Natives falter as exotics prosper: effects of chronic differences in white-tailed deer density on canopy gap regeneration

by

Anthony C. Yacucci

Submitted in Partial Fulfillment of the Requirements

for the Degree of

Master of Science

in the

Biological Sciences

Program

YOUNGSTOWN STATE UNIVERSITY

May, 2023

Natives falter as exotics prosper: effects of chronic differences in white-tailed deer density on canopy gap regeneration

Anthony C. Yacucci

I hereby release this thesis to the public. I understand that this thesis will be made available from the OhioLINK ETD Center and the Maag Library Circulation Desk for public access. I also authorize the University or other individuals to make copies of this thesis as needed for scholarly research.

Signature:

Anthony C. Yacucci, Student	Date

Approvals:

Dr. Ian J. Renne, Thesis Advisor	Date

Dr. Thomas P. Diggins, Committee Member	Date

Dr. Walter P. Carson, Committee Member	Date

Dr. Salvatore A. Sanders, Dean of Graduate Studies	Date

ABSTRACT

Forest canopy gaps are integral for regenerating most plants and maintaining regional diversity. However, native diversity in gaps is often compromised by exotic plant dominance and in the eastern United States, chronic overbrowsing by white-tailed deer (deer; *Odocoileus virginianus*). Notably, decades-long, near ubiquitous deer overabundance limits opportunity to study the dynamics of communities lacking persistent overbrowsing. Here, we ask how does spring and fall herbaceous and woody composition differ between areas with ≥50 years of low (~7 deer/km²) and high deer density (≥20 deer/km²). This was done in 2-14-year-old canopy gaps, ranging in size from 83-522m² (median: 230m^2), in both mesic and drier temperate forest. Paired deer exclosure vs. control plots in two-year-old harvest gaps were also followed for three growing seasons to assess exclusion effects in low deer density areas only. Composition of browsable native and exotic plants (≤2m in height) did not differ between exclosure and control plots, indicating gap regeneration dynamics were unaffected by low deer density after three growing seasons. For spring flora, exotic relative cover increased with gap age, but native and exotic diversity did not differ across gap size, deer density, and habitats. However, for fall flora, exotic cover increased with gap age when deer were abundant, where communities averaged 380% higher non-native coverage. Fewer deer were associated with 75% higher native richness, 50% higher native diversity, and 60% more native cover across gap ages and habitats. Additionally, sapling height and stem density of red (*Quercus rubra*) and pin oak (*Quercus palustris*) were five- to twenty-fold higher with fewer deer. We find that managing white-tailed deer at roughly twice their historic abundance for 67-years facilitates all measured aspects of fall-flowering native understories, including early recruitment of four important canopy species, and reduces exotic plant abundance. Coupling this with our novel theory on short- and long-term

carrying capacity suggests a sustained density of < 8 deer/km² is sufficient to maintain their

forage base and that selective harvests under such conditions are self-replacing. Lastly,

persistently high deer densities will continue to lower native and increase exotic plant

abundance, fundamentally alter gap successional trajectories, and lower deer carrying capacities

in the process.

Table of Contents

List of Figures

List of Tables

INTRODUCTION

In eastern deciduous forests, canopy gaps and herbivory are important drivers of plant community composition (Burton et al., 2021; Nuttle et al., 2013; Royo et al., 2010a; Sabo et al., 2019). Natural and harvest canopy gaps offer critical regeneration sites to many understory and canopy species (Coates, 2002; Hart and Grissino-Mayer, 2009; Shields and Webster. 2007; Webster and Lorimer, 2005), and are typically more diverse relative to adjacent intact forest (Ang et al., 2022; Anderson and Leopold, 2002; Hart and Kupfer, 2011; Kern et al., 2013; Shields and Webster. 2007). Gap size, shape, and orientation affect light availability in the forest understory for 10+ years (Burton et al., 2014, 2021; Gendreau-Berthiaume and Kneeshaw, 2009; Latif and Blackburn, 2010; Valverde and Silvertown, 1997) and thus the types of species that frequently establish in them (Abe et al., 1995; Feldmann et al., 2020; Hart and Grissino-Mayer, 2009; Kern et al., 2013; Poulson and Platt, 1989). For example, advanced regeneration and lateral crown expansion by shade-tolerant and established individuals dominate small gap dynamics (Canham, 1988; Dietze and Clark, 2008; Feldmann et al., 2020; Hart and Grissino-Mayer, 2009), which can alter evenness but does little to richness patterns. On the other hand, larger gaps (e.g. > 250 m^2) facilitate more recruitment from seed, driving species richness increases (Davis et al., 2005), and this is particularly so for shade-intolerant herbaceous and woody species (Canham, 1989; Kern et al., 2013, 2017; Nuttle et al., 2013).

Despite the potential positive effects of different-sized gaps on local and regional diversity, high ungulate densities frequently mitigate them (Ang et al., 2022; Holmes and Webster 2011; Ramirez et al., 2018; Sabo et al., 2023). In the eastern United States, the magnitude of diversity-promotion in canopy gaps largely depends on white-tailed deer abundance (deer; *Odocoileus virginianus* Zimmerman). At low to moderate density (e.g. ≤8

6

deer/km^2), selective browsing by these native herbivores can increase species diversity (Horsley et al., 2003; Nuttle et al., 2014; Royo et al., 2010a; Augustine and DeCalesta, 2003). However, at higher deer densities (e.g., >14 deer/km^2), which are now widespread throughout their range (Côté et al., 2004; McWilliams et al., 2018; Russell et al., 2001), white-tailed deer limit if not prohibit recruitment of browse-sensitive species (Begley-Miller et al., 2014; Burton et al., 2021; Nuttle et al., 2013; Sabo et al., 2019; VanderMolen and Webster, 2021).

Chronic overbrowsing by deer reduces the abundance and reproductive output of palatable species (Augustine and DeCalesta, 2003; Averill et al., 2018; Nuzzo et al., 2017; Royo et al., 2010b; Tanentzap et al., 2011) and if sustained, can lead to local extinction (Goetsch et al., 2011; Peck and Stahl, 1997). For example, overbrowsing causes population declines if not extirpation of preferred native herbs such as trillium (*Trillium* spp. L.; Augustine and DeCalesta, 2003; Kalisz et al., 2014; Knight et al., 2009a) and American ginseng (*Panax quinquefolius* L.; Farrington et al., 2009; McGraw and Furedi, 2005) as well as poor recruitment of woody species such as oak (*Quercus* spp. L.), eastern hemlock (*Tsuga canadensis* (L.) Carrière), hickory (*Carya* spp. L.), and red maple (*Acer rubrum* L.) (Banta et al., 2005; Blossey et al., 2017; Evans and Keen, 2013; Parker et al., 2020; Rossell et al., 2005; VanderMolen and Webster, 2021). In addition, selective browsing of native flora alleviates competition on exotic (Abrams and Johnson, 2012; Averill et al., 2018; Kalisz et al., 2014; Knight et al., 2009b) and unpalatable native plants (Chollet et al., 2013; Shelton et al., 2014; Rooney, 2009; Royo and Carson, 2006), shifting community composition toward a low-productivity forage base through herbivore-altered competitive hierarchies (Barrette et al., 2014; de la Cretaz and Kelty, 2002; Owings et al., 2017; Royo and Carson, 2022).

As deer-altered successional trajectories become increasingly dominated by browse-tolerant and browse-resistant species, and preferred ones decline (Augustine and McNaughton, 1998; Burton et al., 2021; Horsley et al., 2003; VanderMolen and Webster, 2021), the local region's ability to sustain a particular white-tailed deer biomass is compromised. Exclosures are used to quantify impacts of browsing on species composition (Habeck and Schultz, 2015; Sabo et al., 2017; Russell et al., 2001; Redick and Jacobs, 2020), which are generally greater in canopy gaps where plant growth and herbivory rates are higher than in adjacent forest (Kuijper et al., 2009; Nuttle et al., 2013; Sabo et al., 2019; Tahtinen et al., 2014). Importantly, through exclosure vs. control plot comparisons in tissue availability and recruitment rate, excluding deer can reveal potential disparity between short- and long-term carrying capacity (K_{ST} and K_{LT}, respectively), which may be especially pronounced where palatable species are still abundant in the canopy but lack recruitment (see Fig. 2 of Nuttle et al., 2013). We define short-term carrying capacity (K_{ST}) as a system's ability to meet the metabolic demands of an herbivore population while maintaining current forage resources (Monteith et al., 2014; Smythe et al., 2019). For long-term carrying capacity (K_{LT}), we define it as the ability of an area to indefinitely sustain a particular biomass of white-tailed deer. For example, if herbivores consume forage and propagules as they are produced (i.e., they are at their K_{ST}), but recruitment to adulthood is constrained by herbivory, the K_{ST} of an area may be greater than its K_{LT}. This occurs when adult replacement rate of browsable species is lower than their mortality rate (i.e., K_{LT} is declining) but long-lived adults still subsidize K_{ST} via propagule input (e.g., oaks). In this case, exclosures should have higher forage availability and recruitment rates than control plots. Of note, if poor recruitment persists and adults eventually die, K_{ST} will track the inevitably falling K_{LT}. On the other hand, if deer are significantly below their K_{ST}, forage abundance should not differ between

exclosure and control plots, and recruitment should equal if not exceed adult mortality (i.e., deer are respectively at or below their K_{LT}; see Discussion for more details).

A fundamental question emerges as to how high deer density can increase from their historic density of 3-4 deer/km^2 (McCabe and McCabe, 1997) and still indefinitely maintain their forage base (i.e., what elevated deer density remains below their K_{ST} and K_{LT}?). The answer can be approximated via enclosures (Horsley et al., 2003; Nuttle et al., 2014; Tilghman, 1989) or cull-induced deer reductions (de la Cretaz and Kelty, 2002; Nagy et al., 2022; Royo et al., 2010b; Tanentzap et al., 2011; Schmit et al., 2020). However, these studies were conducted in areas with pre-existing, deer-altered, potentially idiosyncratic dynamics and thus estimates of K may be misleading or inaccurate. Indeed, near ubiquitous white-tailed deer overabundance has made finding forests not subjected to sustained overbrowsing difficult, and thus estimating K where deer have not been a key driver of forest dynamics remains elusive. However, Camp James A. Garfield Military Training Center (hereafter Base) in north-east Ohio, which was constructed in 1940 to assemble munitions, provides such an opportunity. Once agricultural land, the fenced, publicly inaccessible, largely forested Base (87.8 km^2) was established when deer densities were still low (Iverson and Iverson, 1999) and has consistently maintained populations near historic levels through annual controlled hunts (Morgan, 1996; 67-year mean: 6.6 deer/km^2; the mean for last 14-years: 7.5 deer/km^2; Fig. 1).

In this study, we measured native and exotic plant diversity, richness, cover, and woody stem number and height in natural and harvest canopy gaps in areas of high vs. low deer density and in exclosure vs. control plots in areas of low deer density only. We asked: 1) does spring and fall floral composition differ in gaps of varying age and size, and do differences depend on white-tailed deer density?, 2) do mesic vs. drier habitats differ in their compositional response to

high vs. low deer density?, and 3) does excluding deer for three growing seasons in wet vs. dry habitats change community composition and woody plant recruitment inside Base, an area of low deer density? Divergence in species composition and woody plant recruitment between exclosure vs. control plots would indicate ~7.5 deer/km^2 alter gap succession and that this density is at or near their K_{ST} at Base. Alternatively, no plot differences would suggest white-tailed deer are significantly below their carrying capacity at Base. In addition, gap size and age may elicit plant compositional responses that depend on deer density and habitat type. If so, then habitat-specific harvest management schemes may have to be adjusted to achieve particular goals (e.g., lower deer density in particular habitats to increase local plant diversity and canopy species recruitment). Lastly, a robust empirical approximation of white-tailed deer carrying capacity can emerge from a secondary forest never experiencing prolonged overbrowsing; this may also serve as a reference for comparing compositional characteristics of other communities to gauge their future behavior in K_{ST} and K_{LT}.

METHODS

Study sites:

Research was conducted primarily at Camp James A. Garfield (Base), a fenced 87.8 km^2 military facility located in Portage and Trumbull County in northeast Ohio, USA. Approximately 75% of Base is classified as forest, most of which is 80 years-old or less, and the remainder is herb- or shrub-dominated (Ogden Environmental & Energy Services 2000). Following the standards of the Federal Geographic Data Committee Vegetation subcommittee, our study sites occur in the following alliances: 1) *Quercus palustris* – (*Quercus bicolor*) Seasonally Flooded Forest, 2) *Acer rubrum* successional forest, 3) *Tsuga canadensis* – *Betula alleghaniensis* Forest, 4) Mixed cold-deciduous successional forest, and 5) *Fagus grandifolia* –

Quercus spp. – *Acer* spp. Forest (Base pers. comm.; also see FGDC 2008). Sites outside of Base are located in adjacent Mahoning and Trumbull County in forested state and municipal parks with similar understory and canopy compositions (pers. obs.).

Canopy gap characteristics:

Canopy gaps in wet and dry habitats were identified through field observations and satellite images. Wet habitats were categorized as forested areas on hydric soil (ODNR 1991) with a canopy primarily composed of pin oak (*Quercus palustris* Münchh) or swamp white oak (*Quercus bicolor* Willd). Dry habitats were defined as upland forested areas (ODNR 1991), with red oak (*Quercus rubra* L.) and shagbark hickory (*Carya ovata* (Mill.) K. Koch) as canopy dominants. Once canopy gaps were identified, their coordinates were entered into ArcGIS-Pro (Esri Inc. 2021) and using historical satellite imagery from the National Agriculture Imagery Program (USDA 2022a) and Google Earth (Google Earth V. 7.3), each gap image was visually compared to determine the approximate year of formation. Because of limitations in image availability, if a gap was present in, say, 2010, absent in 2008, but no image existed in 2009, we assumed the gap formed in the first year it was evident, and thus all gap ages are estimated within one year of their creation. Markers were then placed around the gap edge in ArcGIS-Pro forming a polygon to estimate gap area (m^2). Forty-one 2–14 year-old canopy gaps were identified, which ranged in size from 83 – 522m² (median size: 230m²).

