ANALYZING THE EFFECTS FROM WHITE-TAILED DEER (*Odocoileus virginianus***) BROWSE AT TIMBER HARVEST SITES OF VARYING AGES**

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ABSTRACT White-tailed deer (*Odocoileus virginianus*) are keystone herbivores in the deciduous forests of the eastern United States, capable of significantly altering their habitats. Overpopulation of white-tailed deer leads to excessive herbivory, establishing them as a primary factor in the adverse effects on forest regeneration. Timber harvest sites, which provide abundant food resources, are particularly vulnerable to deer browsing. This study evaluates the impact of deer browse on forest regeneration within timber harvest sites at the West Point Military Reservation, focusing on areas harvested between 2003 and 2021 over a nineteen-year timeframe. At each site, we calculated the number of 1-m² radius plots surveyed along transects determined by harvest size, and our analysis compared tree species abundance, height classes, browse frequency, browse dominance, and competing vegetation in both the overstory and understory. The findings indicate that sugar maple (*Acer saccharum*) demonstrated the highest overall species composition of 74.23% alongside a rich browse dominance of 12.96%, despite exhibiting low browse frequency of 1.70%. Conversely, American hornbeam (*Carpinus caroliniana*) showed the highest browse frequency at 85.71%, but comprised only 0.99% of total browse composition and had a low species representation of 0.11%. Furthermore, all oak species (*Quercus* sp.), which are essential components of the region's mature forests, struggle to transition from the seedling to sapling stage, resulting in oak regeneration failures. The inadequate survival rates of these oak species threaten their ability to maintain dominance and

co-dominance in West Point's forest ecosystems, signaling a potential shift in the forest inventory, composition, and structure with significant ecological repercussions. Late successional species are particularly impacted by deer herbivory, as many do not reach the requisite three to six-foot height class for successful tree establishment in forests due to browsing pressures. In contrast, pioneer species, which constitute the majority of the deer's tree diet, are thriving and outcompeting more sensitive species. This browsing behavior indicates that deer overpopulation is altering tree species dynamics within the forest, leading to a change in our forest ecosystem composition, structure, and function. To mitigate these issues, future management efforts should consider implementing more rigorous hunting regulations, enhancing education and outreach programs for hunters, and exploring alternative population control methods.

1. **INTRODUCTION**

Investigating forest health begins with monitoring tree seedling establishment and growth which drives future forest composition, structure, and function (Lesser et al. 2019). Fauna that utilizes the forest depend on natural regeneration to guarantee its vital resources continue to exist. Regeneration is the ability of a forest to support itself through the growth and survival of seedlings to replace a forest lost to harvest or natural die back (NPS 2020). Forest regeneration is site- and stand-specific influenced by abiotic factors such as light availability and climate, and biotic factors including competing vegetation and wildlife herbivory (Kupferschmid et al. 2019; Lesser et al. 2019). It is essential to identify major stressors that alter forest resilience to implement a sound ecosystem management plan (Quirion and Blossey 2023). High herbivory pressure by large mammals has been featured as the main factor suppressing the forest ecosystem structure and function (Borowski et al. 2021; Schmit et al. 2020).

White-tailed deer (*Odocoileus virginianus*) in eastern U.S. deciduous forests are keystone herbivores which can cause significant alterations to their habitat (Schmit et al. 2020). An overabundance of white-tailed deer has negative cascading effects to the ecological, biological, and cultural communities (Ward and Williams 2020; Westerfield et al. 2019). Dispersion of invasive plant species and earthworms are magnified as high populations of deer traverse a landscape (Waller 2018; Lesser et al. 2019). High densities of deer aid intraspecific disease transmission like epizootic hemorrhagic disease (EHD) and chronic wasting disease (Waller et al. 2017). Furthermore, large quantities of deer intensify economic damage to agriculture and household gardens, transmit tick-borne diseases like Lyme disease from blacklegged ticks (*Ixodes scapularis*), and inflate the rate of deer-vehicle collisions (Ward and Williams 2020; Westerfield et al. 2019). One of the most documented consequences of overabundant deer is excessive herbivory which limits tree sapling development, species diversity, density, and composition of the forest understory (Forrester et al. 2014; Borowski et al. 2021; Ward and Williams 2020; Kupferschmid et al. 2019).

