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RESEARCH ARTICLE

The long-term impacts of deer herbivory in determining temperate forest stand and canopy structural complexity

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Abstract

1. Ungulates place immense consumptive pressure on forest vegetation globally, leaving legacies of reduced biodiversity and simplified vegetative structure. However, what remains unresolved is whether browse-induced changes occurring early in succession ultimately manifest themselves in the developed forest canopy. Understanding the development and persistence of these legacies is critical as canopy structure is an important determinant of forest ecosystem functions such as carbon sequestration and wildlife habitat.
2. We measured how white-tailed deer *Odocoileus virginianus* browse during stand initiation affected canopy structure, tree species richness, diversity, stem density, and basal area on Pennsylvania's Allegheny Plateau using a portable canopy LiDAR system. We capitalized on an historic deer enclosure experiment where forests were subjected to four deer densities (4, 8, 15, and 25 deer/km^2) for 10 years following stand initiation.
3. Deer browsing impacts on the forest canopy are apparent nearly four decades since stand initiation. The highest deer density treatment experienced a significant reduction in tree species diversity, density, and basal area with stands becoming dominated by black cherry *Prunus serotina*. Reductions in overstorey diversity and tree density resulted in a more open canopy with low leaf area and high horizontal leaf variability. Canopies were tallest at the lowest and highest deer densities.
4. *Synthesis and applications*. Using a portable canopy LiDAR system and a former deer enclosure experiment, we show that high deer browsing pressure during stand initiation can have a decades-long impact on stand and canopy structure. High deer densities led to stands with lower species diversity and tree density, which resulted in canopies that were taller and less dense. As remote sensing of the canopy becomes more prevalent, considering the legacy of ungulate herbivory on canopy structure may inform both land management and our understanding of ecological function, such as forest carbon sequestration, maintenance of diverse understory communities, and creation of wildlife habitat

KEYWORDS
deer browsing, disturbance, forest canopy, forest structure, herbivory, lidar, remote sensing, temperate forest management

1 | INTRODUCTION

Forests are influenced by a variety of disturbances, which can have different effects on species composition, successional trajectories, and structure. Forest structure refers to the horizontal and vertical arrangement of vegetation and empty space in a stand—the height of the canopy, whether understories, midstories, and overstories are dense or open, and how that density varies spatially—which impacts carbon sequestration (Gough et al., 2019), wildlife habitat (Fotis et al., 2020), and other important attributes of ecosystem function (Fahey et al., 2018; Mori et al., 2017). Although pulse disturbances (e.g. short-term events that place high pressure on a system, such as windstorms or fire) can transform a stand's structure in minutes, press disturbances (e.g. long-term events that place continuous pressure on a system, such as intense herbivory or certain pathogens) operate continuously over years to decades across a landscape to significantly alter forest structural characteristics and associated ecosystem services (Flower & Gonzalez-Meler, 2015; Graham et al., 2021; Lake, 2000).

Ungulate browsing is a dominant press disturbance in forests worldwide that places consumptive pressure on preferred vegetation, shifting species composition by reducing seedling abundance and diversity, and slowing the pace towards late successional communities (Bernes et al., 2018). In eastern North America, white-tailed deer *Odocoileus virginianus* are the dominant ungulate browser and have a pronounced effect on early successional forest communities where vegetation is concentrated in shorter, more browse vulnerable size classes (Côté et al., 2004; Tilghman, 1989). Deer induced changes in vegetation early in stand development can transform successional trajectories and have long-term ramifications for the future forest's structure and thus, ecosystem function and services (Rooney & Waller, 2003).

Changes in forest structure may not be discernible until the regenerating tree community grows beyond the herbivory filter, a process which accrues over decades (Weisberg & Bugmann, 2003). The influence of vertebrate herbivores on stand structural metrics such as diameter at breast height (DBH) or tree density has received considerable attention (Ramirez et al., 2018; White, 2012). For example, Hidding and colleagues (2013) found that high white-tailed deer browse pressure transformed regenerating boreal forest communities into open spruce (*Picea* spp.) savannas after 15 years, whereas complete or partial protection from browsing allowed the development of a dense young forest characterized by hardwoods and conifers. Similarly, in the Appalachian-Northern hardwood forests of the eastern United States, long-term browsing created understories dominated by striped maple *Acer pensylvanicum*, a subcanopy treelet, while long-term elimination of browsing led to a more diverse understorey community (Kain et al., 2011). Shifts in tree community composition or a species' dominance could then lead to collapses in canopy structure since many trees have species-specific crown architectures that contribute to canopy arrangement (Pretzsch, 2014).