White-tailed deer exclosure vs. control paired plots:

As part of the natural resource management plan at Base, timber harvesting is utilized to maintain the forested ecosystem and the production of quality timber (Morgan, 1995). Nine timber harvest canopy gaps were created in 2017 inside of Base and used for our paired exclosure-control plots. In 2019, two ~10x5-m paired plots were randomly assigned to a

treatment in each gap, which consisted of exclosure plots using a 2m-tall black plastic mesh fence with six 3m-tall t-posts or an unfenced adjacent control situated >100m away from exclosures. In both plots, we placed PVC stakes every 3m to outline a 3x9m plot with a ~1m border surrounding it, creating three 3x3-m subplots. For the duration of our study, only minor damage occurred to the fencing of three exclosures, which were repaired, and in no case was there evidence of deer browsing inside them.

White-tailed deer density estimates:

Base has organized annual white-tailed deer hunts on the property since 1955 and maintains detailed annual hunt data (e.g., hunter days and total deer harvested). In addition, post-hunt winter aerial surveys have occurred in 2002-2003, 2006-2010, 2012-2016, and 2021 to estimate deer density. We used 13 individual years of hunting data with corresponding aerial counts to estimate deer density from 1955-2021. To do so, a pre-hunt population (*PREH)* was estimated by adding the post-hunt aerial count to the total number of deer harvested during each year. To estimate annual deer density, linear regression analysis was preformed using these pre-hunt population estimates (*PREH)* and the total number of hunter days (*HD*) within those same years. From this linear regression, we generated the equation: $PREH_t = 0.45(HD_t) + 421$, where $PREH_t$ is the pre-hunt estimate at year t, and HD_t is hunter days at year t. This was then used to extrapolate an annual pre-hunt population between 1955-2021. Because aerial surveys represent post-hunt populations, we calculated the difference between our pre-hunt estimates from 1955-2021 and the total number of deer harvested annually to determine a final post-hunt population estimate for each year (Fig. 1).

To verify the accuracy of our estimates, we ran a two-tailed paired *t*-test to compare deer density estimated from aerial counts and our post-hunt estimates within the same year. No

difference between them was detected (p = 0.977), indicating that our estimates are robust and precisely reflect post-hunt populations (Fig. A1). Estimated deer density has averaged 6.6 deer/km^2 since 1955, and for the last 14 years, has averaged 7.5 deer/km^2 (Fig. 1).

We did not estimate deer density outside of Base but our observations corroborate other research that consistently reports lower stem density, height, and abundance of browse-preferred species (e.g. *Quercus* sp., red maple [*Acer rubrum* L.], *Rubus* spp,), and increased dominance of unpalatable or browse-tolerant species (e.g. black cherry [*Prunus serotina* Ehrh.], graminoids, garlic mustard [*Alliaria petiolata* L.]) at deer densities from 20 to > 60 deer/km^2 (Anderson & Loucks, 1979; Averill et al., 2018; Boerner & Brinkman 1996; DiTommaso et al., 2014; Horsley et al., 2003; Kalisz et al., 2014; Morrison, 2017; Rooney, 2009; Rossell et al. 2005; Tilghman, 1989). Based on plant community assemblages at our field sites outside of Base, we estimate deer densities to be ≥20 deer/km².
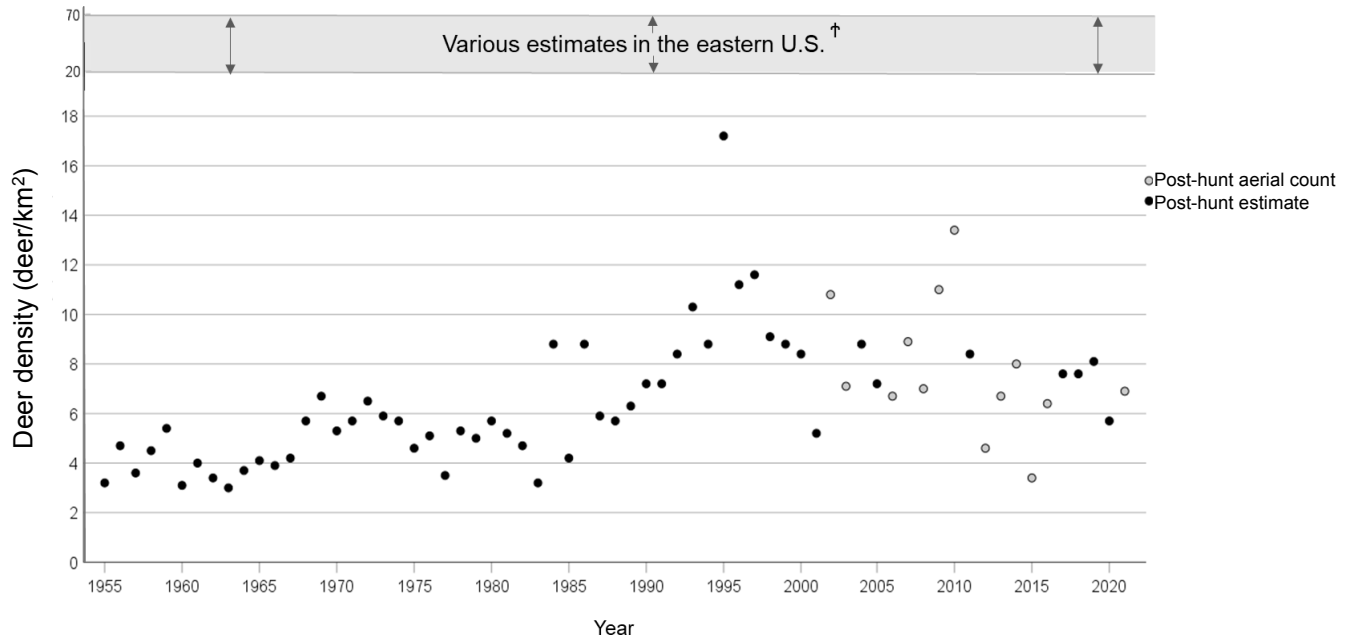
Figure 1. White-tailed deer density estimates within Base from 1955-2021 using our post-hunt population estimates, represented by solid points, and post-hunt aerial counts from 2002-2003, 2006-2010, 2012-2016, and 2021, shown as gray points. The former was calculated using the equation $PREH_t = 0.45(HD_t) + 421$ (see methods-white-tailed deer density estimates). Note that a two-tailed paired *t*-test between aerial counts and our estimated post-hunt populations was p=0.977, suggesting our estimates are precise representations of post-hunt populations. Estimates of white-tailed deer densities throughout much of the eastern U.S.[†] are also shown.

[†] (Adams et al., 2020; Anderson & Loucks, 1979; Averill et al., 2018; Boerner & Brinkman, 1996; DiTommaso et al., 2014; Kalisz et al., 2014; Morrison, 2017; Rooney, 2009; Rossell et al., 2005; Russell et. al., 2001; Urbanek & Nielsen, 2013; Wallingford, 1999; Witham & Jones, 1990)

Vegetation sampling:

From late August to mid-October 2019 and 2021, we estimated the cover of all herbaceous and woody species in the nine paired exclosure-control plots. Absolute cover (i.e. the actual coverage of the plot by a species, regardless of whether it is covered, or covers other vegetation) was determined by estimating how much area was occupied by the canopy of each species within the 0-2 m browse zone. Relative cover, which accounts for layering, was calculated in each plot by dividing the abundance of each species by the total absolute cover for the plot. For each woody species, the number of stems and height of the tallest individual were recorded. In fall 2020-2021, we also sampled 12 additional, randomly placed 3x9 m plots in different-aged and -sized canopy gaps not associated with deer exclosures inside Base , and 20

more in gaps outside of Base. In spring 2021-2022, we sampled spring flora in each plot across all 41 gaps, including those housing exclosure-control plots. However, because all woody species were recorded within six months during the preceding fall season, only herbaceous species were recorded in spring (i.e., forbs, graminoids, ferns). We were able to identify nearly all individuals to species, but where we could not, we identified to genus (e.g., *Carya* spp., *Panicum* spp.).

Statistical analyses:

Each 3x9-m plot was considered an experimental unit, so cover estimates were averaged for each by summing the three subplots and dividing by three. Because seasonality can affect cover estimates, species with a spring (e.g. dwarf ginseng; *Panax trifolius* L.) vs. fall phenology (e.g., Canada goldenrod; *Solidago canadensis* L.) were analyzed separately (i.e., 'spring' and 'fall' analyses). The few species exhibiting a summer phenology (e.g., jack-in-the-pulpit; *Arisaema triphyllum* (L.) Schott) were included in both spring and fall analyses (Table A2). Native vs. non-native designation of each taxon was verified using the PLANTS database (USDA 2022b).

Multiple analysis of covariance:

To evaluate the effect of high vs. low deer density on fall and spring species composition in gaps of varying age and size, we used multiple analysis of covariance (MANCOVA) in SPSS (IBM Corp. 2021). This was carried out using data from all plots inside and outside of Base not associated with an exclosure, as well as 2021 control plot data. A 2×2 factorial design was used to test the effect of deer density (i.e., high vs. low) and habitat type (i.e., wet vs. dry) on native and non-native species richness, absolute cover, relative cover and diversity($e^{H'}$). Gap age and size served as covariates. We used a similar 2x2 factorial design to determine if excluding deer

for three growing seasons affected species composition again using deer density (exclosure vs. control) and habitat type (wet vs. dry) as our independent factors. We then compared response variable differences between 2019 exclosure vs control plot baseline data with those in 2021 using gap size as the only covariate, with no need to include gap age because all gaps were harvested at the same time. We also similarly analyzed 2019 baseline data to assess whether our response variables differed between only exclosure vs. control plots during the year they were constructed to verify no initial compositional differences.

A Shannon diversity index ($H^{'}$) was calculated for each sampling plot using the 'BiodiversityR' package in R (Kindt and Coe, 2005; R core team, 2022), using relative cover as our abundance metric. Diversity values were then converted to effective species number for each plot by using the exponent ($e^{H'}$; Jost, 2006), which provides a value representing the total number of equally distributed species needed to produce a particular diversity value. Prior to full MANCOVA, Box's M test indicated a violation of homogeneity of covariance in our fall and spring data ($p \leq 0.003$), which was rectified via log transformation (after which $p > 0.09$). Although analyses use these log transformed data, all figures, averages, means differences and standard errors show non-transformed data. MANCOVA was repeated for fall data after excluding four spatially correlated wet sites inside Base, because of their atypical dominance by New York fern (*Thelypteris noveboracensis* (L.) Nieuwl.; Fig. A3). Any metric that did not significantly change (p value difference < 0.03) is reported using the full dataset (i.e. with fern sites included). However, for the two variables that did change, MANCOVA results from the partial dataset are also noted (Table 1). Following MANCOVA, any significant univariate main effects, and any interactions, were evaluated using estimated marginal means (EMM). EMM

16

calculates the averages for every response variable across each treatment after adjusting for covariates by holding them at a constant value (mean) for each estimation.

Linear regression analysis:

Linear regression analysis in SPSS (IBM Corp. 2021) was used to test the relationship between any significant covariates and response variables as determined by MANCOVA. Regression was performed using our fall data to determine the association between canopy gap age, and native and exotic abundance in areas of high vs. low deer density. Linear regression analysis was performed a second time for non-native absolute and relative cover in areas of high deer density because of two vertical outlier sites ($\geq 2\sigma$), where the herbaceous and shrub layers were dominated by exotics. Repeating the regression without these sites revealed they had a significant influence on the coefficient of determination (r^2), which measures how much variability is explained by the regression, between non-native absolute and relative cover and canopy gap age, and as such, the statistics from both analyses are included for these variables (Table 2, Fig. 3b, 3c). Because no independent factor was significant during spring, indicating no effect of any treatment of interest on response variables (via MANCOVA), linear regression was not performed for any significant covariate.

Indicator species analysis:

To determine the relationship between plant cover and deer density or habitat, we performed an indicator species analysis (ISA) using the 'indicspecies' package in R (de Cáceres and Legendre, 2009; R core team, 2022). This allows us to evaluate the association between species relative abundance and treatment combinations and was accomplished using point bi-serial correlation coefficient to measure the strength of association between variables. ISA was performed for spring and fall data by grouping deer density (n=2; "Low" vs. "High") and habitat

17

type (n=2; "Wet" vs. "Dry") into four treatment combinations (e.g., high deer density and dry habitat grouped as "High Dry") to elucidate species that were significantly associated with particular ecological conditions (de Cáceres et al., 2010).

Kruskal-Wallis test:

In assessing white-tailed deer density effects on woody regeneration (i.e., stem count and maximum height), we limited our focus to any species and genera that occurred in ≥20% of our plots. Common species such as red oak, pin oak (*Quercus palustris* Münchh), and spicebush (*Lindera benzoin* (L.) Blume) were analyzed by species. Others such as dogwood (*Cornus* spp. L.) and viburnum (*Viburnum* spp. L.) were grouped into genera to meet this ≥20% requirement. Uncommon species that could not be grouped into higher and more inclusive taxa were excluded. Prior to analysis, Levene's homogeneity of variance test in SPSS (IBM Corp. 2021) revealed heteroscedasticity that could not be reduced by log transformation, so woody species were analyzed using Kruskal-Wallis nonparametric independent samples test in SPSS (IBM Corp. 2021).