In New York's Hudson Valley region, the New York State Department of Environmental Conservation (NYSDEC) deemed that regeneration is largely unacceptable due to a high browsing impact from deer (NYSDEC 2021). Furthermore, the state's objective in this region is to reduce the white-tailed deer population by at least 25%, in response to public preference for a decrease in the local deer population (NYSDEC 2021). Historically, white-tailed deer in New York State were nearly hunted to local extinction, coinciding with impacts from significant forest destruction in the 1800s (Weitzel 2023; Halls 1984). By 1878 sightings of deer were so rare, in fact, that a local account published that year in a scientific journal noted the sighting of a white-tailed deer, providing evidence that the species had returned within the confines of the district (Mearns 1898).

Establishment of wildlife agencies permitted the enforcement of hunting regulations and aided regrowth of New Yorks forests in the early 1900's to improve the once declining white-tailed deer population (Blossey et al. 2019; Westerfield et al. 2019). Presently, white-tailed deer are at high densities within most of the eastern U.S. (McShae and Rappole 1992). Current expansion to the deer population is attributed to these early conservation efforts, major changes in land use, reduced human hunting pressure, shifts in societal norms and values, and extermination of natural predators such as gray wolves (*Canis lupus*) and mountain lions (*Pumas concolor*) (Quirion and Blossey 2023; Whyte and Lusk 2019). Historical dynamics have shifted; rather than the forests affecting deer populations, it is now the deer that exert influence over forest ecosystems. This change emphasizes the need to evaluate food source modifications within the forest, which is essential for the effective management of deer populations (Waller 2018).

Wildlife movement across the landscape is generally driven by multiple factors to procure high quality resources such as food, shelter, water, and mates (Quinn 2010) Uniform distribution of resources throughout the environment is rare, affecting wildlife movement patterns as individuals search to obtain desirable resources (Lesser et al. 2019; Quinn 2010). Strongly preferred plant species are pursued by white-tailed deer, even at low densities, enhancing the threats towards vulnerable tree species (Blossey et al. 2019). Desirable tree species may experience reduced regeneration due to selective browsing from deer (Patton et al. 2021). Many studies of high white-tailed deer populations demonstrate that selectivity is the main cause of significant negative effects on forest regeneration (Borowski et al. 2021; Schmit et al. 2020; Ward and Williams 2020). Recent timber harvest sites that provide ready access to abundant food resources are more vulnerable to deer browse compared to other landscapes. Forest regeneration failure

succeeding timber harvests is often the result of excessive herbivory by white-tailed deer (Parker et al. 2020).

In this study, we investigated the effect of white-tailed deer herbivory on regenerating forests across a nineteen-year timeline of recent timber harvest sites at the West Point Military Reservation in New York. Specific study objectives were to (1) quantify the effects of deer browse on the structure, composition, and community of the forest floor at the plot level, (2) examine 2003-2021 timber harvest sites to understand regeneration across time, (3) determine how spatial and temporal factors influence seedling and sapling regeneration and (4) evaluate current whitetailed deer population dynamics. Ultimately, we hope foresters and wildlife managers will be able to utilize the results of this study and others like it to better inform program goals for forest regeneration and deer management (Lesser et al. 2019).

2. STUDY AREA

Our study was conducted at the United States Army Garrison at West Point (USAG-WP) in New York. West Point was founded as a proper U.S. Army Garrison in 1778, but since 1802, it has been the established home to the United States Military Academy (USMA) and its Corps of Cadets (EA Engineering 2018). West Point rests along the Hudson River roughly 50 miles north of New York City. The installation consists of 16,000-acres that is divided into the 1) Main Post (or Cantonment), a roughly 2,000 acre developed area on the west bank of the Hudson River 2) Constitution Island, laying on the east side of the Hudson River, directly across from Main Post and 3) the reservation, west of the cantonment, consists of 14,000 acres mainly comprised of forests used for field training, where most of our sampling took place.

