale among: (1) the present 19-year exclosure survey, (2) the 60-year exclosure survey presented by Goetsch et al. (2011), and (3) the boulder-refugium study presented by Banta et al. (2005). Data are means (with bootstrap 95% confidence intervals), except for the 60-year exclosure, which is not replicated.



be explained by the hypothesis that deer are not having any impact on the plant community in this area. However, the results of the three-dimensional structure survey clearly demonstrate that deer are in fact greatly suppressing plant growth. Between 80 and 200 cm above the soil surface, foliage density was 114-fold greater inside the exclosures compared to the reference plots, where it languished near zero (Fig. 4). All of the species recorded in exclosure plots that had a height potential > 80 cm were trees and shrubs. We suggest that the dense shrub and sapling layer in our exclosure plots could be contributing to the lack of recovery in the ground layer by casting shade on shorter herbaceous species (Boulanger et al. 2018; Simončič et al. 2018). Forest herb abundance and diversity often have a negative relationship to measures of woody plant abundance (Gafta and Peet 2020; Su et al. 2021). Moderate deer densities may increase the percent cover and species richness of the herb community by limiting competition from preferred-browse tree saplings and shrubs (Hegland et al. 2013; Bernes et al. 2018; Boulanger et al. 2018).

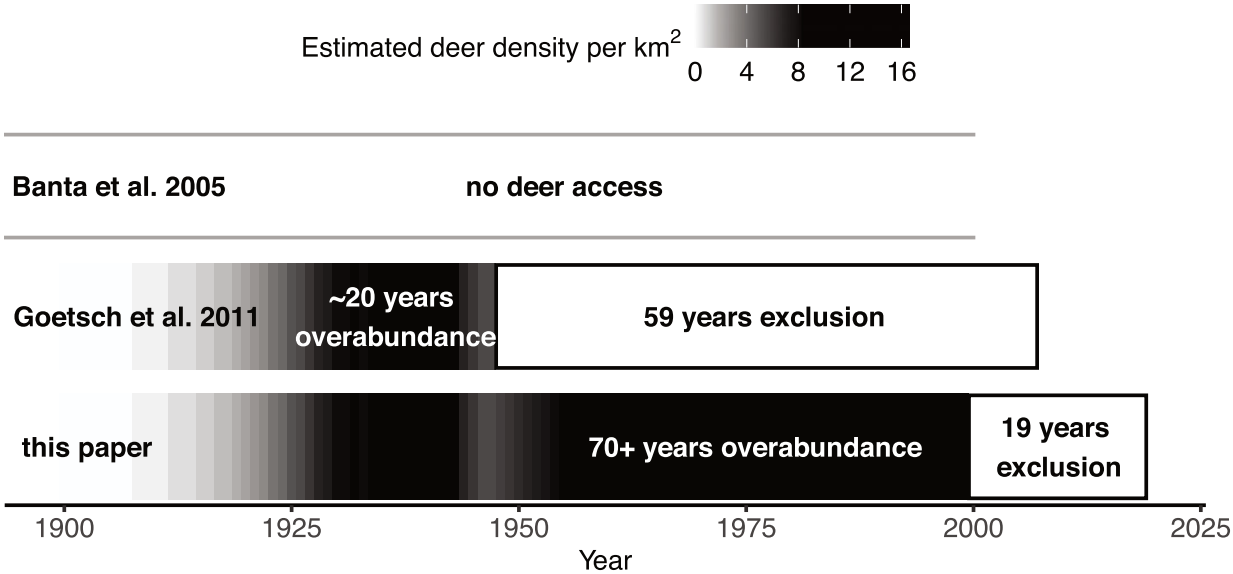
The dramatic increase in foliage density inside our exclosures will almost certainly have important consequences for higher trophic levels. Arthropod abundance is positively associated with the high understory structural complexity found inside deer exclosures (Bressette et al. 2012). Roberson et al. (2016) found that the abundance of web-spinning spiders was twice as high inside exclosures, where foliage complexity was much higher, compared to adjacent reference plots. Songbirds, many of which are insectivores, have been shown to have higher abundance and diversity in association with deer exclosures, as well as enclosures with low deer density, compared to reference plots (deCalesta 1994; Bressette et al. 2012). This is especially true for birds that nest in midstory and understory vegetation (deCalesta 1994; Rushing et al. 2020).

Because there are no data available from the time of exclosure establishment, we are unable to assess the extent to which the difference in foliage density between exclosure and reference plots could be due to pre-existing conditions. However, we doubt whether pre-existing conditions could generate an effect of such magnitude and consistency across plots (Fig. 4, Table A2). Additionally, we note that the dense shrubs and saplings in the exclosure plots appear uniformly young (<20 years), and there were no differences in canopy characteristics between exclosure and reference plots (total BA, species richness, or species composition; Table A1). The only obvious difference in environmental factors between plots of a single pair was a small canopy gap above one of the exclosures, but this did not result in increased foliage density at that site compared to other exclosures (Table A2). Given the size and location of the gap directly above the exclosure, most of the light probably fell north of the plot.