RESULTS

Community composition:

For fall data comparing canopy gap metrics between areas of high vs. low deer density, MANCVOA showed that white-tailed deer density affected native richness, native absolute and relative cover, non-native absolute, and relative cover, and native diversity ($e^{H'}$), but not non-native richness or diversity (Table 1). Areas with high deer densities (outside of Base) averaged 380% higher absolute and relative cover of non-natives, and 60% lower average cover of natives (Fig. 2a, 2b). Areas with fewer deer (inside of Base) also had 75% higher native species richness (Fig. 2c), and 50% higher native community diversity ($e^{H'}$; Fig. 2d). In contrast, species

composition did not differ by habitat type or the covariate gap size (Table 1). However, MANCOVA was marginally significant for the covariate canopy gap age (p=0.074), affecting native relative cover, non-native absolute cover, and a modest effect on non-native relative cover, but not native absolute cover or any metric of richness and diversity ($e^{H'}$; Table 1). Linear regression showed negative relationship between native relative cover and canopy gap age under low deer density (Table 2, Fig. 3a). No significant relationship was observed for any response variable under high deer density (Table 2). However, non-significance in non-native cover outside of Base was driven by two vertical outlier sites that were dominated by two dense shrub and herbaceous layers of exotics; re-running the regression without these sites showed a positive association between high deer density and canopy gap age for non-native absolute and relative cover (Table 2, Fig. 3b, 3c).

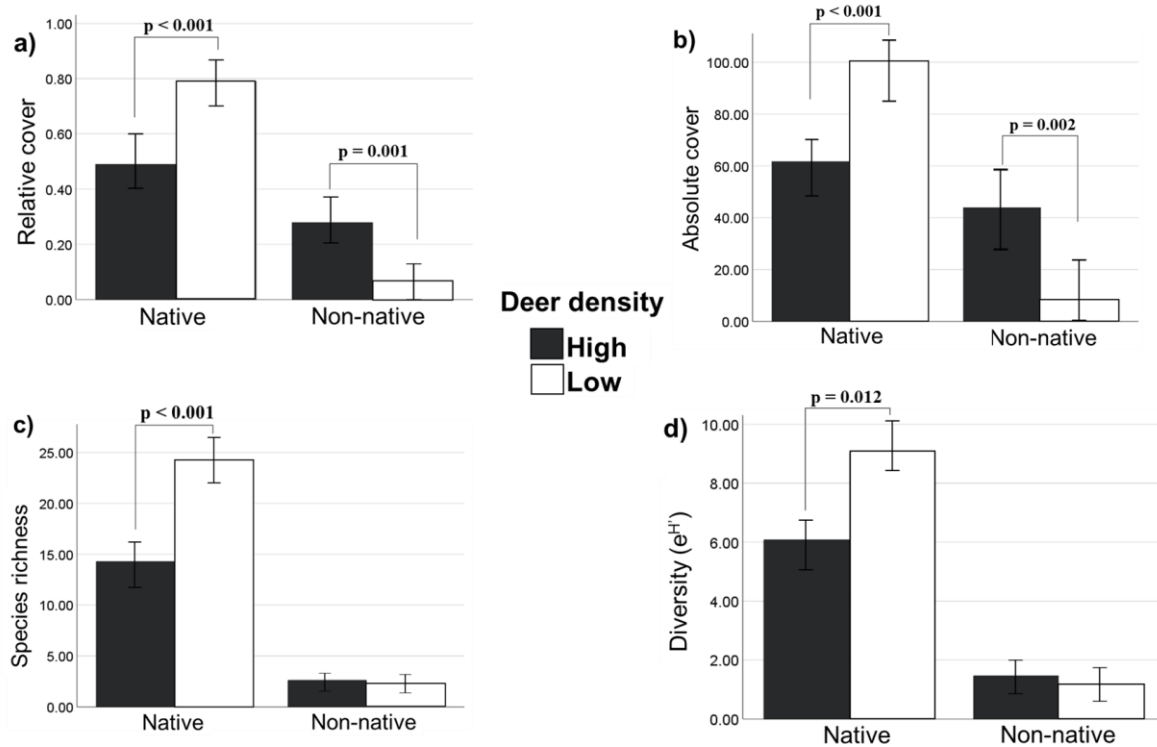**Figure 2.** Effects of high vs. low deer abundance on native and non-native relative cover (a), absolute cover (b), richness (c) and diversity (d) during fall. All presented metrics for native species were higher under low deer abundance. In contrast, relative and absolute cover of non-natives were higher under high deer density. Error bars represent ±95% confidence interval, and all values determined using estimated marginal means.

MANCOVA				
Test	**Variable**	**F-value**	**p-value**	**partial η²**
Multivariate				
	Gap age	$F_{8,28}$= 2.07	0.074	0.371
	Gap size m^2	$F_{8,28}$= 1.14	0.370	0.245
	Deer density (high vs. low)	**$F_{8,28}$= 5.00**	**< 0.001**	**0.588**
	Habitat (wet vs. dry)	$F_{8,28}$= 1.15	0.360	0.248
	Deer density * Habitat	$F_{8,28}$= 1.89	0.101	0.339
Univariate				
Deer density	**Native richness**	**$F_{1,35}$= 26.81**	**< 0.001**	**0.434**
	Non-native richness	$F_{1,35}$= 0.005	0.944	0.000
	Native absolute cover	**$F_{1,35}$= 16.34**	**< 0.001**	**0.318**
	Native relative cover	**$F_{1,35}$= 20.74**	**< 0.001**	**0.372**
	Non-native relative cover	**$F_{1,35}$= 12.68**	**0.001**	**0.266**
	Non-native diversity (e$^{H'}$)	$F_{1,35}$= 0.159	0.692	0.005
	Native diversity (e$^{H'}$)	$F_{1,35}$= 2.57 **($F_{1,31}$= 7.16)**	0.118 **(0.012)**	0.068 **(0.188)**
	Non-native absolute cover	$F_{1,35}$= 4.57 **($F_{1,31}$= 9.53)**	**0.040** **(0.004)**	**0.115** **(0.235)**
Gap age	Native richness	$F_{1,35}$= 1.76	0.193	0.048
	Non-native richness	$F_{1,35}$= 1.37	0.249	0.038
	Native absolute cover	$F_{1,35}$= 1.61	0.212	0.044
	Native relative cover	**$F_{1,35}$= 7.78**	**0.008**	**0.182**
	Non-native relative cover	$F_{1,35}$= 3.66	0.064	0.095
	Non-native diversity (e$^{H'}$)	$F_{1,35}$= 1.33	0.256	0.037
	Native diversity (e$^{H'}$)	$F_{1,35}$= 0.055	0.816	0.002
	Non-native absolute cover	**$F_{1,35}$= 4.74**	**0.036**	**0.119**

Table 1. Statistics from multiple analysis of covariance (MANCOVA) using fall data. Numbers in parentheses indicate the change in value when the New York fern sites were excluded (partial dataset). Metrics from the full dataset determined using log transformed data, and values using the partial dataset were calculated using non-log transformed data. All significant values and variables are bolded ($p \leq 0.05$). The covariate of gap age was marginally significant for the multivariate test ($p > 0.05$, at p= 0.074).
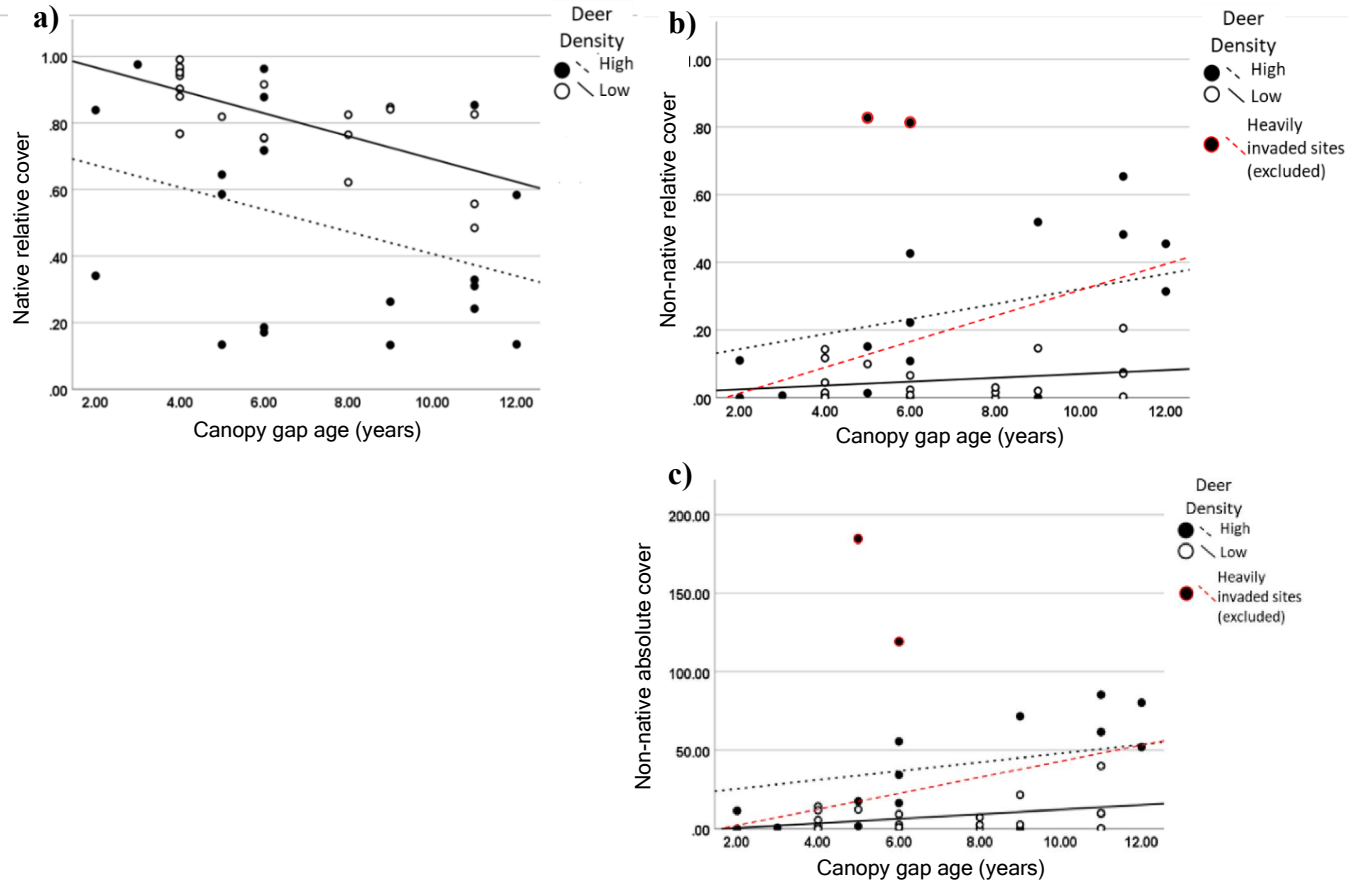
Figure 3. Linear regression of native relative cover (a), and non-native relative (b) and absolute cover (c) across canopy gap ages during fall. The red dashed lines indicate the change in the fit line when two vertical outliers were excluded for non-native absolute and relative cover, while black dashed lines show linear fits with these sites.

	High deer density							**Low deer density**						
	Slope	Intercept	Std. Error	r²	Adjusted r²	t-score	p-value	Slope	Intercept	Std. Error	r²	Adjusted r²	t-score	p-value
Native relative cover	-0.033	0.740	0.020	0.128	0.080	-1.628	0.128	-0.034	1.036	0.009	0.456	0.427	-3.988	**<0.001**
Non-native absolute cover	2.813 (5.206)	19.88 (-10.747)	3.487 (1.884)	0.035 (0.323)	-0.019 (0.281)	0.807 (2.763)	0.430 **(0.014)**	1.462	-2.363	0.766	0.161	0.117	1.909	0.070
Non-native relative cover	0.022 (0.034)	0.099 (-0.052)	0.02 (0.014)	0.066 (0.274)	0.015 (0.229)	1.132 (2.458)	0.272 **(0.026)**	0.006	0.013	0.005	0.064	0.015	1.139	0.269

Table 2. Linear regression of native and exotic abundance in areas of high vs. low deer density as a function of canopy gap age during fall. Numbers in parentheses indicate the alternative values after vertical outliers were excluded for non-native absolute and relative cover. All significant values at p ≤ 0.05 are bolded.

MANCOVA from our spring sampling indicated no effect of deer density, habitat or gap size on native and non-native richness, cover, and diversity ($e^{H'}$; Multivariate; $F_{8,28} \leq 1.54$, p >0.188). Canopy gap age was a significant covariate affecting non-native relative cover only ($F_{1,35}=5.03$, p=0.031, partial $\eta^2=0.126$), but because no effect was observed for deer density, habitat type or any interaction, linear regression was not performed.