The Hudson Highlands is the ecoregion that West Point dwells in which drives the forest composition and structure. The Hudson Highlands landscape is comprised of ridges, valleys, and exposed bedrock throughout the terrain. The Hudson River, adjacent to the installation, cuts through the highlands leaving steep cliff faces on both sides of the river. Soils are shallow, rocky, and highly acidic (Bryce et al. 2010). The most common forest type on the facility and in the Hudson Highlands is the Appalachian oak-hickory forest, mainly composed of white oak (*Quercus alba*), northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), bitternut hickory (*Carya cordiformes*), shagbark hickory (*Caraya ovata*), and hophornbeam (*Ostrya virginiana*) (NYNHP 2023). Particularly, northern red oak is the dominant mature timber stand on the reservation (EA Engineering 2018). West Point's climate is characterized as humid continental, with wet hot summers and snowy frozen winters. West Point's average annual high temperature was 61°F with an average annual low temperature of 42°F. The total average annual rainfall was 50.67" per year. Average annual wind speed was 5.2 mph (World Climate 2023). The installation mainly consists of slopes greater than 20%. Elevations range from near sea level up to 1,433 feet (EA Engineering 2018).

Since the 1950s, timber harvests have expanded significantly, driven by the growth of the forestry program that have influenced forest composition (EA Engineering 2018). As these forestry initiatives developed, the frequency and intensity of timber harvests also increased. Additionally, West Point's forests have been shaped by various historical factors, including forest fires that have altered substantial portions of the landscape over time. Furthermore, West Point has a long-running hunting program in coordination with the natural resources section which increases pressure on the deer population. Presently, a primary focus of land use revolves around intensive cadet training. The evolving requirements of training necessitate development across

the installation, including construction projects and the expansion of military ranges that encroach upon the surrounding forests. Cadet training encompasses various activities such as small arms, mortar, and artillery training, land navigation, field exercises, and the development of general military and leadership skills. This training is essential for fulfilling West Point's mission and has direct implications for land use and personnel accessibility. Consequently, these factors significantly influence the area's wildlife, vegetation, and overall land management strategies.

3. METHODS

3.1. Study design

We surveyed regeneration, vegetation competition, and browse data at timber harvest sites that occurred from 2003 through 2021, covering a nineteen-year timeline across USAG-West Point (**Table 1**). Timber harvests did not occur every year at West Point, but rather on occasional years, in which sometimes multiple harvests occurred. We selected the applicable timber harvest sites for this survey, excluding a few sites that did not accurately represent the

Harvest Name	Training Area	Harvest Year	Size (acres)	# Plots	Survey Date
Kelly Farm	B	2008	11.38	21	5/16
Mineral Springs	L	2021	18.62	23	5/17
Kelly Farm		2008	11.86	21	5/20
Area L South	L	2013	16.15	22	5/31
Area L North	L	2013	47.7	35	6/7 & 6/14 & 6/20
Firebreak 22	S	2005	62	41	6/25 & 6/26
Bull Pond	Ω	2011	55.04	38	$7/3$ & $7/8$
Mine Lake	T1	2007	60.04	40	$7/10 \& 7/11$
Long Mountain	U ₁	2003	35	30	$7/17$ & $7/18$
West Burke	N	2021	15.41	22	$7/23$ & $7/25$
M South	M	2018	24.6	26	7/30 & 8/1
Prep School/DOL	J2	2009	62	41	8/28 & 9/3

Table 1. Descriptions of the twelve timber harvest sites selected to survey, ranked by the earliest to latest survey date.

landscape. We divided the 2013 Area L timber sale into two separate areas, north and south. This removed the 0.5-mile-long logging road between those areas that did not accurately portray the harvest site. A total of twelve study sites were chosen, with an average timber harvest size of 35 acres. The largest timber harvests measured 62 acres each in 2005 and 2009, while the smallest was 11.38 acres in 2008. In total, we surveyed 419.8 acres of timber harvest sites. To explore the study sites and generated maps, examine the [Survey Maps.](https://armyeitaas-my.sharepoint-mil.us/personal/alyssa_m_jaffee_ctr_army_mil/Documents/Documents/research%20docs/regeneration%20survey%20maps%202024.pdf)