Although there is evidence of disturbances such as ice storms, forest pathogens, and fire leaving a unique mark on temperate forest canopies (Atkins et al., 2020; Fahey et al., 2016), very few studies identify the effects of long-term vertebrate herbivory on canopy structure (Côté et al., 2004; Nuttle et al., 2011). To our knowledge, only one study has quantified deer density impacts on a mature forest's canopy height, finding that increased deer populations led to taller canopies in Britain (Eichhorn et al., 2017). Nevertheless, herbivore impacts on canopy structure remain understudied and elusive due to a lack of operational and accessible technologies to quantify canopy structural metrics. To make field-based, observational insights on the relationships between herbivores and canopy structure, researchers must possess tools that permit simple and reliable quantification of post-disturbance canopy structural metrics for vegetation strata that are far taller than the observer (Ritchie et al., 1993).

In this study, we capitalize on a controlled browsing experiment initiated in 1979–1980 on the Allegheny Plateau, USA, where forests regenerated under four controlled white-tailed deer densities for 10 years (Tilghman, 1989). We use a Portable Canopy LiDAR (PCL) system to rapidly characterize deer-induced changes in canopy structure in these now 36-year-old stands (Figure 1). While PCL has been used to measure canopy structural complexity of temperate forests in light of several disturbances (Atkins et al., 2020; Fahey et al., 2016; Hardiman et al., 2013), this technology has not been applied to study the influence of deer browse, the eastern North American forest's dominant press disturbance. This controlled browsing experiment, using deer enclosures rather than exclosures, has only been replicated once, in the boreal forests of Quebec, Canada (Tremblay et al., 2007). These experimental stands provide a unique opportunity to examine the legacy of deer browse pressure during stand initiation on forest canopy structure after nearly four decades of growth, during which stratification has occurred and stems of species that will characterize the main canopy for the next several decades are established (Hibbs, 1983). In this work, our primary goal is to assess the impacts of varying deer density during stand initiation on (a) long-term forest species diversity, composition, and stand structure, and (b) long-term canopy complexity.

2 | MATERIALS AND METHODS

2.1 | Study site and design

This experiment took place at four sites within the Allegheny Plateau Region of northwestern and north-central Pennsylvania, USA. Sites were distantly located in Elk County (710 m elevation; 41°34′22″N, 78°28′30″W), Warren County (550 m elevation; 41°38′48″N, 79°08′11″W), Forest County (550 m elevation; 41°34′40″N, 79°06′19″W), and McKean County (670 m elevation; 41°38′21″N, 78°19′33″W; Horsley et al., 2003). Each location was composed of 60- to 70-year-old second-growth stands of black cherry *Prunus serotina*, red maple *Acer rubrum*, and sugar maple *Acer saccharum* prior to the establishment of the experimental treatments (Tilghman, 1989). Within the four sites, a 65 ha deer enclosure with 2.5 m high fencing