Species composition

White-tailed deer density strongly affected several woody species, especially those preferred as forage by deer. For example, in areas of low deer density inside Base, red and pin oak respectively had eight and twenty times higher average stem densities, and five and sixteen times higher average maximum heights than where deer are more abundant outside of Base (Table 3, Fig. 4). Additionally, areas with fewer deer had 25% higher mean stem density and 8% higher mean maximum height of *Viburnum* spp. (Table 3, Fig. 4). Average height of ash (*Fraxinus spp* L.) and stem density of red maple were also three and twenty-two times higher at Base, respectively, vs. outside Base (Table 3, Fig. 4). Except for the non-native glossy buckthorn (*Rhamnus frangula* L.), which had five times higher mean stem density and height under low deer density (Table 3, Fig. 4), no other low-palatability woody species were affected by deer density (Table A4).
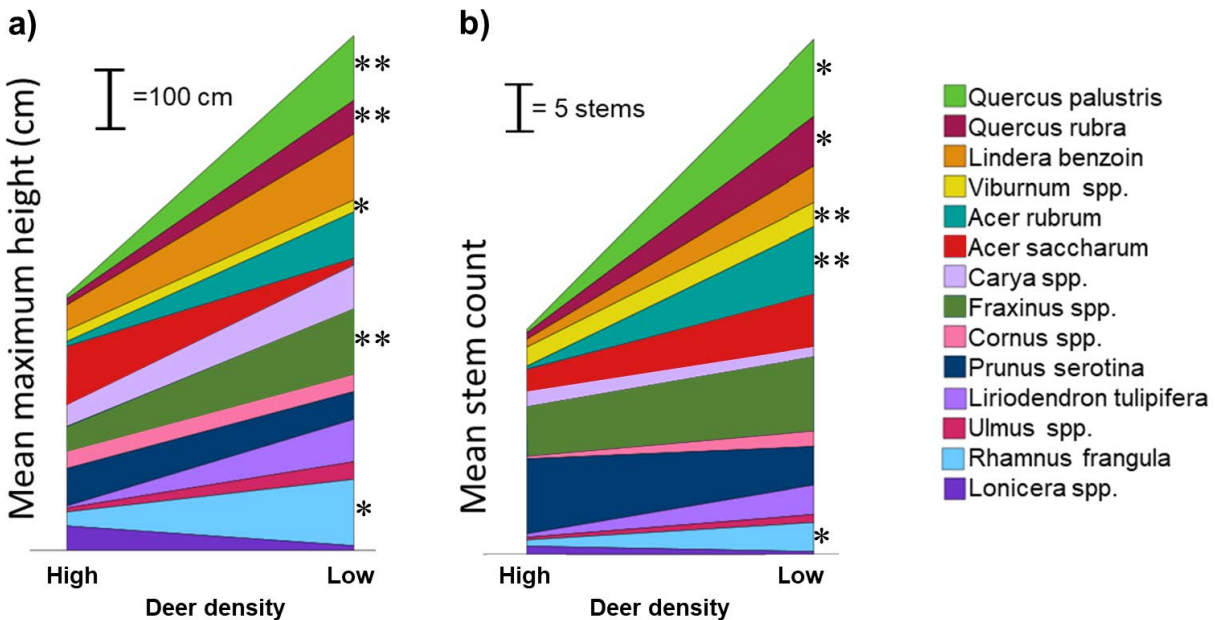
Figure 4. Woody regeneration of taxa occurring in ≥20% of plots under high vs. low deer densities. Shown are mean maximum height (cm) (a) and mean stem count (b) in the 2 m browse zone. Each color denotes a different taxon in the order they appear in the graphs and legend, from top to bottom. Significance is indicated by * (p<0.05) and ** (p<0.025). Graph brackets indicate scale, where ⊤ = 100 cm in height (a) and ⊤ = a stem count of 5 (b).

Species	Metric	Deer Density	Mean	Std. Deviation	H	Sig.
Quercus palustris	Stem Count	Low	8.7	16.7		
		High	0.4	0.94	4.94	p = 0.026
	Maximum Height (cm)	Low	98.7	142.4		
		High	6.1	12.5	5.80	p = 0.016
Quercus rubra	Stem Count	Low	5.6	11.4		
		High	0.7	1.9	4.43	p = 0.035
	Maximum Height (cm)	Low	51.04	71.3		
		High	9.1	22.3	5.71	p = 0.017
Viburnum spp.	Stem Count	Low	2.7	5.05		
		High	2.15	5.9	5.07	p = 0.024
	Maximum Height (cm)	Low	18.1	18.4		
		High	16.8	42.2	3.90	p = 0.048
Acer rubrum	Stem Count	Low	7.7	15.5		
		High	0.35	0.67	5.10	p = 0.024
Fraxinus spp.	Maximum Height (cm)	Low	98.7	96.3		
		High	36.6	71	5.72	p = 0.017
Rhamnus frangula	Stem Count	Low	3.3	5.0		
		High	0.7	1.5	4.20	p = 0.04
	Maximum Height (cm)	Low	101.1	131.6		
		High	21.3	46.5	4.29	p = 0.038

Table 3. Woody species that significantly differed in mean stem count and/or mean maximum height (cm) between areas of high (N=20) vs. low (N=21) deer abundance (p<0.05), with test statistics (H) determined by Kruskal-Wallis tests.

Twenty-two indicator species from fall and seven from spring were associated with one or more of the treatment combinations (i.e., white-tailed deer density and habitat type; Table 4). Indicators of high deer density included non-native or browse-resistant native species such as creeping jenny (*Lysimachia nummularia* L.), common gypsyweed (*Veronica officinalis* L.), garlic mustard (*Alliaria petiolata* L.), and *Panicum* spp. (Table 4). Conversely, nearly all indicators of low deer density were native, including woody species such as red oak, black oak (*Quercus velutina* Lam), and spicebush as well as herbs such as Allegheny blackberry (*Rubus allegheniensis* Porter), partridgeberry (*Mitchella repens* L.) and Canada goldenrod (*Solidago canadensis* L.) (Table 4).

Fall				
Deer abundance	**Habitat type**	**Species**	**Corr. Coef.**	**p-value**
High	Dry			
		Panicum spp.	0.420	0.0381
High	Wet			
		Geum spp.	0.492	0.0046
		Lycopus uniflorus	0.467	0.0201
		Lysimachia nummularia *	0.471	0.0076
		Veronica officinalis *	0.454	0.0082
High	Wet & Dry			
		Parthenocissus quinquefolia	0.408	0.0424
Low	Dry			
		Oxydendrum arboreum	0.550	0.0026
		Rubus allegheniensis	0.529	0.0032
		Mitchella repens	0.479	0.0266
		Geum urbanum *	0.428	0.0133
		Quercus velutina	0.433	0.0141
		Quercus rubra	0.567	0.0008
		Liriodendron tulipifera	0.436	0.0148
		Cornus florida	0.521	0.0016
		Rhynchospora spp.	0.355	0.0034
		Carex glaucodea	0.479	0.0245
		Solidago canadensis	0.430	0.0353
		Tilia americana	0.365	0.0238
Low	Wet			
		Thelypteris noveboracensis	0.586	0.0014
		Lindera benzoin	0.464	0.0230
		Quercus palustris	0.587	0.0009
		Ulmus spp.	0.427	0.0385
Spring				
High	Wet			
		Alliaria petiolata *	0.462	0.0147
		Symplocarpus foetidus	0.448	0.0275
Low	Dry			
		Fragaria virginiana	0.486	0.0100
		Carex swanii	0.546	0.0001
		Carex blanda	0.470	0.0114
		Oxalis spp.	0.528	0.0022
Low	Wet			
		Arisaema triphyllum	0.437	0.0283

Table 4. Indicator species analysis (ISA) showing plant species significantly associated with high vs. low deer abundance in wet vs. dry habitats ($p < 0.05$); "*" designates non-native species. Indicator species were determined by evaluated associations between species relative cover and site characteristics (i.e., deer abundance and habitat type). ISA was performed once for each season.

Paired exclosure vs. control plots

Analysis of 2019 baseline data, which were collected when exclosure-control plots were built, revealed no difference in native or non-native richness, cover, or diversity ($e^{H'}$) between exclosure vs. control plots (Table 5). After three growing seasons, no differences in these

variables were detected between exclosure vs. control plots in fall or spring (Table 5). Species

composition also did not differ between habitat type and gap size in fall or in spring (Table 5).

MANCOVA				
Test	Variable	F value	p-value	partial η^2
2019 baseline				
Multivariate				
	Gap size m^2	$F_{8,8}$= 2.06	0.163	0.674
	Exclosure vs. control plot	$F_{8,8}$= 1.80	0.212	0.643
Fall				
Multivariate				
	Gap size m^2	$F_{8,6}$= 0.90	0.566	0.546
	Exclosure vs. control plot	$F_{8,6}$= 2.29	0.165	0.753
	Habitat (wet vs. dry)	$F_{8,6}$= 3.45	0.075	0.821
	Exclosure vs. Control * Habitat	$F_{8,6}$= 1.31	0.381	0.636
Spring				
Multivariate				
	Gap size m^2	$F_{8,6}$= 1.63	0.285	0.685
	Exclosure vs. control plot	$F_{8,6}$= 0.90	0.568	0.545
	Habitat (wet vs. dry)	$F_{8,6}$= 1.08	0.477	0.590
	Exclosure vs. Control * Habitat	$F_{8,6}$= 0.73	0.668	0.494

Table 5 Statistics from multiple analysis of covariance (MANCOVA) from paired exclosure vs. control plot comparisons. Table shows the output from 2019 baseline data, response variable differences after two years of exclusion during fall (i.e., difference between 2019 and 2021), and spring sampling.

DISCUSSION
Gap dynamics in areas of high vs. low deer density

Natural and harvest canopy gaps offer critical regeneration sites to many understory and

canopy species (Coates, 2002; Hart and Grissino-Mayer, 2009; Shields and Webster. 2007;

Webster and Lorimer, 2005), and are typically more diverse relative to adjacent intact forest

(Ang et al., 2022; Anderson and Leopold, 2002; Hart and Kupfer, 2011; Kern et al., 2013;

Shields and Webster. 2007). However, chronic, near ubiquitous overbrowsing by deer has been

degrading native plant diversity for decades in eastern deciduous forests (Begley-Miller et al.,

2014; Burton et al., 2021; Nuttle et al., 2013; Sabo et al., 2019; VanderMolen and Webster,

2021) and opportunity is limited to study the dynamics of communities unaffected by such

persistent overbrowsing. To the best of our knowledge, ours is the first study to elucidate

differences in gap successional trajectories in areas with >50 years of low (~7 deer/km^2) and

high deer density (>20 deer/km^2). Evaluating community composition along a canopy gap

chronosequence inside and outside of Base also provides an opportunity to assess current forest

regeneration as a function of historically and currently different deer densities. This was done in

different-sized gaps, ranging in age from 2- to 14-years old, in mesic vs. dry habitat types.

Our results for fall-flowering plants indicate that all vegetation metrics of the native flora

were higher following five decades of low compared to high deer density. For example, native

cover, richness, and diversity were 50-75% higher in areas of low deer density (Fig. 2).

However, where deer were more abundant, exotic cover increased as gaps aged, where non-

native cover averaged 380% higher than areas with low deer density. In addition, sapling height

and stem density of northern red as well as pin oak were between five- and 20-fold higher at

Base, indicating varying deer density affects early recruitment of some canopy dominants. In

fact, indicator species analysis revealed that nine native woody species were associated with

fewer deer in both wet and drier forest, and none were associated with high deer density (Table

4). Furthermore, according to the 2016 Ohio forest inventory, declining oak regeneration has

been observed throughout the state where they are continuously being overbrowsed and

gradually replaced by more shade tolerant species such as maples (*Acer* spp.), resulting in limited

success in recruiting into the sapling stage (i.e. 1- 4 inch d.b.h.; Albright et al., 2018).

Collectively, these findings suggest that annual deer management at Base, which has kept their

average deer density at no more than twice their historic abundance of 3-4 deer/km^2 (McCabe

and McCabe, 1997), has fostered significantly higher native diversity and abundance in fall than

outside of Base. In contrast, high deer densities were strongly associated with reductions in all

metrics of native plant composition, including canopy species recruitment, as well as facilitation of exotic species growth (also see Knight et al., 2009b; Averill et al., 2018).

We predicted that non-native richness and diversity would be higher in areas of high deer density because of greater propagule pressure than at Base. This prediction is based on the positive correlation between exotic propagule pressure and human settlement (Stohlgren et al., 2006), public roadways (von der Lippe and Kowarik, 2007), and hiking trails (Liedtke et al., 2020), and the fact that our plots outside of Base were in small forests surrounded by suburbia. However, non-native richness and diversity did not differ across our deer density gradient. This suggests regional species pools for shade-tolerant non-native are lower in diversity than anticipated or that colonization and growth by exotics is low in suburban locales with high deer densities. While there is little doubt that shade-tolerant exotic plants are regionally less diverse than those that are shade-intolerant (see Eschtrush and Battles, 2011; Martin et al., 2009), we also suggest that dense exotic understories reduce establishment of native as well as exotic plants. Indeed, as gaps aged, exotic cover increased, suggesting that competition for light intensified, in part driven by greater dominance of already established exotics as well as canopy closure.

Despite differences in all measured aspects of vegetation in fall, we found no differences in native and exotic compositional components measured in spring. This difference is likely a legacy effect of the past land use history at Base coupled with the fact that most spring-flowering plants have poorer dispersal potential than their fall-flowering counterparts (Bellemare et al., 2002; Flinn and Vellend 2005; Verheyen et al., 2003). In short, there simply has not been enough time for them to colonize a large, relatively young forest that was formerly agricultural field. However, the species poor spring flora has also been attributed to deer herbivory during

27

periods when densities exceeded the historical average at Base (Fig. 1; Morgan, 1995). Although deer have since decreased inside Base (Fig. 1), we suspect the co-occurrence of periodic heavier browsing and land-use history accounts for the current depauperate spring understory, as previous reports have indicated small populations occurring on or near a rocky gorge which has likely served as refugia from herbivory and land-use history (Morgan, 1995). To test these hypotheses, we suggest seed additions inside and outside of new exclosures to assess whether seed limitation, browsing-induced low recruitment at 7.5 deer/km^2, or a combination of both still limits their spread. Additionally, we propose this be done in canopy gaps as well as under a closed canopy to foster species across a range of shade tolerance.

We reiterate that Base was largely abandoned farmland in 1940 and was founded at a time when deer density began to rise in the eastern US (Cote et al., 2004; Iverson and Iverson, 1999; Leopold et. al., 1947). As such, it represents an 88 km^2 area that has undergone secondary succession with atypically low deer densities. Based on current trends outside of Base, the prognosis for many native plants is poor but is promising for those that are exotic (Averill et al., 2018; Eschtrush and Battles, 2009; Kalisz et al., 2014; Knight et al., 2009b). We add that many phytophagous insects depend on abundant and diverse native flora (Ehrlich and Raven, 1964), and loss of which consequently lowers energy flow to higher trophic levels (DeCalesta, 1994; Nuttle et al., 2011). Lastly, as forests decline in high quality (native) forage species and increase in those of low palatability, the ability of a region to sustain a particular deer biomass is compromised (see below; also see Nuttle et al., 2013; Rooney, 2009; Royo and Carson, 2006; Royo and Stanovick, 2019).