We collected data at the plot level at timber harvest sites during mid-spring to late summer 2024 from 16 May to 3 September. The dimensions of each harvest site, including size, shape, and topography, determined the number and arrangement of transects and plots. We generated plots and transects for each site on paper maps using hand tools such as a ruler, map scale, calculator, and conversions. The number of transects varied per harvest site, ranging from 4 to 11, which we evenly spaced and oriented parallel to each other, typically following the perpendicular contours of elevation. The distance between transects varied from 156 ft to 352 ft. Our protocol determined the number of 1-square-meter (1 m^2) radius plots at each site dependent on harvest acreage. We established 20 plots for the first 10 acres and added one additional plot for every 2.5 acres. For example, if a harvest size was 30 acres, then 28 plots would be established: 20 plots for the first 10 acres then 8 additional plots for the remaining 20 acres. Harvest sites of 10 acres or fewer were sampled with 20 plots (Parker et al. 2020). We evenly spaced the plots along each transect. The number of plots on each transect varied per transect length. Each transect included a 50ft buffer on both sides, ensuring that the plots started at least 50 ft in from the harvest boundary line. The distances between plots for each harvest site varied from 81 ft to 207 ft. We surveyed a total of 360 $1-m^2$ radius plots.

3.2.Browse observations on seedlings and saplings

For each $1-m^2$ radius plot, we identified seedling and sapling species, tallied the number of trees into four height classes $(0-5", >5-12", >12", 3",$ and $>3"$), and recorded the number of browsed trees per species. We lumped some tree species into genera, such as hickories (*Carya* sp.), when identification by species was difficult due to their young age. A seedling or sapling was counted if it measured under 6 ft in height, with a DBH no greater than 4.5". Seedlings are young trees that have recently emerged from seeds, marking a critical time for forest establishment. They are typically defined as being under 3 feet tall. In contrast, a sapling is a young tree that has surpassed the seedling stage and is growing towards maturity, usually ranging from 3 to 10 feet tall. A tree was considered browsed if there was observed damage to any portion of the plants primary or lateral branches likely caused by deer browse (Parker et al., 2020). All browsing was assumed to be caused by white-tailed deer (Miller et al. 2009). Any plot that fell into standing water or on roads was kept and documented as 'not applicable'. Trees that originated as a shoot from an existing tree or stump were not counted, as it does not qualify as an individual.

3.3. Competing vegetation in the over and understory

We recorded ocular estimates of plot coverage by non-vegetated ground, dominant competing vegetation, and overstory canopy for each 1-m² radius plot (Miller et al. 2009). Nonvegetated ground is recorded as the compiled percent of rock, woody debris, litter, moss, and bare ground per plot. Competing ground vegetation is considered herbaceous plants, shrubs, or vines that fight for the same resources as tree saplings or seedlings. For each plot, we identified a singular dominant competing ground species by name and recorded the percent it covered from a standing position (Miller et al. 2009). We documented ocular estimates of the percent of closed

tree canopy from each plot center. Overstory and understory estimates were documented separately in the data sheet. Any notes we had for each plot were documented in the note space. The [regeneration data sheet](https://armyeitaas-my.sharepoint-mil.us/personal/alyssa_m_jaffee_ctr_army_mil/Documents/Documents/research%20docs/new%20data%20form.pdf) is attached at the end for reference.

4. RESULTS

4.1.Forest regeneration composition and diversity

With a species richness (S) of 25 and 12,413 total individuals, close to 75% of the total tree species were sugar maples (*Acer saccharum*) (**Table 2**). Meaning about 75% of all trees under six feet across survey sites were sugar maples. Following the exceptionally high prevalence of sugar maples, the top five dominant species represented include sweet birch (*Betula lenta*), red maple (*Acer rubrum*), chestnut oak (*Quercus montana*), and species of hickory (*Carya sp.*) comprising a combined 94.02% of the total composition (**Table 2**). Notably, Northern red oak (*Quercus rubra*) represented only 0.99% of the total composition, while white oak (*Quercus alba)* accounted for merely 0.26% of the total. The total calculated Shannon-Weiner Index (Hˈ) was 1.10.

Sugar maples (*A. saccharum*) represented the highest number of individuals in the 0–5-inch size class, totaling 8,961 (**Table 3.**). However, in the subsequent size class of greater than five inches and up to 12 inches, there were only 170 sugar maples, resulting in a substantial mortality rate of 98%. This mortality rate was significantly higher than most other species observed. In the oldest size class of greater than three feet and up to six feet, sweet birch (*B. lenta*) comprised the largest group, with 86 individuals. Notably, only 1.04% of all individuals attained the size class heights of greater than three feet and up to six feet, and fewer than half of all species (12 out of 25 species) were documented to reach this size class (**Table 3**).