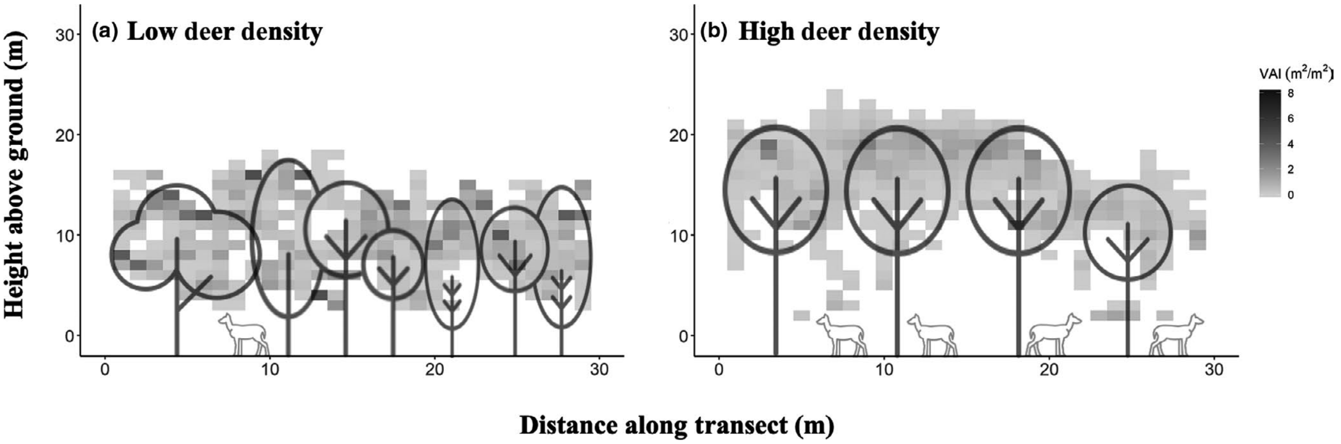

FIGURE 1 Example of a 'hit grid' showing different canopy structures between low and high deer density treatments, as measured by the portable canopy LiDAR system. The tree silhouettes represent a hypothetical stand and canopy structure based on the LiDAR returns. Darker bins indicate greater laser return density and increased canopy foliage (VAI: vegetative area index), with data processed in the FORESTR R package (Atkins, Bohrer, et al., 2018). Figure 1a is representative of the more diverse and dense canopies associated with the low deer density treatments (Gap Fraction: 1.4%; VAI: 7.2; Rugosity 4.1; Mean Max Height: 14.9), whereas Figure 1b is representative of the open, savanna-like stands of black cherry associated with high deer densities (Gap Fraction: 14.3%; VAI: 4.8; Rugosity: 8.6; Mean Max Height: 19.3) (Trees from Made by Made & Deer from Berkah Icon; The Noun Project)

was assembled. Two enclosures were established in 1979 and the other two enclosures in 1980, each constructed and operated in direct consultation with the Pennsylvania Game Commission through designation of all sites as State Game Propagation Areas. Each 65 ha site was subdivided with fencing to establish experimental manipulations of deer populations at densities of 4, 8, 15, and 25 deer/km^2, for a total of four replicates of each density treatment (Figure 2; Tilghman, 1989). The lowest deer density treatments (4 deer/km^2) were 26 ha, whereas the rest of the stands were 13 ha. Nested within each deer density treatment were three different overstorey conditions: clearcut, cut to 60% residual relative density, and uncut. Clearcuts represented 10% of each deer density treatment's area (1.3 or 2.6 ha). We considered only the clearcut areas in this study as the entire stand was re-initiated and deer had a direct influence on all trees currently in the overstorey. All enclosures were disassembled in 1990, after which deer could travel unimpeded. One treatment (15 deer/km^2) at State Game Land 30 was harvested prior to our study, reducing our sample size to 15 treatment areas. For a more detailed description of the experimental design, initial conditions, and vegetative trajectories, see Horsley et al. (2003).

2.2 | Forest species diversity, stand structure, & canopy structural complexity

In June and July 2016, we measured forest stand structure, species composition, and canopy structure, approximately 36 years after stand re-initiation and deer browsing. All field work was conducted with an approved study plan and memoranda of understanding between participating landowners. Within each deer density treatment, we randomly placed three, 30 × 5 m parallel belt transects spaced at least 30 m away from one another. Within each transect, we identified and measured the diameter at breast height (DBH) of all trees >5 cm DBH. From DBH, basal area was calculated at the transect level (150 m^2) and then extrapolated to a per hectare basis (10,000 m^2). Shannon diversity was calculated with basal area as the unit of abundance using R package VEGAN (Oksanen et al., 2020).

Canopy structural complexity was measured using a ground-based portable canopy LiDAR system (PCL; Parker et al., 2004). The PCL measures the arrangement of leaves and branches within a canopy using an upward-facing infrared laser at 2,000 Hz and is an economical means to rapidly collect and calculate multiple, high-resolution canopy structural metrics at the stand scale. Canopy structural metrics were calculated using the FORESTR R package (Atkins, Bohrer, et al., 2018). Although FORESTR can calculate nearly two dozen canopy structural parameters, we focused on metrics that characterize four different aspects of canopy structural complexity and are commonly studied in relation to disturbance; vegetation area index (VAI; the density of vegetation within the canopy, or the density of LiDAR returns within each 1 × 1 m column along PCL transect), mean outer canopy height (MOCH; average maximum return height of lasers along transect), gap fraction (the openness of the canopy, or the ratio of PCL sky hits to vegetation returns), and rugosity (canopy structural complexity, or the vertical and horizontal heterogeneity in leaf, branch and stem distributions; Atkins, Bohrer, et al., 2018; Atkins et al., 2020). These metrics correlate well with important ecophysiological responses including above-ground primary productivity (ANPP, Fotis et al., 2018; Hardiman, Gough, et al., 2013) and leaf traits (Fotis & Curtis, 2017), and can characterize habitat heterogeneity features that predict wildlife diversity (e.g. Ishii et al., 2004; avian diversity, Seavy et al., 2009; squirrel habitat, Fotis et al., 2020).