28

Estimating short- and long-term carrying capacities of white-tailed deer

The long-term prognosis for local and regional plant diversity is encouraging when the contemporary disturbance regimes under which resident species have evolved match their historic spatial frequency and magnitude (Pickett and White, 1985; Ross et al., 2002). Significant alterations to this inevitably change the survivorship and fecundity schedules of the inhabitants, ultimately manifesting themselves in community compositional change (Bengtsson et al., 2000; Perring et al., 2018; Royo et al., 2010b). In the last half century, the unprecedented increase in deer populations from their historic density of 3-4 deer/km^2 (McCabe and McCabe, 1997) represents such a force, with well-documented reductions in native palatable species (Augustine and DeCalesta, 2003; Nuzzo et al., 2017; Royo et al., 2010b; Tanentzap et al., 2011) and facilitation of browse-resistant species (Kalisz et al., 2014; Knight et al., 2009b; Royo and Carson, 2006; Sabo et al., 2019; VanderMolen and Webster, 2021). Our study corroborates these findings, namely, that native species falter while exotic species prosper under chronic overbrowsing by deer, which becomes more pronounced as gaps age (also see Nuttle et al., 2013). Importantly, these near ubiquitous regional trends in deer-driven vegetational change were entirely absent at Base, a 87.8 km^2, fenced military facility that has maintained its deer population near historic levels for over six decades (see Fig. 1).

Given regional trends toward deer-induced dominance of browse-tolerant and browse-resistant species, a fundamental question emerges as to what deer density (or biomass) can currently be sustained in a given area (i.e., what is their short-term nutritional carrying capacity or K_{ST}). The answer depends exclusively on the immediate abundance and diversity of browsable plant species, including their range in forage quality, as well as current deer metabolic

intake rates. We define short-term carrying capacity (K_{ST}) as a system's ability to meet the

metabolic demands of an herbivore population while maintaining current forage resources

(Monteith et al., 2014; Smythe et al., 2019). For long-term carrying capacity (K_{LT}), we define it

as the ability of an area to indefinitely sustain a particular biomass of white-tailed deer. When

forage is consumed as it is produced, a population is, by definition, at its K_{ST}. When this occurs,

vegetation in exclosures should diverge from control plots as herbivores alter plant competitive

hierarchies (Suding and Goldberg, 2001; Tripler et al., 2005). Alternatively, when deer are well

below their K_{ST}, exclosure vs. control plots should not differ in composition. At Base, we found

that, relative to control plots, excluding deer for three growing seasons in large gaps (median:

385 m²) did not change native and exotic community metrics. This is in contrast to findings of

compositional divergence between exclosure and control plots in the same or shorter time in

similar-sized gaps, but where deer are more abundant (Augustine and Frelich, 1998; Burton et

al., 2021; Forrester et al., 2014; Horsley et al., 2003; Hupperts et al., 2022). We therefore

conclude that deer below their K_{ST} at Base.

K_{ST}, for good reason, has been the focus of many studies, which investigate the short-

term dynamics between available forage and deer density (McLeod, 1997; Mysterud, 2006).

However, of arguably greater importance is the long-term consequence of poor early recruitment

of canopy species to K_{ST} (e.g., important canopy species like oak; also see Fig. 2 of Nuttle et al.,

2013). Long-lived canopy species such as oaks subsidize K_{ST} via propagule input (Kaneko et al.,

2020; La Saout et al., 2014) and thus their recruitment is critical to the long-term carrying

capacity (K_{LT}). In our discussion, we focus exclusively on deer as the herbivore but

acknowledge myriad factors affect K_{ST} and K_{LT}, including weather, other herbivores, disturbance,

and regional species pools (Jesmer et al., 2021). K_{ST} remains the same when recruitment rate to

adulthood equals adult mortality rate, declines when adult recruitment is less than that of adult mortality, and vice versa. We found that where deer densities were low, no difference in early recruitment of canopy species was found between exclosure vs. control plots. However, outside of Base, where deer are estimated to be ≥ 20 deer/km^2, native plant richness, diversity and cover were reduced by at least 50% (Fig. 1), with >80% lower stem density and height in two oak species (Fig. 4, Table 3). Seven other native woody species were also significantly associated with low deer density (Table 4). Collectively, these findings suggest the K_{LT} at Base is higher than outside of it. Moreover, K_{ST} may remain higher than K_{LT} for extended periods because of the inherent lag between poor recruitment of important canopy species and adult mortality in these long-lived species. This 'carrying capacity debt' begins to get paid when unreplaced adults begin to die.

ACKNOWLEDGEMENTS:

REFERENCES

Abe, S., Masaki, T., Nakashizuka, T., 1995. Factors influencing sapling composition in canopy gaps of a temperate deciduous forest. Vegetatio 120, 21–32. https://doi.org/10.1007/BF00033455

Abrams, M.D., Johnson, S.E., 2012. Long-term impacts of deer exclosures on mixed-oak forest composition at the Valley Forge National Historical Park, Pennsylvania, USA. J. Torrey Bot. Soc. 139, 167–180. https://doi.org/10.3159/TORREY-D-11-00075.1

Adams, H.L., Kissell, R.E., Ratajczak, D., Warr, E.L., Applegate, R.D., Barrett, L., Lavacot, T., Graves, D., 2020. Relationships among white-tailed deer density, harvest, and landscape metrics in TN, USA. Eur. J. Wildl. Res. 66, 19. https://doi.org/10.1007/s10344-019-1353-8

Albright, T.A., Butler, B.J., Crocker, S.J., Kurtz, C.M., Lister, T.W., McWilliams, W.H., Miles, P.D., et. al., 2018. Ohio Forests 2016. Resource Bulletin NRS-118. Newtown Square, PA. Department of Agriculture, Forest Service, Northern Research Station. 24 p. https://doi.org/10.2737/NRS-RB-118

Anderson, K.L., Leopold, D.J., 2002. The role of canopy gaps in maintaining vascular plant diversity at a forested wetland in New York State. J. Torrey Bot. Soc. 129, 238–250.

Anderson, R.C., Loucks, O.L., 1979. White-tailed deer (Odocoileus virginianus) influence on structure and composition of Tsuga canadensis forests. J. Appl. Ecol. 16, 855–861.

Ang, J.M.A., Kusumoto, D., Mitsugi, M., Suzuki, M., 2022. Regeneration of tree species after 11 years of canopy gap creation and deer exclusion in a warm temperate broadleaved forest over-browsed by sika deer. PeerJ 10, 1–19. https://doi.org/10.7717/peerj.14210

Augustine, D.J., DeCalesta, D., 2003. Defining deer overabundance and threats to forest communities: from individual plants to landscape structure. Ecoscience 10, 472–486. https://doi.org/10.1080/11956860.2003.11682795

Augustine, D.J., Frelich, L.E., 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. Conserv. Biol. 12, 995–1004. https://doi.org/10.1046/j.1523-1739.1998.97248.x

Augustine, D.J., McNaughton, S.J., 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J. Wildl. Manage. 62, 1165. https://doi.org/10.2307/3801981

Averill, K.M., Mortensen, D.A., Smithwick, E.A.H., Kalisz, S., McShea, W.J., Bourg, N.A., Parker, J.D., Royo, A.A., et. al., 2018. A regional assessment of white-tailed deer effects on plant invasion. AoB Plants 10:plx047. https://doi.org/10.1093/aobpla/plx047

Banta, J.A., Royo, A.A., Kirschbaum, C., Carson, W.P., 2005. Plant communities growing on boulders in the Allegheny National Forest: evidence for boulders as refugia from deer and as a bioassay of overbrowsing. Nat. Areas J. 25, 10–18.

Barrette, M., Bélanger, L., De Grandpré, L., Ruel, J.C., 2014. Cumulative effects of chronic deer browsing and clear-cutting on regeneration processes in second-growth white spruce stands. For. Ecol. Manage. 329, 69–78. https://doi.org/10.1016/j.foreco.2014.06.020

Begley-Miller, D.R., Hipp, A.L., Brown, B.H., Hahn, M., Rooney, T.P., 2014. White-tailed deer are a biotic filter during community assembly, reducing species and phylogenetic diversity. AoB Plants 6:plu030. https://doi.org/10.1093/aobpla/plu030

Bellemare, J., Motzkin, G., Foster, D.R., 2002. Legacies of the agricultural past in the forested present: An assessment of historical land-use effects on rich mesic forests. J. Biogeogr. 29, 1401–1420. https://doi.org/10.1046/j.1365-2699.2002.00762.x

Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. For. Ecol. Manage. 132, 39-50.

Blossey, B., Dávalos, A., Nuzzo, V., 2017. An indicator approach to capture impacts of white-tailed deer and other ungulates in the presence of multiple associated stressors. AoB Plants 9:plx034. https://doi.org/10.1093/aobpla/plx034

Boerner, R.E.J., Brinkman, J.A., 1996. Ten years of tree seedling establishment and mortality in an Ohio deciduous forest. J. Torrey Bot. Soc. 123, 309–317. https://doi.org/10.2307/2996780

Burton, J.I., Mladenoff, D.J., Forrester, J.A., Clayton, M.K., 2014. Experimentally linking disturbance, resources and productivity to diversity in forest ground-layer plant communities. J. Ecol. 102, 1634–1648. https://doi.org/10.1111/1365-2745.12319

Burton, J.I., Mladenoff, D.J., Forrester, J.A., Clayton, M.K., 2021. Effects of forest canopy gaps on the ground-layer plant community depend on deer: Evidence from a controlled experiment. J. Veg. Sci. 32:e12969. https://doi.org/10.1111/jvs.12969

Canham, C.D., 1988. Growth and canopy architecture of shade-tolerant trees. Ecology 69, 786–795.

Canham, C.D., 1989. Different responses to gaps among shade-tolerant tree species. Ecology 70, 548–550. https://doi.org/10.2307/1940200

Chollet, S., Baltzinger, C., Saout, S. Le, Martin, J.L., 2013. A better world for bryophytes? A rare and overlooked case of positive community-wide effects of browsing by overabundant deer. Ecoscience 20, 352–360. https://doi.org/10.2980/20-4-3627

Coates, K.D., 2002. Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. For. Ecol. Manage. 155, 387–398. https://doi.org/10.1016/S0378-1127(01)00574-6

Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Syst. 35, 113–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725

Davis, M.A., K., T., J., G.P., 2005. Invasibility: the local mechanism driving community assembly and species diversity. Ecography 28, 696–704.

De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574. https://doi.org/10.1890/08-1823.1

De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. Oikos 119, 1674–1684. https://doi.org/10.1111/j.1600-0706.2010.18334.x

De la Cretaz, A.L., Kelty, M.J., 2002. Development of tree regeneration in fern-dominated forest understories after reduction of deer browsing. Restor. Ecol. 10, 416–426. https://doi.org/10.1046/j.1526-100X.2002.02037.x

DeCalesta, D.S., 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. J. Wildl. Manage. 58, 711–718. https://doi.org/10.2307/3809685

Dietze, M.C., Clark, J.S., 2008. Changing the gap dynamics paradigm: Vegetative regeneration control on forest response to disturbance. Ecol. Monogr. 78, 331–347. https://doi.org/10.1890/07-0271.1

DiTommaso, A., Morris, S.H., Parker, J.D., Cone, C.L., Agrawal, A.A., 2014. Deer browsing delays succession by altering aboveground vegetation and belowground seed banks. PLoS One 9, e91155. https://doi.org/10.1371/journal.pone.0091155

Ehrlich, P.R., Raven, P.H., 1964. Butterflies and plants: a study in coevolution. Evolution 18, 586–608.

Esri inc. (2021). ArcGIS Pro (Version 2.8). Esri Inc. https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview.

Eschtruth, A.K., Battles, J.J., 2009. Acceleration of exotic plant invasion in a forested ecosystem by a generalist herbivore. Conserv. Biol. 23, 388–399. https://doi.org/10.1111/j.1523-1739.2008.01122.x

Eschtruth, A.K., Battles, J.J., 2011. The importance of quantifying propagule pressure to understand invasion: an examination of riparian forest invasibility. Ecology 92, 1314-1322.

Evans, J.P., Keen, E.M., 2013. Regeneration failure in a remnant stand of pignut hickory (Carya glabra) on a protected barrier island in Georgia, USA. Nat. Areas J. 33, 171–176. https://doi.org/10.3375/043.033.0207

Farrington, S.J., Muzika, R.M., Drees, D., Knight, T.M., 2009. Interactive effects of harvest and deer herbivory on the population dynamics of American ginseng. Conserv. Biol. 23, 719–728. https://doi.org/10.1111/j.1523-1739.2008.01136.x

Feldmann, E., Glatthorn, J., Ammer, C., Leuschner, C., 2020. Regeneration dynamics following the formation of understory gaps in a Slovakian beech virgin forest. Forests 11. https://doi.org/10.3390/F11050585

FGDC., 2008. Federal Geographic Data Committee National Vegetation Classification. FGDC-STD-005-2008 (Version 2). Federal Geographic Data Committee Vegetation Subcommittee, US Geological Survey, Reston, Virginia, USA https://www.fgdc.gov/standards/projects/vegetation/NVCS_V2_FINAL_2008-02.pdf

Flinn, K.M., Vellend, M., 2005. Recovery of forest plant communities in post-agricultural landscapes. Front. Ecol. Environ. 3, 243-250. https://doi.org/10.2307/3868486

Forrester, J.A., Lorimer, C.G., Dyer, J.H., Gower, S.T., Mladenoff, D.J., 2014. Response of tree regeneration to experimental gap creation and deer herbivory in north temperate forests. For. Ecol. Manage. 329, 137–147. https://doi.org/10.1016/j.foreco.2014.06.025

Gendreau-Berthiaume, B., Kneeshaw, D., 2009. Influence of gap size and position within gaps on light levels. Int. J. For. Res. 1–8. https://doi.org/10.1155/2009/581412

Goetsch, C., Wigg, J., Royo, A.A., Ristau, T., Carson, W.P., 2011. Chronic over browsing and biodiversity collapse in a forest understory in Pennsylvania: results from a 60 year-old deer exclusion plot. J. Torrey Bot. Soc. 138, 220–224. https://doi.org/10.3159/TORREY-D-11-00013.1

Google Earth Pro 7.3, 2017. Obtained from https://www.google.com/earth/versions/.