Table 2. The table presents the total number and percent composition of tree species documented during the study. Tree species are listed by their scientific names and organized in order of highest to lowest percent.

The majority of trees were observed in the 0–5-inch size class, comprising 86.16% of the total composition (**Table 3**). As the size classes increased, the total percent composition and in most cases the number of individuals per species size class exhibited a corresponding decrease. Northern red oak (*Q. rubra*) struggled to transition from seedling to sapling stage, barely reaching two individuals in the 3'-6' size class. However, a few species, notably invasive species

such as devil's walking stick (*Aralia spinosa*) and tree of heaven (*Ailanthus altissima*), deviated from this trend, exhibiting a higher number of individuals in the larger size classes. Additionally, native species such as American beech (*Fagus grandifolia*) and hophornbeam (*Ostrya virginiana*) also displayed a departure from the typical size class distribution, with a greater representation in the larger size categories.

Species	$0" - 5"$	$>5"$ -12"	>12 "-3'	$>3'-6'$
Acer pensylvanicum	112	14	17	5
Acer rubrum	728	102	18	0
Acer saccharum	8961	170	73	10
Ailanthus altissima	1	6	2	1
Aralia spinosa	1	14	8	1
Betula lenta	311	230	232	86
Carpinus caroliniana	$\overline{4}$	3	7	θ
Carya sp.	75	152	133	4
Fagus grandifolia	9	$\mathbf{1}$	24	14
Fraxinus sp.	$\overline{2}$	1	θ	$\overline{0}$
Liriodendron tulipifera	131	43	23	$\overline{2}$
Nyssa sylvatica	11	2	θ	$\overline{0}$
Ostrya virginiana	10	16	28	$\overline{2}$
Pinus sp.	6	0	0	0
Populus deltoides	θ	0	1	
Populus grandidentata	0		0	0
Populus tremuloides	0		0	0
Prunus serotina	21	3	3	0
Quercus alba	17	8	7	0
Quercus montana	209	124	53	0
Quercus rubra	69	39	13	2
Sassafras albidum	9	9	6	0
Tilia americana	$\overline{0}$	$\overline{0}$	0	1
Tsuga canadensis	3	0	0	0
Ulmus sp.	5	0	2	0
Total	10695	939	650	129
Percent $(\%)$	86.16	7.56	5.24	1.04

Table 3. Tree species and collective study sample by size classes, including the total number by size class per species and percent by size class of collective study sample, arranged in alphabetical order.

(**Table 4**).

The Pearson *r* correlation test was used to determine if there is a relationship between the twelve (N) timber harvest sites ages and their Shannon-Diversity Indices (Hˈ). Results showed that there was no statistically significant relationship between species diversity index (Hˈ) and timber harvest age ($r = 0.04$, $p = 0.897$) (**Table 4**). The Pearson *r* correlation coefficient was used to find whether there is a relationship between the species richness (S) and the harvest site age at

each timber harvest site. The results show that there was no statistically significant relationship between species richness and ages of harvest sites $(r = -0.51, p = 0.874)$

Shannon diversity index (H') and species richness (S) to the age of the 12 timber harvest sites (N). $(\alpha = 0.05)$.

Table 4. The Pearson correlation coefficient (r) is comparing the

4.2.Deer browse intensity and preference

A total of 21 out of the 25 species exhibited observable browse by white-tailed deer. The overall percentage of browse across all regenerating trees was 9.76% (**Table 5**). **Figure 1** excludes any species with a sample size (N) of fewer than four, as these are not considered statistically significant. The three species not represented in **Figure 1** are American basswood (*Tilia americana*), eastern hemlock (*Tsuga canadensis*), and ash species (*Fraxinus sp*.), each of which showed some degree of browse. The four species without any observable browse were

bigtooth aspen (*Populus grandidentata*), eastern cottonwood (*Populus deltoides*), species of pine (*Pinus sp.*), and quaking aspen (*Populus tremuloides*).