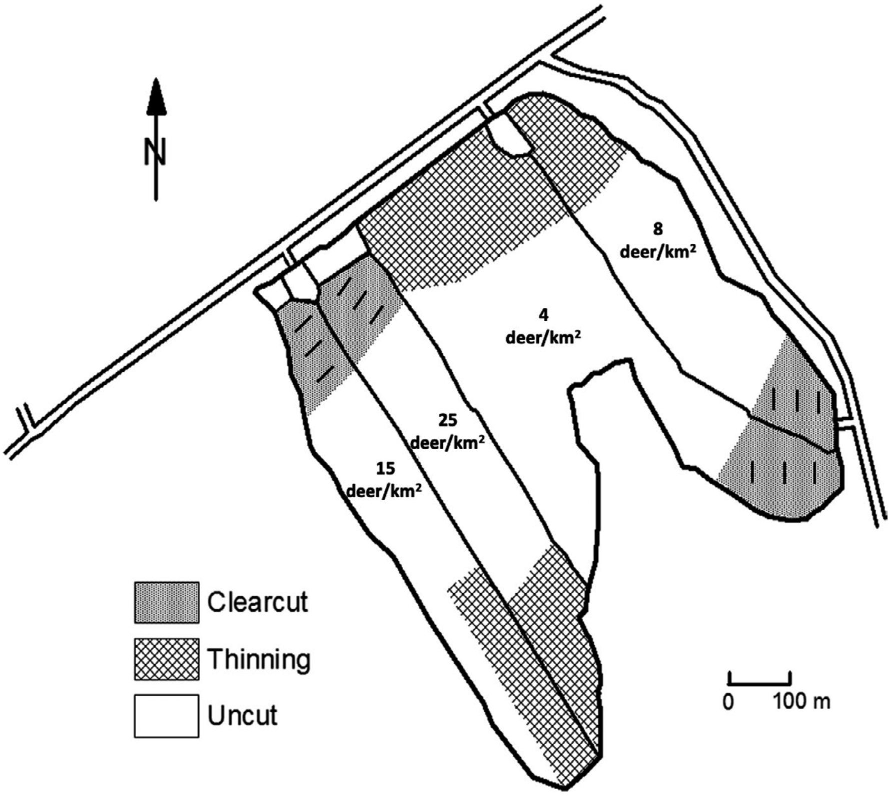

FIGURE 2 Map of one of four deer enclosures showing the different deer density and forest management treatments with each line in the clearcut location representing a 30 × 5 m belt transect. Deer populations were maintained for approximately 10 years within the enclosure experiment (1989–1990). This study evaluated stand and canopy structure in the clearcut sections of each deer density treatment

2.3 | Statistical analysis

We used analysis of variance (ANOVA) to assess treatment effects on stand structural attributes, species diversity, and canopy structural metrics using general linear mixed models (Proc GLIMMIX; SAS 9.4, SAS Institute, Inc.). Our experiment is a nested randomized complete block design where deer density is considered a fixed effect and both site and transect are considered random effects. This design assumes independent transects nested within each deer density treatment. This is modelled on Nuttle and colleague's (2014) approach within the same experiment and is reasonable given that tree basal area was low and distance between transects (≥30 m) was large, which likely exceeds direct canopy interaction distance between each transect (Lorimer, 1983). We tested this assumption by running exploratory analyses that modelled spatial autocorrelation among transects using a second, spatial power random effect. These models either had poorer fit (i.e. higher AICc) or failed to converge, and did not change interpretation, suggesting spatial autocorrelation was minimal (See Appendix Tables S1 and S2). Nevertheless, we present those results so the reader can draw their own conclusions about potential spatial dependence.

Normality was tested using the Shapiro–Wilk test. Vegetation area index, rugosity, basal area, and tree species diversity (H′) were normally distributed. Gap fraction, MOCH, DBH, species richness, and stem density were right-skewed. For these, continuous response variables were modelled using a gamma distribution, whereas count data used Poisson (richness) or negative binomial distribution (stem density). We graphically examined the normality of the residuals, tested the homogeneity of the variance using boxplots and Levene's tests. Where necessary, this residual variance was adjusted using a second random statement with a ‘group=’ option. All models used a Kenward–Roger denominator degrees of freedom adjustment method. Where a significant (critical value = 0.05) deer density treatment effect was detected, we tested pairwise differences among deer density treatments with the LSMEANS function statement and used the Tukey–Kramer adjustment for multiple comparisons (Lenth, 2016).