Habeck, C.W., Schultz, A.K., 2015. Community-level impacts of white-tailed deer on understorey plants in North American forests: a meta-analysis. AoB Plants 7:plv119. https://doi.org/10.1093/aobpla/plv119

Hart, J.L., Grissino-Mayer, H.D., 2009. Gap-scale disturbance processes in secondary hardwood stands on the Cumberland Plateau, Tennessee, USA. Plant Ecol. 201, 131–146. https://doi.org/10.1007/s11258-008-9488-9

Hart, J.L., Kupfer, J.A., 2011. Sapling richness and composition in canopy gaps of a southern Appalachian mixed Quercus forest. J. Torrey Bot. Soc. 138, 207–219. https://doi.org/10.3159/TORREFY-D-11-00006.1

Holmes, S.A., Webster, C.R., 2011. Herbivore-induced expansion of generalist species as a driver of homogenization in post-disturbance plant communities. Plant Ecol. 212, 753–768. https://doi.org/10.1007/s11258-010-9858-y

Horsley, S.B., Stout, S.L., DeCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol. Appl. 13, 98–118. https://doi.org/10.1890/1051-0761(2003)013[0098:WTDIOT]2.0.CO;2

Hupperts, S.F., Webster, C.R., Froese, R.E., Bal, B., Dickinson, Y.L., 2022. Influence of Strip Clearcuts, Deer Exclusion and Herbicide on Initial Sapling Recruitment in Northern Hardwood Forests. Forests 13. https://doi.org/10.3390/f13071149

IBM Corp. Released 2021. IBM SPSS Statistics for Windows, Version 28.0. Armonk, NY: IBM Corp. https://www.ibm.com/products/spss-statistics

Iverson, A.L., Iverson, L.R., 1999. Spatial and temporal trends of deer harvest and deer-vehicle accidents in Ohio. Ohio J. Sci. 9.

Jesmer, B.R., Kauffman, M.J., Courtemanch, A.B., Kilpatrick, S., Thomas, T., Yost, J., Monteith, K.L., Goheen, J.R., 2021. Life-history theory provides a framework for detecting resource limitation: a test of the Nutritional Buffer Hypothesis. Ecol. Appl. 31. https://doi.org/10.1002/eap.2299

Jost, L., 2006. Entropy and diversity. Oikos 113, 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Kalisz, S., Spigler, R.B., Horvitz, C.C., 2014. In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives. PNAS 111, 4501–4506. https://doi.org/10.1073/pnas.1310121111

Kaneko, M., Takeshita, K.M., Tanikawa, K., Kaji, K., 2020. Seasonal variation in and nutritional implications of the diet composition of a sika deer (Cervus nippon) population in a heavily browsed habitat: contribution of canopy subsidies. Mammal Study 45, 327–336.

Kern, C.C., Burton, J.I., Raymond, P., D'Amato, A.W., Keeton, W.S., Royo, A.A., Walters, M.B., Webster, C.R., Willis, J.L., 2017. Challenges facing gap-based silviculture and possible solutions for mesic northern forests in North America. Forestry 90, 4–17. https://doi.org/10.1093/forestry/cpw024

Kern, C.C., Montgomery, R.A., Reich, P.B., Strong, T.F., 2013. Canopy gap size influences niche partitioning of the ground-layer plant community in a northern temperate forest. J. Plant Ecol. 6, 101–112. https://doi.org/10.1093/jpe/rts016

Kindt, R., Coe, R., 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre (ICRAF), Nairobi, Kenya.

Knight, T.M., Caswell, H., Kalisz, S., 2009a. Population growth rate of a common understory herb decreases non-linearly across a gradient of deer herbivory. For. Ecol. Manage. 257, 1095–1103. https://doi.org/10.1016/j.foreco.2008.11.018

Knight, T.M., Dunn, J.L., Smith, L.A., Davis, J.A., Kalisz, S., 2009b. Deer facilitate invasive plant success in a Pennsylvania forest understory. Nat. Areas J. 29, 110–116. https://doi.org/10.3375/043.029.0202

Kuijper, D.P.J., Cromsigt, J.P.G.M., Churski, M., Adam, B., Jedrzejewska, B., Jedrzejewski, W., 2009. Do ungulates preferentially feed in forest gaps in European temperate forest? For. Ecol. Manage. 258, 1528–1535. https://doi.org/10.1016/j.foreco.2009.07.010

Latif, Z.A., Blackburn, G.A., 2010. The effects of gap size on some microclimate variables during late summer and autumn in a temperate broadleaved deciduous forest. Int. J. Biometeorol. 54, 119–129. https://doi.org/10.1007/s00484-009-0260-1

Le Saout, S., Chollet, S., Chamaillé-Jammes, S., Blanc, L. Padié, S. et al., 2014. Understanding the paradox of deer persisting at high abundance in heavily browsed habitats. Wildlife Biology 20, 122–135.

Leopold A., Sowls L.K., Spencer D.L., 1947. A survey of over-populated deer ranges in the United States. J. Wildl. Manage. 11, 162–177.

Liedtke, R., Barros, A., Essl, F., Lembrechts, J.J., Wedegärtner, R.E.M., Pauchard, A., Dullinger, S., 2020. Hiking trails as conduits for the spread of non-native species in mountain areas. Biol. Invasions 22, 1121–1134. https://doi.org/10.1007/s10530-019-02165-9

Martin, P.H., Canham, C.D., Marks, P.L., 2009. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. Front. Ecol. Environ. 7, 142–149. doi:10.1890/070096

McCabe, T.R., and McCabe, R.E., 1997. Recounting whitetails past. In: McShea, W.J., Underwood, H.B., Rappole, J.H. (Eds.), The Science of Overabundance: Deer Ecology and Population Management. Smithsonian Press, Washington, DC, pp.11-26.

McGraw, J.B., Furedi, M.A., 2005. Deer browsing and population viability of a forest understory plant. Science 307, 920–922. https://doi.org/10.1126/science.1107036

McLeod, S.R., 1997. Is the concept of carrying capacity useful in variable environments? Oikos 79, 529–542.

McWilliams, W.H., Westfall, J.A., Brose, P.H., Dey, D.C., D'Amato, A.W., Dickinson, Y.L., et. al., 2018. Subcontinental-scale patterns of large-ungulate herbivory and synoptic review of restoration management implications for midwestern and northeastern forests. Gen. Tech. Rep. NRS-182. Newt. Square, PA U.S. Department of Agriculture, Forest Service, Northern Research Station. 24 p.

Monteith et al., 2014. Life-History Characteristics of Mule Deer: Effects ofNutrition in a Variable Environment. Wildlife Monographs, https://doi.org/10.1002/wmon.1011

Morgan, T., 1995. Integrated natural resource management plan: Ravenna Army Ammunition Plant. https://www.rvaap.org [accessed Feb. 2023]

Morgan, T., 1996. Natural resources and environmental overview of the The Ravenna Army Ammunition Plant with thoughts on the future. Am. Curr. 22. http://www.nanfa.org/ac/ravenna-army-plant-environmental-overview.pdf

Morrison, J.A., 2017. Effects of white-tailed deer and invasive plants on the herb layer of suburban forests. AoB Plants 9:plx058. https://doi.org/10.1093/aobpla/plx058

Mysterud, A., 2006. The concept of overgrazing and its role in management of large herbivores. Wild. Biol. 12, 129-141.

Nagy, C., Ng, C., Veverka, N., Weckel, M., 2022. Assessment of a 15-year white-tailed deer management program and woody recovery in a suburban forest preserve. For. Ecol. Manage. 503, 119748. https://doi.org/10.1016/j.foreco.2021.119748

Nuttle, T., Ristau, T.E., Royo, A.A., 2014. Long-term biological legacies of herbivore density in a landscape-scale experiment: Forest understoreys reflect past deer density treatments for at least 20 years. J. Ecol. 102, 221–228. https://doi.org/10.1111/1365-2745.12175

Nuttle, T., Royo, A.A., Adams, M.B., Carson, W.P., 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. Ecol. Monogr. 83, 3–17. https://doi.org/10.1890/11-2263.1

Nuttle, T., Yerger, E.H., Stoleson, S.H., Ristau, T.E., 2011. Legacy of top-down herbivore pressure ricochets back up multiple trophic levels in forest canopies over 30 years. Ecosphere 2(1):art4. https://doi.org/10.1890/ES10-00108.1

Nuzzo, V., Dávalos, A., Blossey, B., 2017. Assessing plant community composition fails to capture impacts of white-tailed deer on native and invasive plant species. AoB Plants 9. https://doi.org/10.1093/aobpla/plx026

Ohio Department of Natural Resources (ODNR). Ohio wetlands inventory – Mahoning, Trumbull County (1987), Published 1991. ODNR GIS Services Columbus Ohio. https://ohiodnr.gov/wps/portal/gov/odnr/business-and-industry/services-to-business-industry/gis-mapping-services/metadata-downloads [accessed May 2022]

Ogden Environmental and Energy Services, 2000. Environmental baseline summary report: Ravenna training and Logistic site- Portage and Trumbull Counties, Ohio. Cincinnati, Ohio. https://www.rvaap.org/docs/pub/F_EBSR_RTLS_40_00AC.pdf

Owings, C.F., Jacobs, D.F., Shields, J.M., Saunders, M.R., Jenkins, M.A., 2017. Individual and interactive effects of white-tailed deer and an exotic shrub on artificial and natural regeneration in mixed hardwood forests. AoB Plants 9:plx024. https://doi.org/10.1093/aobpla/plx024

Parker, H.A., Larkin, J.T., Heggenstaller, D., Duchamp, J., Tyree, M.C., Rushing, C.S., Just Domoto, E., Larkin, J.L., 2020. Evaluating the impacts of white-tailed deer (Odocoileus virginianus) browsing on vegetation in fenced and unfenced timber harvests. For. Ecol. Manage. 473, 118326. https://doi.org/10.1016/j.foreco.2020.118326

Peck, L.J., Stahl, J.E., 1997. Deer management techniques employed by the Columbus and Franklin County Park District, Ohio. Wildl. Soc. Bull. 25, 440–442.

Perring, M.P., Bernhardt-Romermann, M., Baeten, L., Midolo, G., Blondeel, H., et al., 2018. Global environmental change effects on plant community composition trajectories depend upon management legacies. Glob. Chang. Biol. 24, 1722–1740.

Pickett, S.T.A., White, P.S., 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, FL, pp 371–384.

Poulson, T.L., Platt, W.J., 1989. Gap light regimes influence canopy tree diversity. Ecology 70, 553–555. https://doi.org/10.2307/1940202

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ramirez, J.I., Jansen, P.A., Poorter, L., 2018. Effects of wild ungulates on the regeneration, structure and functioning of temperate forests: a semi-quantitative review. For. Ecol. Manage. 424, 406–419. https://doi.org/10.1016/j.foreco.2018.05.016

Redick, C.H., Jacobs, D.F., 2020. Mitigation of deer herbivory in temperate hardwood forest regeneration: a meta-analysis of research literature. Forests. 1220 https://doi.org/10.3390/f11111220

Rooney, T.P., 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecol. 202, 103–111. https://doi.org/10.1007/s11258-008-9489-8

Ross, K.A., Fox, B.J., Fox, M.D., 2002. Changes to plant species richness in forest fragments: fragment age, disturbance and fire history may be as important as area. J. Biogeog. 29, 749-765.

Rossell, C.R., Gorsira, B., Patch, S., 2005. Effects of white-tailed deer on vegetation structure and woody seedling composition in three forest types on the Piedmont Plateau. For. Ecol. Manage. 210, 415–424. https://doi.org/10.1016/j.foreco.2005.02.035

Royo, A.A., Carson, W.P., 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can. J. For. Res. 36, 1345–1362. https://doi.org/10.1139/x06-025

Royo, A.A., Carson, W.P., 2022. Stasis in forest regeneration following deer exclusion and understory gap creation: A 10-year experiment. Ecol. Appl. https://doi.org/10.1002/eap.2569

Royo, A. A, Collins, R., Adams, M.B., Kirschbaum, C., Carson, W.P., 2010a. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. Ecology 91, 93–105. https://doi.org/10.1890/08-1680.1

Royo, A.A., Stanovick, J.S., 2019. Deer browsing overwhelms extended leaf phenology benefits: A test case with Rubus allegheniensis and a recalcitrant hay-scented fern layer. For. Ecol. Manage. 448, 294–299. https://doi.org/10.1016/j.foreco.2019.06.019

Royo, A. A., Stout, S.L., deCalesta, D.S., Pierson, T.G., 2010b. Restoring forest herb communities through landscape-level deer herd reductions: is recovery limited by legacy effects? Biol. Conserv. 143, 2425–2434. https://doi.org/10.1016/j.biocon.2010.05.020

Russell, F.L., Zippin, D.B., Fowler, N.L., 2001. Effects of white-tailed deer (Odocoileus virginianus) on plants, plant populations and communities: a review. Am. Midl. Nat. 146, 1–26. https://doi.org/10.1674/0003-0031(2001)146[0001:eowtdo]2.0.co;2

Sabo, A.E., Forrester, J.A., Burton, J.I., Jones, P.D., Mladenoff, D.J., Kruger, E.L., 2019. Ungulate exclusion accentuates increases in woody species richness and abundance with canopy gap creation in a temperate hardwood forest. For. Ecol. Manage. 433, 386–395. https://doi.org/10.1016/j.foreco.2018.11.004

Sabo, A.E., Forrester, J.A., Kruger, E.L., Mladenoff, D.J., 2023. Herbaceous plant height is an early indicator of groundlayer response to an experimental manipulation of forest structure and deer pressure. For. Ecol. Manage. 536, 120902. https://doi.org/10.1016/j.foreco.2023.120902

Sabo, A.E., Frerker, K.L., Waller, D.M., Kruger, E.L., 2017. Deer-mediated changes in environment compound the direct impacts of herbivory on understorey plant communities. J. Ecol. 105, 1386–1398. https://doi.org/10.1111/1365-2745.12748

Schmit, J.P., Matthews, E.R., Brolis, A., 2020. Effects of culling white-tailed deer on tree regeneration and Microstegium vimineum, an invasive grass. For. Ecol. Manage. 463, 118015. https://doi.org/10.1016/j.foreco.2020.118015

Shelton, A.L., Henning, J.A., Schultz, P., Clay, K., 2014. Effects of abundant white-tailed deer on vegetation, animals, mycorrhizal fungi, and soils. For. Ecol. Manage. 320, 39–49. https://doi.org/10.1016/j.foreco.2014.02.026

Shields, J.M., Webster, C.R., 2007. Ground-layer response to group selection with legacy-tree retention in a managed northern hardwood forest. Can. J. For. Res. 37, 1797–1807. https://doi.org/10.1139/X07-052

Smythe, S.E., Sanchez, D.M., Epps, C.W., 2019. Contrasting winter moose nutritional carrying capacity models on a dynamic landscape. J. Fish Wildl. 10, 163–179.