The browse dominance reflects the total combined number of browsed individuals and the contribution of each species to that total as a percentage. The species with the highest

recorded browse composition was sweet birch (*B. lenta*), accounting for 26.67% (**Figure 1**). Other notable species with a significant browse dominance were hickories (*Carya sp.*) at 16.18%, chestnut oak (*Q. montana*) at 14.12%, sugar maple (*A. saccharum*) at 12.96%, and red maple (*A. rubrum*) at 9.74% (**Figure 1**). All remaining species each accounted for less than 5% of the browse dominance.

Figure 1. This bar chart displays 18 species, including their scientific names, that exhibited observable browsing by whitetailed deer. The blue bars indicate the percent frequency of individual species being browsed, while the orange bars represent the percent occurrence of browse per species.

The browse frequency reflects the occurrence that a given species is impacted by deer browse. The species with the highest browse frequency was American hornbeam (*Carpinus caroliniana*), recorded at 85.71%. There were six additional species that exhibited a browse frequency greater than 50%. These species included American beech (*F. grandifolia)*, American hophornbeam (*O. virginiana*), devils walking stick (*A. spinosa*), sassafras (*Sassafras albidum*), hickory species (*Carya* sp.), and white oak (*Q. alba*) (**Figure 1**).

Although sugar maple contributed 12.96% to the browse dominance it had a strikingly low browse frequency of only 1.70%. Overall, while American hornbeam had the highest browse frequency at 85.71%, it constituted merely 0.99% of the total browse dominance, highlighting the complex relationship between browse frequency and browse composition in forest ecosystems.

4.3.Over and understory competition

The percent of canopy cover generally exhibited low variability, particularly clustered in the higher percentages. The median for overstory shading was 70% with and interquartile range of 60-90% (**Figure 2**). Several outliers, low percentages, were observed in the canopy cover data indicating some extreme values. Percent of canopy cover was observed to increase with time preceding the timber harvest sale. The R^2 value of 0.487 indicated a moderate positive correlation between increase in canopy cover and time since the harvest (**Figure 3**).

Figure 2. Box plot comparing the distribution of all recorded percentages of non-vegetated ground (orange) and canopy cover (blue). The plot displays the distribution of both data sets in quartiles, showing the median (x), interquartile range (dark shaded area), and any outliers (dots).

In contrast, the percent of non-vegetated ground was more evenly distributed with most data points clustered around the middle interquartile range at 20- 80%. The median was 48% with a relatively consistent spread across the entire range of values (**Figure 2**). The R^2 value of 0.248 suggested a weak relationship between the percent of non-vegetated ground to the time since the timber harvest sale (**Figure 3**).

Figure 3. The scatter chart illustrates the relationship between the average percent of canopy cover (blue) and non-vegetated ground (orange) to the number of years since the timber harvest. Linear trendlines, represented by dashed lines, are shown with their respective r-squared value (R2) for both the canopy cover (R2 =0.487) and non-vegetated ground (R2 = 0.248).

There were 37 different categories of dominant competing vegetation across the landscape, in which eight invasive species were represented. The percent composition highlights species representation within the landscape. The average percent cover of species per plot indicates their spatial distribution within the surveyed area. Eighteen species each contributed less than one percent to the total composition; due to their small sample sizes, the data for these species were excluded from analysis. The category labeled 'Nothing' indicates sites with bare ground devoid of competing vegetation. Sites deemed not surveyable due to the presence of roads, water bodies, or fenced-off areas were classified as not applicable (N/A) and excluded from the analysis.

Grass species had the highest percent composition at 18.9%, indicating that grass was the dominant competing vegetation type across the surveyed areas (**Figure 4**). Japanese stiltgrass (*Microstegium vimineum*) exhibited the highest average percent cover at 58.2%, indicating a significant distribution rate within selected areas the species was present. The top five dominant species included grass species, blueberry species (*Vaccinium* sp.), hay-scented fern (*Dennstaedtia punctilobula*), Japanese stiltgrass (*Microstegium vimineum*), and Japanese barberry (*Berberis thunbergii*). More than half of these dominant species, including hay-scented fern, Japanese stiltgrass, and Japanese barberry, are considered highly problematic invasives at West Point. Although these invasive species were represented by a smaller proportion than native species, their average percent cover reveals a more significant impact; when present, they tend to

Figure 4. Column chart illustrating the percent composition (blue) across the landscape and average percent cover (orange) per plot for each dominant competing vegetation. This is ranked in order from the highest percent composition to the lowest.

dominate areas. For example, multiflora rose comprised only 1.4% of the overall population but had an average spatial coverage of 41%, highlighting the challenges posed by invasive species.