3 | RESULTS

3.1 | Stand diversity, composition and structure

We found a significant decrease in the Shannon diversity of tree species with increased deer density ($p = 0.001$, $F = 6.43$, Table 1) nearly 36 years after the initiation of the enclosure experiment, wherein the highest deer density treatments (15 and 25 deer/km^2) were relatively depauperate and dominated by black cherry *Prunus serotina*. The lowest deer density treatments had greater representation of pin cherry *Prunus pensylvanica*, red maple *Acer rubrum*, and birch *Betula* spp. as well as black cherry (Figure 3; Table 2). Across deer density treatments, black cherry's proportional abundance steadily increased with greater deer browse pressure (4 deer/km^2 = 15.6%, 8 deer/km^2 = 18.4%, 15 deer/km^2 = 39.5%, 25 deer/km^2 = 60.4%), being the highest at the 25 deer/km^2, whereas the proportional abundance of all other species generally decreased (Table 2). While average species richness was also low at the 15 and 25 deer/km^2 treatment, there were no significant differences in

TABLE 1 Canopy complexity metrics (VAI, Mean Outer Canopy Height, Gap Fraction, Rugosity) and stand metrics (Species Richness, Stem Density, Basal Area, Shannon Diversity) of trees as measured in 2016 within the clearcut sections of deer density treatments on the Allegheny Plateau

	Canopy metrics				Stand metrics			
Treatment	VAI (m^2/m^2)	MOCH (m)	Gap fraction (%)	Rugosity (m)	Richness (S)	Stem density (N/ha)	Basal area (m^2/ha)	Diversity (H')
4 deer/km^2	7.53 ± 0.07^a	13.68 ± 0.70	0.81 ± 0.23^a	7.40 ± 0.80^{ab}	4.67 ± 0.22	$2,487 \pm 191^a$	36.14 ± 1.89^a	1.17 ± 0.14^a
8 deer/km^2	7.34 ± 0.18^a	12.09 ± 0.46	0.90 ± 0.26^a	5.85 ± 0.49^b	5.25 ± 0.29	$2,210 \pm 106^{ab}$	27.64 ± 1.89^{bc}	1.25 ± 0.14^a
15 deer/km^2	7.62 ± 0.12^a	12.32 ± 0.64	0.65 ± 0.22^a	9.01 ± 0.70^a	4.56 ± 0.63	$2,550 \pm 178^a$	34.94 ± 2.27^{ab}	0.91 ± 0.15^{ab}
25 deer/km^2	6.17 ± 0.25^b	14.96 ± 1.15	4.70 ± 1.35^b	8.72 ± 0.92^a	3.92 ± 0.60	$1,721 \pm 191^b$	25.78 ± 1.89^c	0.73 ± 0.14^b
Effect	$F_{3,17.2} = 9.45$; $p = 0.0007$	$F_{3,3.2} = 3.97$; $p = 0.0505$	$F_{3,39.6} = 8.02$; $p = 0.0003$	$F_{3,18.3} = 7.98$; $p = 0.0013$	$F_{3,16.7} = 1.51$; $p = 0.2474$	$F_{3,18.1} = 3.80$; $p = 0.0284$	$F_{3,39.4} = 6.44$; $p = 0.001$	$F_{3,38.4} = 6.43$; $p = 0.0012$

richness among density treatments ($p = 0.25$, $F = 1.51$, Table 1; see also Tilghman, 1989). Stem density and basal area also decreased at the highest deer density. Stem density was highest at 4 and 15 deer/km^2, had a moderate decrease at 8 deer/km^2 and then was significantly lower than every other treatment at 25 deer/km^2 ($p = 0.03$, $F = 3.80$, Table 1). Basal area was highest at 4 deer/km^2 and 15 deer/km^2, moderately lower at 8 deer/km^2, and lowest at 25 deer/km^2 ($p = 0.001$, $F = 6.44$, Table 1). Both metrics varied with intermediate deer browsing but were consistently the lowest within the 25 deer/km^2 treatment.

3.2 | Canopy structure

The highest deer density treatment also had significant effects on canopy complexity. Stands established at the highest browsing levels showed the lowest VAI ($p < 0.001$, $F = 9.45$, Table 1). There were no significant differences in VAI between the 4, 8 or 15 deer/km^2 stands. There was a concomitant increase in gap fraction for canopies in the 25 deer/km^2 treatment ($p < 0.001$, $F = 39.64$, Table 1), but little difference in this metric between the 4, 8 and 15 deer/km^2 treatments. Both VAI and gap fraction were strongly negatively correlated with one another and are treated as corresponding variables in the discussion ($r = -0.92$, Appendix Figure S1).

Rugosity, a measure of the heterogeneity in vertical and horizontal leaf, branch and stem distribution, showed substantial variation among deer density treatments. Rugosity was highest at 15 and 25 deer/km^2, lowest at 8 deer/km^2, and intermediate in the 4 deer/km^2 treatment ($p = 0.001$, $F = 7.98$, Table 1). Mean outer canopy height also varied among treatments, with trees in the 4 and 25 deer/km^2 treatments being an average of 1–3 m taller than trees in the 8 and 15 deer/km^2 treatments ($p = 0.051$, $F = 3.97$, Table 1).