Stohlgren, T.J., Barnett, D., Flather, C., Fuller, P., Peterjohn, B., Kartesz, J., Master, L.L., 2006. Species richness and patterns of invasion in plants, birds, and fishes in the United States. Biol. Invasions 8, 427–447. https://doi.org/10.1007/s10530-005-6422-0

Suding, K.N., Goldberg, D., 2001. Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation. Ecology 82, 2133–2149.

Tahtinen, B., Murray, B.D., Webster, C.R., Tarasoff, C.S., Burton, A.J., 2014. Does ungulate foraging behavior in forest canopy gaps produce a spatial subsidy with cascading effects on vegetation? For. Sci. 60, 819–829. https://doi.org/10.5849/forsci.13-080

Tanentzap, A.J., Bazely, D.R., Koh, S., Timciska, M., Haggith, E.G., Carleton, T.J., Coomes, D.A., 2011. Seeing the forest for the deer: do reductions in deer-disturbance lead to forest recovery? Biol. Conserv. 144, 376–382. https://doi.org/10.1016/j.biocon.2010.09.015

Tilghman, N.G., 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. J. Wildl. Manage. 53, 524-532. https://doi.org/10.2307/3809172

Tripler, C.E., Canham, C.D., Inouye, R.S., Schnurr, J.L., 2005. Competitive hierarchies of temperate tree species: Interactions between resource availability and white-tailed deer. Ecoscience 12, 494–505. https://doi.org/10.2980/i1195-6860-12-4-494.1

Urbanek, R.E., Nielsen, C.K., 2013. Influence of landscape factors on density of suburban white-tailed deer. Landsc. Urban Plan. 114, 28–36. https://doi.org/10.1016/j.landurbplan.2013.02.006

USDA Farm Service, 2022a. National Agricultural Imagery Program (NAIP). Aerial Photography Field Office, Salt Lake City, UT USA. https://doi.org/10.5066/F7QN651G . Imagery obtained from www.earthexplorer.usgs.gov [accessed Aug. 2022]

USDA National Resource Conservation Service, 2022b. The PLANTS Database. National Plant Data Team, Greensboro, NC USA. http://plants.usda.gov. [accessed Feb. 2022]

Valverde, T., Silvertown, J., 1997. Canopy closure rate and forest structure. Ecology 78, 1555–1562. https://doi.org/10.1890/0012-9658(1997)078[1555:CCRAFS]2.0.CO;2

VanderMolen, M.S., Webster, C.R., 2021. Influence of deer herbivory on regeneration dynamics and gap capture in experimental gaps, 18 years post-harvest. For. Ecol. Manage. 501, 119675. https://doi.org/10.1016/j.foreco.2021.119675

Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., Foster, D.R., 2003. Response of forest plant species to land-use change: a life-history trait-based approach. J. Ecol. 91, 563–577. https://doi.org/10.1046/j.1365-2745.2003.00789.x

Von Der Lippe, M., Kowarik, I., 2007. Long-distance dispersal of plants by vehicles as a driver of plant invasions. Conserv. Biol. 21, 986–996. https://doi.org/10.1111/j.1523-1739.2007.00722.x

Wallingford, B.D., 2000. Estimating county deer population sizes & growth rates. Bureau of Wildlife Management, Pennsylvania Game Commission. https://www.pgc.pa.gov/InformationResources/MediaReportsSurveys/AnnualWildlifeManagementReports/Pages/default.aspx [accessed Feb. 2023]

Webster, C.R., Lorimer, C.G., 2005. Minimum opening sizes for canopy recruitment of midtolerant tree species: a retrospective approach. Ecol. Appl. 15, 1245–1262. https://doi.org/10.1890/04-0763

Witham, J.H., Jones, J.M., 1990. White-tailed deer abundance on metropolitan forest preserves during winter in northeastern Illinois. Wildl. Soc. Bull. 18, 13–16.

APPENDIX 1

White-tailed deer density comparison between aerial count and calculated post-hunt estimates at Base.

Figure A1. White-tailed deer density within Camp James A. Garfield (Base), comparing the difference between our post-hunt population estimates (calculated using the equation $PREH_t = 0.45(HD_t) + 421$ (see methods 2.4)) and post-hunt aerial counts.
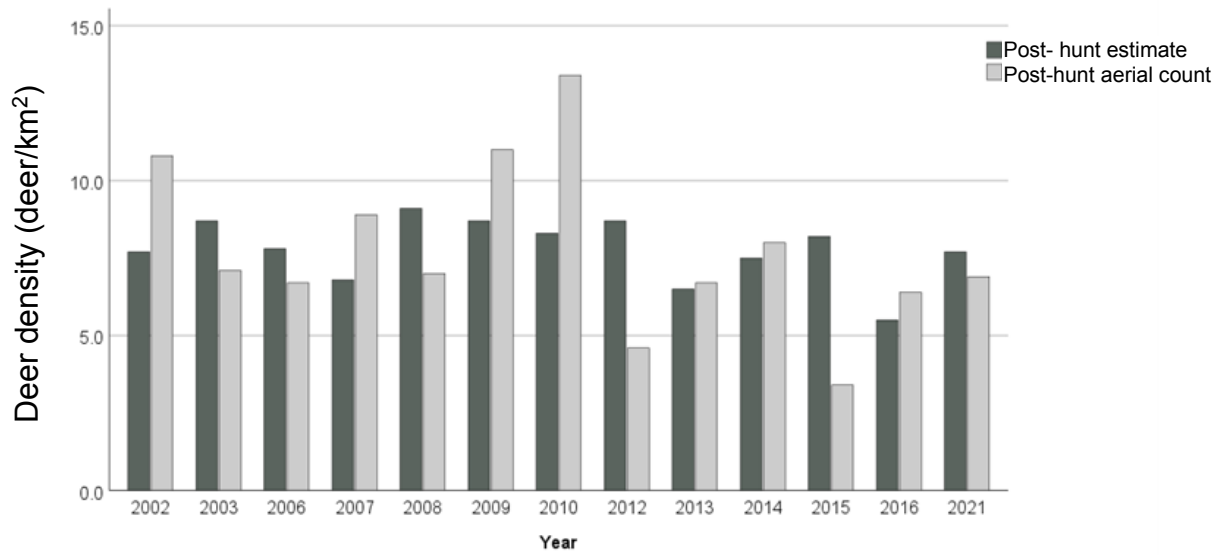
APPENDIX 2

Species phenology

Table A2. Full list of species sampled, an 'X' under spring and/or fall indicates which analysis each

species was included in. Those with a spring and fall phenology were analyzed separately, while those

with more of a summer phenology were included in both analyses and thus display a 'X' under spring and

fall.

Species		Analysis	
Scientific name	**Common name**	**Spring**	**Fall**
Acalypha rhomboidea	Commom threeseed mercury		X
Acer rubrum	Red maple		X
Acer saccharum	Sugar maple		X
Agrimonia	Agrimonies		X
Agrimonia gryposepala	Agrimony		X
Agrostis perennans	Autumn bentgrass		X
Alliaria petiolata	Garlic mustard	X	
Allium canadense	Wild garlic	X	
Allium schoenoprasum	Chive	X	
Allium tricoccum	Ramp	X	
Anemone quinqofolia	Wood anemone	X	
Anemone virginiana	Tall thimbleweed	X	
Anthoxanthum odoratum	Sweet vernal grass	X	X
Ambrosia trifida	Giant ragweed		X
Apocynum spp.	Dogbane	X	X
Arisaema triphyllum	Jack-in-the-pulpit	X	X
Asclepias incarnata	Swamp milkweed	X	X
Aster spp.	Aster		X
Berberis thunbergii	Japanese barberry		X
Boehmeria spp.	Nettle		X
Boehmeria cylindrica	False nettle		X
Brassica spp.	Brassica		X
Cardamine spp.	Cresses	X	
Cardamine bulbosa	Bulbous bittercress	X	
Cardamine concatenata	Cutleaf toothwort	X	
Carex spp.	Carex		X
Carex blanda	Eastern woodland sedge	X	X
Carex bromoides	Brome-like-sedge		X
Carex pennsylvanica	Pennsylvania sedge	X	X
Carex communis	Fibrous-root sedge	X	X
Carex crinita	Fringed sedge	X	
Carex glaucodea	Blue sedge	X	X
Carex gracillima	Graceful sedge	X	X
Carex intumescens	Greater bladder sedge		X
Carex laxiflora	Broad loose-flowered sedge	X	
Carex lupulina	Hop sedge		X

Carex muskingumensis	Palm sedge		X
Carex pallescens	Pale sedge		X
Carex radiata	Eastern star sedge	X	X
Carex stricta	Tussock sedge	X	X
Carex swanii	Swan's sedge	X	X
Carex vulpinoidea	Fox sedge		X
Carpinus caroliniana	American hornbeam		X
Carya spp.	Hickory		X
Chamerion angustifolium	Fireweed		X
Chelone spp.	Turtlehead		X
Cimicifuga spp.	Bugbane		X
Circaea alpina	Small enchanter's nightshade	X	X
Circaea lutetiana	Broadleaf enchanter's nightshade	X	X
Claytonia virginica	Spring beauty	X	
Clematis virginiana	Devil's darning needles		X
Conopholis spp.	Cancer-root		X
Cornus alternifolia	Alternateleaf dogwood		X
Cornus florida	Flowering dogwood		X
Cornus racemosa	Gray dogwood		X
Cornus sericea	Redosier dogwood		X
Corydalis spp.	Fumewort	X	X
Crataegus spp.	Hawthorne		X
Cyperus rotundus	Nut grass		X
Cryptotaenia canadensis	Canadian honewort	X	X
Cynodon dactylon	Bermudagrass	X	X
Desmodium nudiflorum	Nakedflower ticktrefoil		X
Dipsacus fullonum	Teasel		X
Dichanthelium clandestinum	Deertongue		X
Doellingeria umbellata	Flat-topped aster		X
Dryopteris spp.	Wood fern		X
Dryopteris carthusiana	Spinulose wood fern		X
Epifagus virginiana	Beechdrops		X
Epilobium spp.	Willowherbs		X
Epilobium ciliatum	Fringed willowherb		X
Epilobium coloratum	Purpleleaf willowherb		X
Erechtites hieraciifolius	American burnweed		X
Erigenia bulbosa	Harbinger of spring	X	
Erythronium americanum	Trout lily	X	
Eupatorium perfoliatum	Common boneset		X
Euonymus alatus	Burningbush		X
Euonymus obovata	Running strawberry buch		X
Eurybia divaricata	White wood aster		X
Fagus grandifolia	American beech		X
Floerkea proserpinacoides	False mermaidweed	X	
Fragaria virginiana	Virginia strawberry	X	X
Fraxinus spp.	Ash		X
Galium spp.	Bedstraw	X	X
Galium aparine	Cleavers	X	X
Galium odoratum	Sweetscented bedstraw	X	X

Galium palustre	Common marsh bedstraw	X	X
Geranium maculatum	Spotted geranium	X	
Geum spp.	Avenses	X	X
Geum aleppicum	Yellow avens	X	X
Geum canadense	White avens	X	
Geum urbanum	Herb bennet	X	X
Solidago gigantea	Giant goldenrod		X
Glyceria striata	Fowl mannagrass	X	X
Helenium spp.	Sneezeweed		X
Hieracium spp.	Hawkweed		X
Hydrophyllum	Waterleaf	X	
Hypericum spp.	St. Johnswort		X
Impatiens capensis	Jewelweed		X
Juncus spp.	Rush		X
Lactuca spp.	Lettuce	X	X
Laportea canadensis	Wood nettle		X
Leersia Virginica	Whitegrass	X	X
Ligustrum sinense	Chinese privet		X
Lindera benzoin	Northern spicebush		X
Liriodendron tulipifera	Tuliptree		X
Lobelia inflata	Indian Tobacco		X
Lonicera japonica	Japanese honeysuckle		X
Lonicera spp.	Honeysuckle		X
Lonicera morrowii	Morrow's honeysuckle		X
Lonicera tatarica	Tatarian honeysuckle		X
Ludwigia alternifolia	Seedbox		X
Lycopus uniflorus	Northern bungleweed		X
Lysimachia nummularia	Creeping jenny	X	X
Maianthemum canadense	Canada mayflower	X	
Maianthemum spp.	False solomon's seal	X	
Mentha arvensis	Wild mint		X
Mertensia virginica	Virginia bluebells	X	
Mitchella repens	Partridgeberry	X	X
Mimulus alatus	Monkeyflower		X
Monarda spp.	Monarda	X	X
Myosotis scorpioides	True forget-me-not	X	X
Nyssa sylvatica	Blackgum		X
Oclemena acuminata	Whorled wood aster		X
Onoclea sensibilis	Sensitive fern		X
Osmorhiza claytonii	Clayton's sweetroot	X	X
Osmunda cinnamomea	Cinnamon fern	X	X
Ostrya virginiana	Hophornbeam		X
Oxalis spp.	Woodsorrel	X	X
Oxydendrum arboreum	Sourwood		X
Packera aurea	Golden ragwort	X	
Panax trifolius	Dwarf ginseng	X	
Panicum spp.	Panic grass		X
Panicum capillare	Witchgrass		X
Parthenocissus quinquefolia	Virginia creeper	X	X