Our results stand in stark contrast to two previous case studies from the ANFR. The first is a survey of the herb and shrub layers in the oldest deer exclosure in the eastern United States, built in 1948 in the same region as our study. Goetsch et al. (2011) found that percent cover was 6 times higher, richness 4 times higher, and Shannon diversity 13 times higher inside the fence than in an adjacent reference plot (Fig. 5). We see four potentially explanatory differences between our study and that of Goetsch et al. (2011). First, the older exclosure was in operation for almost 60 years at the time of sampling, about three times longer than our exclosures (Fig. 6). The longer deer are excluded, the more likely that browse-sensitive species made uncommon by heavy browsing will colonize the protected area. Nineteen years may simply be an insufficient period of time for many species to arrive in the exclosures, especially for those that reproduce primarily vegetatively or have limited seed dispersal distances. Given another 40 years, we would predict greater recovery of species diversity.

Second, the period of over-browsing prior to exclusion was more than three times greater for our exclosures than for that of Goetsch et al. (2011; about 20 years versus 70+ years; Fig. 6). It is possible that some plant populations could persist through 20 years of over-browsing (i.e., before establishment of the exclosure) via some degree of browse resistance, retreating to refugia, or seed-banking. For example, some perennial herbs can withstand decades of

Fig. 6. Comparison of timescales of deer overabundance and exclusion between our exclosures and that of Goetsch et al. (2011) as well as the boulder-top refugia of Banta et al. (2005). Deer density estimates for the Allegheny National Forest Region are derived from Royo and Stout (2019) and Whitney (1990).



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over-browsing by drawing on extensive belowground carbohydrate reserves (Webster et al. 2005; Lapointe et al. 2010; Wilbur et al. 2017). Local browse refugia, such as tall boulders and treefall mounds above the reach of deer, routinely harbor vulnerable species that are rare or absent on the forest floor (Comisky et al. 2005; Krueger and Peterson 2006). However, persisting through the 70+ years of over-browsing that preceded our exclosures is much less likely.

Third, Goetsch et al. (2011) estimate their stand age at 60–80 years. Since the exclosure was 59 years old at the time of sampling, it must have been erected at some point within the first 21 years of forest succession. This may have allowed divergence of the exclosure from the reference plot more rapidly than would fences erected in mature stands, like those of the present study, where species composition was more established. High deer density during early succession is reported to result in alternative successional trajectories and divergent "alternate stable state" communities (e.g., Horsley and Marquis 1983; Stromayer and Warren 1997; Hidding et al. 2013; Nuttle et al. 2014).

The fourth factor that may have contributed to the discrepancy between the two studies is the size of the protected area. The exclosure of Goetsch et al. (2011) was 33%–515% larger than our exclosures (4000 m^2 versus 650–3000 m^2). As exclosure size increases, the probability of additional species being included in the protected community would likely also increase. The limited spatial scale of exclosure experiments means that they are likely to miss plant species that have been made uncommon on the landscape by deer browsing. Landscape-scale deer density reduction experiments do not entail that limitation (e.g., Royo et al. 2010). In the absence of data from the time of establishment, we can only speculate as to how this factor might have differentially affected the divergent understories.

A second contrasting case study from the ANFR is Banta et al. (2005) on boulder refugia. Tall and relatively flat boulders in this area can support higher stem density and richness than adjacent reference plots on the soil surface (Banta et al. 2005; Comisky et al. 2005). Permanently out of the reach of deer, plant communities on boulder-tops could provide a window into what a healthy understory might look like without decades of heavy browse pressure (Fig. 6). However, the degree to which boulders can prevent the complete loss of sensitive species from a landscape (as in Rooney and Dress 1997) is unclear, given that their total surface area is quite small (Banta et al. 2005). In addition, many boulders may lack adequate substrate for some plant species, especially trees. Our exclosure plots lag behind Banta et al.'s (2005) boulder-top communities in percent cover but have similar richness and diversity of understory herbs (Fig. 5). This lower herb cover again may be due in part to shading by the dense shrub and sapling layer at present, which we suggest may thin out over time as these woody components grow farther above the ground flora or are excluded through competition. Banta et al. (2005) also noted a high level of divergence in community composition, with forbs and shrubs dominating the boulder-tops while ferns and grasses dominated the forest floor (Sørensen's coefficient 0.16). Our plots showed similarly elevated shrub cover inside the exclosure in 2013 and fern cover outside in both years, but there were no significant differences for shrubs in 2019 or forbs in either year (Table 2). As previously mentioned, our Sørensen's coefficients (0.662 for 2013 and 0.755 for 2019) and PERMANOVA results ($p = 0.036$,

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$r^2 = 0.11$ for exclosure treatment) demonstrate an overall lack of divergence. In light of this contrast, tall boulders like those of Banta et al. (2005) function as natural deer exclusion zones without the interference of legacy effects seen in our exclosures.