4 | DISCUSSION

The legacy of deer browse is still widely apparent in the experimental forest's species composition, stand structure, and canopy structural complexity, despite the deer density treatments having ended nearly three decades ago. As deer are present at high densities throughout eastern North American forests, our results indicate that this severe press disturbance can have a dramatic influence on forest structure at multiple levels for many years.

High deer density at stand initiation led to low tree diversity in the overstorey, with black cherry being the dominant canopy species (Figure 3; Table 2). These results contribute to extensive literature showing that high deer browsing results in low plant diversity (Goetsch et al., 2011; Habeck & Schultz, 2015; Russell et al., 2017). Our observation that high deer densities favour black cherry growth is also supported by Royo et al. (2021) and by prior studies in stand development within our experiment (Horsley et al., 2003; Nuttle et al., 2011; Tilghman, 1989), further demonstrating the persistent

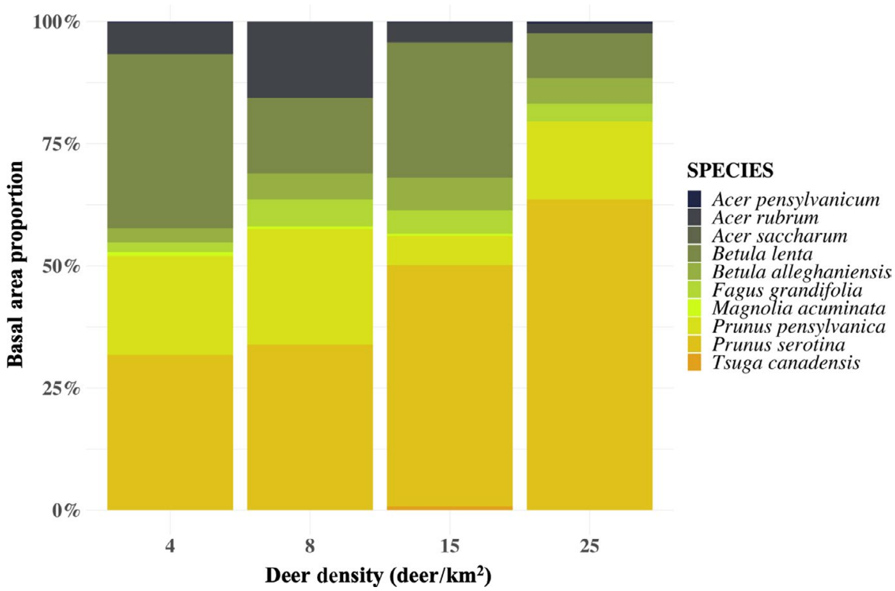

FIGURE 3 Proportional breakdown of species by basal area within each deer density treatment. As deer densities increase, so does the canopy dominance of unpalatable black cherry *Prunus serotina* (orange), while more shade-tolerant species decrease

TABLE 2 Tree species density and proportional abundance by deer density treatment (APCE = *Acer pensylvanicum*; ACRU = *Acer rubrum*; BELEN = *Betula lenta*; BETAL = *Betula alleghaniensis*; FAGR = *Fagus grandifolia*; MAGAC = *Magnolia acuminata*; PRPN = *Prunus pensylvanica*; PRSR = *Prunus serotina*). Species that did not appear in more than two density treatments (*Tsuga canadensis* and *Acer saccharum*) were not included

	Species density (N/ha)								
Treatment	ACPE	ACRU	BELEN	BETAL	FAGR	MAGAC	PRPN	PRSR	Total
4 deer/km^2	17 (0.7%)	211 (8.5%)	1006 (40.5%)	94 (3.8%)	172 (6.9%)	22 (0.9%)	567 (22.8%)	389 (15.6%)	2,487
8 deer/km^2	6 (0.3%)	394 (17.8%)	489 (22.1%)	100 (4.5%)	344 (15.6%)	11 (0.5%)	461 (20.9%)	406 (18.4%)	2,210
15 deer/km^2	15 (0.6%)	163 (6.4%)	652 (25.6%)	141 (5.5%)	400 (15.7%)	7 (0.3%)	89 (3.5%)	1007 (39.5%)	2,550
25 deer/km^2	17 (1.0%)	61 (3.5%)	133 (7.7%)	78 (4.5%)	178 (10.3%)	0	217 (12.6%)	1039 (60.4%)	1,721

legacy of deer browsing on stand diversity. Black cherry, being cyanogenic, is unpalatable to deer, making it one of the primary tree species to survive following the intense browse pressure in the 25 deer/km^2 treatment (Horsley et al., 2003). Other ecologically and economically valuable tree species, such as maple and birch, remain in low abundance in the 25 deer/km^2 treatments after 36 years (Figure 3).