5. DISCUSSION

Our study confirms that white-tailed deer (*Odocoileus virginianus*) do not significantly impact early successional species that occur in high populations. However, there is a discernible trend indicating a direct effect on late successional species, particularly those with lower population densities (DiTommaso et al. 2014). Notably, the five species with the highest browse composition—sweet birch, hickory, sugar maple, red maple, and chestnut oak—align with the list of the five dominant regenerating species. This suggests that the main species being browsed are those most readily available in the landscape. Such restrictions not only affect individual species but may also have broader implications for forest dynamics and the recovery of postdisturbance ecosystems.

Succession is defined as the series of changes following a disturbance, creating opportunities for species colonization (Horn 1974). Pioneer species, characterized by rapid growth rates, shade intolerance, and the ability to quickly populate disturbed areas are the first species to appear after disturbance (Witynski, 2021). In contrast, late successional species exhibit slower-growth, increased shade-tolerance, and often have lower overall populations (Cortese, 2023). Sweet birch, a recognized pioneer species, shows exceptional growth rates, often growing twice as fast as other species such as sugar maple and red maple (Lamson, 1990). At West Point, pioneer trees including sweet birch and hickories, serve as the primary food resource among tree saplings and seedlings for white-tailed deer, constituting most of their diet without adversely impacting their population (**Figure 1**). Sweet birch's ability to thrive in disturbed areas

underscores its essential role in soil stabilization, enhancing wildlife biodiversity, and the early stages of forest regeneration (Cortese 2023).

Late successional species face challenges from white-tailed deer herbivory, with many failing to reach the tallest height class at 3-6 feet, indicating that browsing limits their development into mature trees (**Table 3**). Species such as American hornbeam, American beech, American hophornbeam, and sassafras demonstrate high browse selection frequency, yet they exist as small populations, significantly reducing their chances of survival (**Figure** 1). Given the low percentage and limited number of species reaching the tallest height class, the impacts of over foraging are pronounced. The selective foraging behavior of white-tailed deer, influenced by food availability, landscape characteristics, and seasonal variations, results in a disproportionate impact on specific plant species and their parts (Sample et al. 2023; Nudds 1980).

Contrary to expectations, sugar maples exhibited the highest species composition. This outcome can be attributed to their prolific seeding and significant shade tolerance, which are characteristic of late successional species (Godman 1990). However, concerningly, the mortality rate of sugar maples can reach as high as 98% between the first and second size classes (**Table 3**). Their survival is hindered by sensitivity to surface moisture conditions and shallow root systems that limit their growth potential, particularly in our forests where high canopy cover from 60% to 90%—restricts light availability (**Figure 2**). Furthermore, our observations suggest that deer browsing has minimal impact on the death rates of sugar maples in comparison to species that are more heavily browsed.

Intensified herbivory on Northern red oak (*Quercus rubra*) has emerged as a significant concern in our study. Given that Northern red oak serves as the dominant species in our mature timber stands and has the capacity to produce a substantial number of seedlings, we anticipated a greater representation of this species within the overall species composition. Alongside Northern red oak, chestnut oak (*Quercus montana*) and white oak (*Quercus alba*) are also crucial components of our predominant mature forest type. Nevertheless, all oak species are experiencing challenges transitioning from the seedling to sapling stage, a critical phase for establishing individual trees in the forest ecosystem. Research has indicated that oak species in eastern North America often face regional regeneration failures, although areas with lower deer densities, such as tribal lands, demonstrate a contrasting scenario where oak species thrive (Reo & Karl 2010). Oaks not only constitute an important timber resource but also serve as a primary food source for wildlife and exhibit an intermediate preference for deer (Blossey et al. 2019). Despite the substantial seed production from mature overstory trees and successful germination, the extensive deer browsing linked to an overpopulation significantly hinders the establishment of Northern red oak seedlings, leading to a pronounced regeneration debt (Blossey et al. 2019). The failure of oak species to survive at adequate rates threatens their ability to maintain dominance and co-dominance in our forests. This decline suggests an imminent shift in forest inventory, composition, and structure that may have far-reaching ecological implications.