The failure of our exclosure communities to recover diversity over time may be attributed to severe and long-term over-browsing in this area that had nearly or completely extirpated many of the most sensitive species prior to plot establishment (Rooney and Dress 1997). We suspect species not capable of persisting during prolonged over-browsing are not likely to recolonize within only 20 years of reduced deer density (Webster et al. 2005). Taken in light of previous studies on deer browsing legacy effects, our findings suggest that some outside recruitment source, whether human introductions or natural refugium reservoirs, will be needed if plant diversity is to recover in eastern forests, even if deer are brought down to presettlement densities.

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Data availability

Data generated and analyzed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare that there are no competing interests.

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Appendix A

Table A1. Basal areas of canopy tree species at each plot location (m^2/ha). Plot pair numbers correspond to those on the site map in Fig. 1. "R" denotes a reference plot, and "E" denotes an exclosure plot.

	1		2		3		4		5		6		Mean ± SD	
	R	E	R	E	R	E	R	E	R	E	R	E	R	E
Acer rubrum	6.2	14.8	14.8	8.3	2.3	0.7	6.6	0.4	7.0	1.5	5.8	3.2	7.1 ± 4.1	4.8 ± 5.7
Acer saccharum	0.9	1.2							4.2	1.3		0.3	0.9 ± 1.7	0.5 ± 0.6
Amelanchier arborea												0.2	0.0 ± 0.0	0.0 ± 0.0
Betula lenta			6.8										1.1 ± 2.8	0.0 ± 0.0
Betula alleghaniensis								0.8					0.0 ± 0.0	0.1 ± 0.3
Carpinus caroliniana	0.1												0.0 ± 0.0	0.0 ± 0.0
Liriodendron tulipifera										2.6			0.0 ± 0.0	0.4 ± 1.1
Magnolia acuminata				3.6							4.7	4.5	0.8 ± 1.9	1.4 ± 2.1
Nyssa sylvatica					0.5	1.0	0.2				4.9	1.0	0.9 ± 1.9	0.3 ± 0.5
Ostrya virginiana	0.1												0.0 ± 0.0	0.0 ± 0.0
Prunus serotina	9.1	7.0					2.8	2.6	0.6	0.8			2.1 ± 3.6	1.7 ± 2.8
Quercus alba		1.8		7.1	0.6	3.1			0.6				0.2 ± 0.3	2.0 ± 2.8
Quercus montana			5.7	3.4					11.5	0.7	2.2	6.8	3.2 ± 4.6	1.8 ± 2.8
Quercus rubra	12.0	31.9	8.4	4.5	39.8	29.1	46.9	55.5	19.2	21.0	34.1	16.2	26.7 ± 15.7	26.4 ± 17.3
Quercus velutina							2.6						0.4 ± 1.0	0.0 ± 0.0
Tilia americana									3.4	0.6			0.6 ± 1.4	0.1 ± 0.2
Tsuga canadensis						0.2							0.0 ± 0.0	0.0 ± 0.1
Total	28.4	56.8	35.7	26.9	43.1	34.1	59.0	58.1	46.4	28.3	51.7	32.1	44.1 ± 11.0	39.4 ± 14.2

Table A2. Plot-level % visibility occluded (mean ± SD) in the 2015 understory structural survey.

	Reference				Exclosure			
Height interval	1	2	3	5	1	2	3	5
180–200 cm	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	34.9 ± 21.2	19.5 ± 36.2	30.5 ± 12.9	13.1 ± 12.1
160–180 cm	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	29.0 ± 28.1	20.4 ± 26.3	50.3 ± 32.6	21.9 ± 13.3
140–160 cm	1.0 ± 2.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	24.5 ± 16.4	24.9 ± 18.2	46.1 ± 28.2	9.9 ± 9.0
120–140 cm	1.3 ± 2.8	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	19.7 ± 14.2	25.8 ± 10.8	47.8 ± 20.2	15.8 ± 17.5
100–120 cm	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	19.8 ± 12.6	27.4 ± 13.0	43.2 ± 23.9	12.6 ± 12.5
80–100 cm	3.5 ± 5.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	11.2 ± 8.9	36.1 ± 24.0	48.2 ± 16.9	23.2 ± 15.2
60–80 cm	15.2 ± 15.3	0.0 ± 0.0	1.1 ± 2.3	0.0 ± 0.0	10.5 ± 5.4	35.4 ± 16.0	29.8 ± 20.4	26.0 ± 19.2
40–60 cm	20.0 ± 5.0	1.0 ± 1.8	2.6 ± 4.2	11.6 ± 13.4	16.8 ± 5.4	35.0 ± 5.5	14.5 ± 3.5	33.7 ± 34.9
20–40 cm	45.9 ± 25.6	22.1 ± 15.1	15.2 ± 10.2	27.4 ± 31.4	57.0 ± 26.8	43.8 ± 8.1	17.8 ± 7.6	56.4 ± 28.0
0–20 cm	85.3 ± 12.0	23.4 ± 20.1	54.2 ± 31.6	82.9 ± 5.9	97.6 ± 2.3	46.8 ± 30.4	43.0 ± 38.8	94.2 ± 4.4

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