High deer density treatments had low tree density and basal area as well, similar to the results of Horsley et al. (2003) who found that increasing deer density reduced stem density 5 years post-treatment. However, this browse effect on tree density was not observed by Nuttle et al. (2011) at 10- and 25-year post-treatment, who found little difference in tree density between treatments. They hypothesized that low-palatability species, such as black cherry, were able to regenerate and fill niche space of high-palatability species, consistent with Leibold's edibility hypothesis (Leibold, 1989; Nuttle et al., 2011). We suggest that over time, high deer densities at our site led to a recalcitrant understorey, with unpalatable hay-scented fern *Dennstaedtia punctilobula* spreading during stand initiation and eventually dominating the understorey of most of the 25 deer/km^2 stands (Nuttle et al., 2014). As these stands began self-thinning, the fern understories prevented tree regeneration through shading and resource competition, as has been seen in other parts of Pennsylvania (Royo & Carson, 2006). The legacy effect of deer browse on tree density we observed has therefore likely re-emerged due to compositional differences in the regeneration layer among treatments, whereby a recalcitrant understorey prevented further tree regeneration following the self-thinning of uneaten, shade intolerant black cherry in high deer density areas. These results underscore the importance of long-term monitoring of stands afflicted by deer browse (or other press disturbance agents), as the effects of herbivory on stand structure may take decades to fully develop. Furthermore, these sparce black cherry stands at 25 deer/km^2 had the lowest basal area and thus, the lowest above-ground biomass, as both metrics are highly correlated ($r = 0.99$; Appendix Table S3). Low tree basal area at the highest deer density indicates that overabundant herbivore populations can cause reductions in above-ground carbon stocks over time through species community change (White, 2012).

The combination of changes in tree species composition and stand structure in the highest deer density treatment translated into changes in canopy structure: a stark decrease in VAI and increase in canopy gap fraction at 25 deer/km^2. Functionally, this implies a reduction in the density and connectivity of canopy leaves, with foliage now highly aggregated and clustered around black cherry stems (Figure 1). This finding aligns with Canham et al. (1994) who found that black cherry had the lowest crown depth (the proportion of tree height to tree-crown depth) of many common temperate tree species and Sullivan et al. (2017) who found that shade intolerant species have narrower canopies. The deer browse effect on crown geometries and canopy structure, as quantified with the PCL, may also signal the beginning of a shift in forest structure to an alternative state, one described by Stromayer and Warren (1997) as a 'deer savanna'. In our system, high deer browse pressure caused significant changes in species composition, gap fraction, and VAI, with black cherry dominating the overstorey and hay-scented fern dominating the understorey.

The impact of deer on VAI presented herein is more similar to pulse disturbances, such as fire and ice storms, than press disturbances, such as acid rain or some pathogens. Deer, fire, and ice storms each reduce canopy VAI through species compositional changes, leaf combustion, or stem collapse, respectively (Atkins et al., 2020; Fahey et al., 2020). In contrast, acidification and pathogens such as hemlock wooly adelgid have shown relatively little influence on VAI, potentially because these slow-acting disturbances allow for foliar replacement in the canopy over time (Atkins et al., 2020). However, the impact of herbivory on canopy vegetative density is likely to be longer-lasting than a single fire or ice storm event. Deer have changed the stand's VAI through lasting shifts in species composition and canopy architecture rather than through moderate canopy combustion or breakage, which likely only have a short temporal signature. These long-term reductions in canopy density by deer can then influence ecological function, as VAI is strongly correlated with the fraction of photosynthetically active radiation (fPAR) absorbed by the canopy (Atkins et al., 2018) and influences wildlife such as arthropods, bird species, reptiles, and other arboreal species (Cuddington, 2011; Nuttle et al., 2011; Ulyshen, 2011).

Rugosity showed less straightforward treatment responses. The increase in rugosity associated with higher deer densities and gap fraction is similar to Fotis et al. (2018) who found that stands with low stem densities had more open canopies and greater horizontal variability, which contributes to greater rugosity. Since all of our stands are still in the stem exclusion phase, stands in the low deer density treatment are dense and less horizontally complex than stands in the high deer density treatment, causing a difference in rugosity. Our findings are consistent with the canopy structural classification system of Fahey et al. (2019), where dense forests in the stem exclusion phase have low rugosity and young, patchy canopies have slightly higher rugosity.