Interestingly, while higher concentrations of invasive species are often anticipated in timber harvest plots due to the influx of disturbances that may introduce new invasives or spread existing ones, native species have continued to dominate in these areas. Less intense and older timber harvest sites tend to exhibit greater canopy cover, which promotes better conditions for native species (Martínez-Meléndez et al., 2021). In contrast, invasive plants such as Japanese barberry, Japanese stiltgrass, and hay-scented fern flourish in areas with high deer populations, which facilitates their spread and may enable them to outcompete native flora (Gorchov et al.

2021). Our observations link the rapid expansion rates of invasive species to canopy openings, disturbances, competition with native species, and increased deer populations in timber harvest sites. However, these findings may be influenced by the intensity and type of timber harvest, as well as the pre- and post-harvest treatments—details that remain unaccounted for due to missing historical data.

Herbivory by deer, influenced by selective browsing preferences, significantly affects the regeneration dynamics in forests (Patton et al. 2021; Borowski et al. 2021). A Shannon diversity index (H') value of 1.1 suggests a moderate level of biodiversity within the studied community, indicating a mixture of species, with some exhibiting greater dominance influenced by deer browsing in conjunction with other ecological factors (Nolan 2005). Currently, our forests differ markedly from their historical states, largely due to introduced tree diseases. Species such as American beech, which is impacted by both beech leaf disease and beech bark disease, have experienced a notable decline in the recruitment of new individuals in the smallest size class. Similarly, eastern hemlock, affected by the hemlock woolly adelgid, showed an insignificant sample size, with individuals in the smallest size class failing to grow further. These developments illustrate the interrelated impacts of disease and herbivory on forest structure. The interactions among overpopulation of deer and the spread of new diseases are transforming the composition of these complex ecosystems. The increasing browsing intensity from deer overpopulation exacerbates the stress on already declining populations, creating a cycle that threatens forest regeneration and biodiversity.

This browsing behavior alters species composition, enabling certain plants to thrive at the expense of others, likely linked to an overpopulation of deer. Overall, high white-tailed deer populations are affecting the regeneration of late successional species at post-timber harvest

sites, ultimately inhibiting their growth into mature trees and altering the forest composition. These findings emphasize the complexity of herbivore foraging behavior and underscore the need to understand these dynamics to inform management strategies aimed at maintaining healthy forest ecosystems and ensuring the sustainability of both plant and animal populations.

6. MANAGEMENT IMPLICATIONS

In analyzing past timber harvest sales, it became evident that there was minimal to no information available regarding the forest conditions prior to the timber sale and the subsequent impacts following the sale. For future timber harvests, it is essential to assess and document the intensity and type of cut to fully understand its potential impacts. One effective cut method is selective harvesting that involves choosing individual trees to remove from a forest, while leaving parts of the original ecosystem to avoid radical changes. Additionally, conducting a preharvest survey to evaluate the understory, canopy cover, regeneration, forest type, and tree species will provide valuable insights into the forest's condition before any alterations are made to the landscape. Furthermore, effective management and monitoring of invasive species is crucial both before and during logging, as well as after the harvest. Implementing best management practices is vital, given that invasive species tend to thrive in disturbed areas (Gorchov et al., 2021).

Given the overpopulation of white-tailed deer, a reduction in their numbers through recreational hunting presents a viable management strategy. However, it is important to note that the primary interest of many hunters has shifted from population control to recreational pursuits, leading to a decline in hunting's effectiveness as a means of managing deer populations (Reo & Karl 2010). Current deer management efforts are often shaped by socio-cultural and political factors, making it challenging to achieve significant reductions in deer numbers necessary for

promoting adequate forest regeneration. The prevailing management goal for white-tailed deer typically aims at optimizing recreation opportunities while minimizing human-wildlife conflicts and reducing damage to native vegetation (Bookhout, 1996). However, achieving balance in these competing interests often complicates the management of deer populations, potentially undermining forest health. To effectively address the challenges posed by overpopulation, it may be advisable to completely reevaluate existing management strategies and develop new solutions that directly target a reduction in the white-tailed deer population.

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