Other temperate forest disturbances have had variable influences on rugosity. Ice storms, hemlock wooly adelgid, and now white-tailed deer browse increase rugosity, age-related senescence decreases rugosity, while fires, historic logging, beech bark disease, and acidification have little effect (Atkins et al., 2020; Wales et al., 2020). The variable response of rugosity to disturbance type indicates that multiple canopy structural metrics should be considered to gain a more holistic perspective on which aspect(s) of the canopy change. As our stands continue to develop, rugosity could become a useful metric to predict NPP in light of herbivory disturbance, as it is strongly correlated with greater net primary productivity within maturing stands (Gough et al., 2019, 2021). Furthermore, since stand age and time since disturbance are of particular importance when measuring rugosity, but are often difficult to standardize across studies, long-term experimental studies such as ours are particularly important to better understand these disturbance–canopy interactions (Wales et al., 2020).

We found that tree canopies were tallest at the lowest (4 deer/km^2) and highest (25 deer/km^2) deer density treatments. This pattern may have been driven by differences in preferred browse species at each end of the deer density spectrum, with palatable pin cherry favoured at 4 deer/km^2 and unpalatable black cherry at 25 deer/km^2 (Figure 3; Table 2). Both *Prunus* species are shade intolerant and fast growing, making the low and high deer density canopies taller than those dominated by more shade-tolerant species such as beech, maple and birch (Table 1; Figure 3; Canham et al., 1994). Differences in canopy height and composition could influence each stand's total above-ground biomass and ability to support various wildlife habitat types (Fotis et al., 2020; Seavy et al., 2009; Sullivan et al., 2017; Wang et al., 2021). These results support other studies showing that press disturbances can have a positive impact on MOCH through species-specific influences. For instance, soil acidification likely increases MOCH by favouring upper canopy growth and loss of subcanopy species (Atkins et al., 2020). Eichhorn et al. (2017) found that increased deer densities led to taller canopies in southern England, although the mechanism for this effect was unclear. Our experiment provides clear evidence that high deer densities impact canopy height decades after stand establishment by altering the relative abundance of tree species that vary in shade tolerance and growth rate. Such species-specific influences by press disturbances may be an important mechanism affecting changes in canopy height and structure.

Effective management of forest structure and canopy complexity in light of current or future disturbances is becoming a priority due to structure's many connections to ecosystem function and resilience (Fahey et al., 2018; Seidl et al., 2016). Using a PCL, we have gained insight on how a decade of deer browse disturbance can leave a distinct signal on the canopy, with high deer density leading to high rugosity, gap fraction, and canopy height, with low VAI. Since ungulates are at high densities in many forests globally, our work provides a basis for generalizing how intense herbivory may affect key canopy structural traits over time (Bernes et al., 2018). By allowing ungulate populations to remain at high densities, forest managers are indirectly changing stand and canopy structure, which likely has important long-term ramifications on many associated ecosystem functions. Therefore, long-term monitoring of canopy structure in forests with heavily managed ungulate populations could serve as an indicator of both ecological function and management success (Gatica-Saavedra et al., 2017).

5 | CONCLUSIONS

Using a long-term deer enclosure experiment, our study is the first to apply a PCL system to determine how varying deer densities affect canopy structure. We show that deer leave a unique legacy on the structure of northern hardwood forests at multiple levels, from species diversity to canopy complexity, and that these changes can be detected with the PCL. Over three decades after the conclusion of the experimental treatments, at the highest deer density treatment we saw decreases in tree diversity, basal area, tree density, canopy VAI, and increases in gap fraction and rugosity. Furthermore, we found that tree density and basal area varied widely with different deer browse intensities due to changes in species composition and that these effects of deer browse may take decades to become fully pronounced. Although the influence of herbivory is pervasive across many forest types (Bernes et al., 2018; Patton et al., 2018), there has been little prior quantitative evidence of the legacy of browsing pressure on canopy structure in temperate forests. Deer herbivory may be one of the most important drivers of forest composition and canopy structure over long time-scales, which could have significant ramifications on wildlife habitat (Fotis et al., 2020), carbon sequestration and storage (Fotis et al., 2018; Gough et al., 2020; Hardiman et al., 2011), light-use efficiency (Atkins, Fahey, et al., 2018; Hardiman, Gough, et al., 2013), and timber extraction (Miller et al., 2009) in the present and into the future.

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CONFLICT OF INTEREST

The authors have declared no conflicts of interest.

AUTHORS' CONTRIBUTIONS

S.P.R. collected the data and led writing of the manuscript; A.A.R., S.P.R. and A.T.F. analysed the data; all authors equally contributed to project ideas and methodology. All authors also provided feedback on manuscript and gave final publication approval.

DATA AVAILABILITY STATEMENT

Data are available in the Dryad Digital Repository https://doi.org/10.5061/dryad.b8gtht7dn (Reed et al., 2021).

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SUPPORTING INFORMATION

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