Penstemon digitalis	Foxglove beardtongue		X
Persicaria sagittata	Arrowleaf tearthumb	X	X
Persicaria virginiana	Jumpseed	X	X
Phalaris arundinacea	Reed canarygrass	X	X
Phytolacca americana	Pokeweed		X
Pilea pumila	Canadian clearweed		X
Pinus strobus	Eastern white pine		X
Plantago lanceolata	Narrowleaf plantain	X	X
Poa annua	Annual bluegrass	X	X
Poa palustris	Fowl bluegrass	X	X
Poa pratensis	Kentucky bluegrass	X	X
Poa spp.	Grass		X
Podophyllum peltatum	Mayapple	X	
Polyganatum spp.	Solomon's seal	X	
Polygonum spp..	Smartweed		X
Polygonum pennsylvanicum	Pennsylvania smartweed		X
Polystichum acrostichoides	Christmas fern	X	X
Populus spp.	Cottonwood		X
Potentilla Simplex	Common cinquefoil	X	
Prenanthes alba	White rattlesnakeroot		X
Prenanthes crepidinea	Nodding rattlesnakeroot		X
Prenanthes spp.	Rattlesnakeroot		X
Prunella vugaris	Selfheal		X
Prunus pensylvanica	Pin cherry		X
Prunus serotina	Black cherry		X
Prunus virginiana	Chokecherry		X
Quercus alba	White oak		X
Quercus bicolor	Swamp white oak		X
Quercus palustris	Pin oak		X
Quercus rubra	Northern red oak		X
Quercus velutina	Black oak		X
Ranunculus acris	Tall buttercup	X	
Ranunculus ficaria	Lesser celandine	X	
Ranunculus hispidus	Hispid buttercup	X	
Ranunculus recurvatus	Hooked crowfoot	X	
Ranunculus repens	Creeping buttercup	X	
Ranunculus sceleratus	Cursed crowfoot	X	
Rhamnus frangula	Glossy buckthorn		X
Ribes spp.	Gooseberry		X
Rosa multiflora	Multiflora rose		X
Rubus allegheniensis	Allegheny blackberry		X
Rubus hispidus	Bristly dewberry		X
Rubus idaeus	American red raspberry		X
Rumex crispus	Curly dock	X	
Rhynchospora	Rhynchospora	X	X
Sambucus spp.	Elderberry		X
Sanicula canadensis	Canadian blacksnakeroot	X	
Sassafras albidum	Sassafras		X
Schedonorus arundinaceus	Tall fescue		X

Scirpus spp.	Sedge		X
Scirpus cyperinus	Woolgrass		X
Scirpus hattorianus	Mosquito bulrush		X
Scutellaria laterifolia	Blue skullcap		X
Senecio spp.	Ragwort	X	
Smilax spp.	Greenbriers		X
Solanum dulcamara	Bittersweet nightshade	X	X
Solidago altissima	Tall goldenrod		X
Solidago caesia	Blue-stemmed goldenrod		X
Solidago canadensis	Canada goldenrod		X
Solidago flexicaulis	Zigzag goldenrod		X
Solidago juncea	Early goldenrod		X
Solidago patula	Roughleaf goldenrod		X
Solidago rugosa	Wrinkleleaf goldenrod		X
Solidago spp.	Goldenrod		X
Solidago speciosa	Showy goldenrod		X
Solidago uliginosa	Swamp goldenord		X
Spiraea tomentosa	Steeplebush		X
Sorghastrum nutans	indiangrass		X
Sporobolus heterolepis	Praire dropseed		X
Stellaria media	Common chickweed	X	
Symphoricarpos albus	Common snowberry	X	X
Symphyotrichum ericoides	White heath aster		X
Symphyotrichum lanceolatum	White panicle aster		X
Symphyotrichum lateriflorum	Calico aster		X
Symphyotrichum novae-angliae	New England aster		X
Symphyotrichum puniceum	Purplestem aster		X
Symphytum officinale	Common comfrey	X	X
Symplocarpus foetidus	Skunk cabbage	X	
Taraxacum officinale	Common dandelion	X	X
Thalictrum spp.	Meadow rue	X	X
Thelypteris noveboracensis	New York fern		X
Tilia americana	American basswood		X
Toxicodendron radicans	Poison ivy	X	X
Trifolium pratense	Red clover		X
Tsuga canadensis	Eastern hemlock		X
Ulmus spp.	Elm		X
Verbena stricta	Hoary verbena		X
Verbesina spp.	Crownbeards		X
Verbesina alternifolia	Wingstem		X
Veronica officinalis	Common gypsyweed	X	X
Veronica serpyllifolia	Brightblue speedwell	X	X
Viburnum acerfolium	Mapleleaf viburnum		X
Viburnum cassinoides	Possumhaw		X
Viburnum dentatum	Southern arrowwood		X
Viburnum lentago	Nannyberry		X
Viburnum prunifolium	Blackhaw		X
Viburnum spp.	Viburnum		X
Viola blanda	Sweet white violet	X	

Viola hastata	Halberdleaf violet	X	
Viola macloskeyi	Small white violet	X	X
Viola palustris	Marsh violet	X	
Viola sagittata	Arrowleaf violet	X	
Viola sororia	Common blue violet	X	X
Viola spp.	Violet	X	
Vitis spp.	Grape vines		X

APPENDIX 3

Graph of native species composition in fall

Figure A3. Relative cover of native species at each site during fall sampling, where each color represents a species in order of appearance in the legend. The number above each bar specifies native species richness. Sites with a * indicate those that were excluded from the second MANCVOA analysis due to the atypical dominance of New York fern (see methods- data analyses).
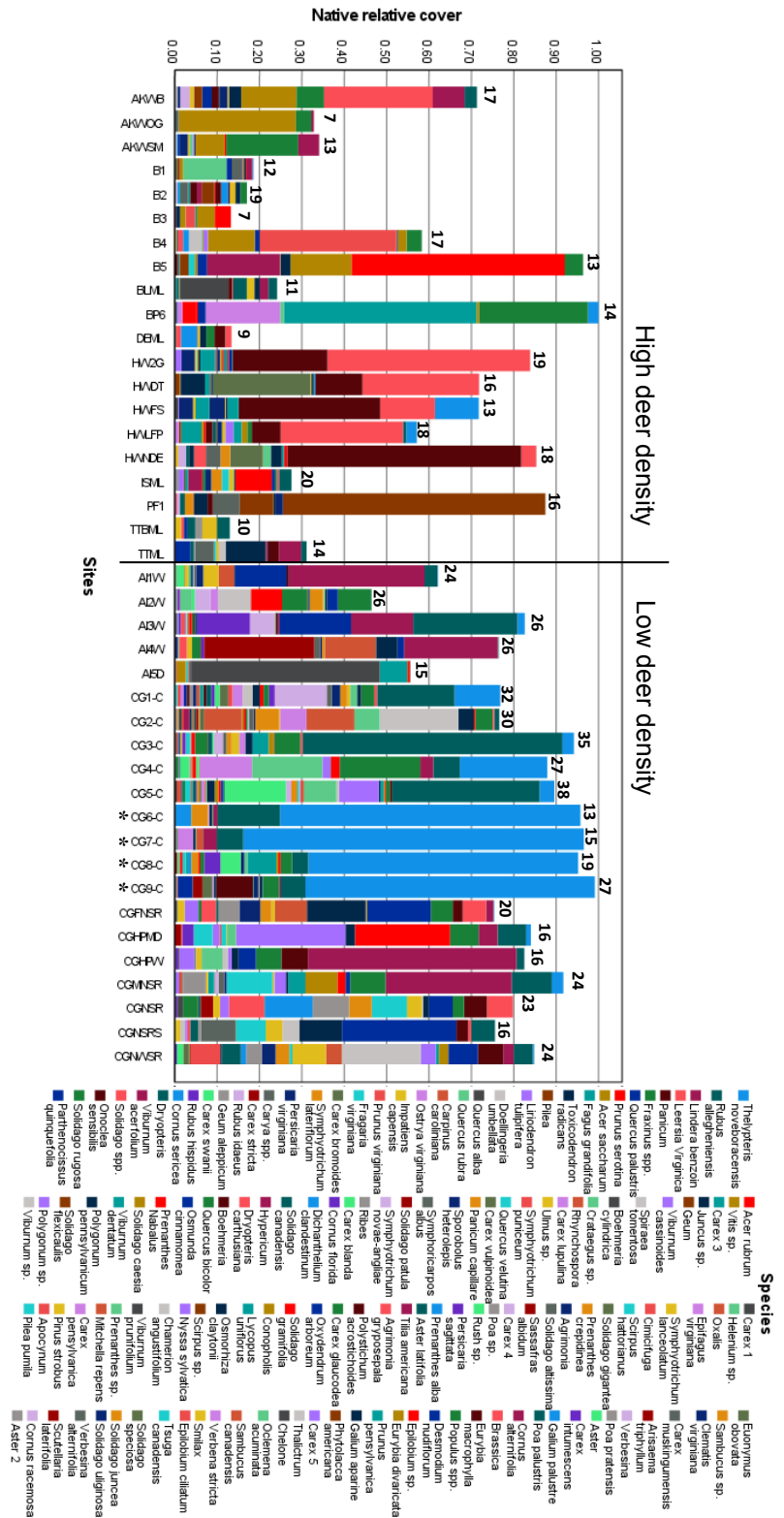
APPENDIX 4

Woody species descriptive statistics

Table A4. Descriptive statistics of woody regeneration of taxon occurring in ≥20% of plots under high (N=20) vs. low (N=21) deer density showing mean maximum height and mean stem count (cm) in the 2m browse zone. Significance (p ≤ 0.05), mean ranks (non-arithmetic, non-parametric) and test statistics (H) all determined by Kruskal-Wallis test.

	Deer Density	Mean	Std. Deviation	Mean rank	H	Sig.
Quercus palustris Stem count	Low	8.71	16.73	24.43	4.94	0.026
	High	0.40	0.94	17.40		
Quercus palustris Max height	Low	98.70	142.44	24.71	5.80	0.016
	High	6.10	12.51	17.10		
Quercus rubra Stem count	Low	5.57	11.40	24.31	4.43	0.035
	High	0.70	1.89	17.52		
Quercus rubra Max height	Low	51.04	71.26	24.76	5.71	0.017
	High	9.14	22.33	17.05		
Lindera benzoin Stem Count	Low	3.81	6.95	24.02	3.34	0.068
	High	0.95	2.14	17.83		
Lindera benzoin Max height	Low	100.87	121.20	23.81	2.80	0.094
	High	38.86	59.64	18.05		
Viburnum spp. Stem count	Low	2.71	5.05	24.67	5.07	0.024
	High	2.15	5.87	17.15		
Viburnum spp. Max height	Low	18.14	18.43	24.14	3.90	0.048
	High	16.76	42.22	17.70		
Acer rubrum Stem count	Low	7.67	15.54	24.62	5.10	0.024
	High	0.35	0.67	17.20		
Acer rubrum Max height	Low	71.12	201.73	23.62	2.68	0.102
	High	7.62	13.54	18.25		
Acer saccharum Stem count	Low	5.76	14.25	21.21	0.02	0.895
	High	2.35	4.30	20.78		
Acer saccharum Max height	Low	9.68	13.04	19.69	0.65	0.421
	High	88.39	133.01	22.38		
Carya spp. Stem count	Low	1.29	1.65	22.19	0.52	0.471
	High	1.90	4.91	19.75		
Carya spp. Max height	Low	67.49	139.31	23.02	1.48	0.224
	High	33.53	100.80	18.88		

Fraxinus spp. Stem Count	Low	8.33	12.99	23.67	2.25	0.134
	High	5.55	10.69	18.20		
Fraxinus spp. Max height	Low	98.70	96.34	25.21	5.72	0.017
	High	36.58	71.04	16.58		
Cornus spp. Stem Count	Low	1.76	5.20	23.69	3.38	0.066
	High	0.30	0.80	18.18		
Cornus Spp. Max height	Low	26.85	50.06	23.57	3.08	0.079
	High	27.43	102.24	18.30		
Prunus serotina Stem Count	Low	4.33	9.17	22.10	0.44	0.508
	High	8.45	24.76	19.85		
Prunus serotina Max height	Low	42.33	119.51	21.57	0.12	0.729
	High	57.15	153.03	20.40		
Liriodendron tulipifera Stem Count	Low	3.33	9.79	22.98	2.45	0.118
	High	0.40	1.57	18.93		
Liriodendron tulipifera Max height	Low	64.59	144.57	23.14	2.88	0.090
	High	3.05	9.38	18.75		
Ulmus spp. Stem count	Low	0.90	1.51	22.71	1.45	0.228
	High	0.30	0.66	19.20		
Ulmus spp. Max height	Low	26.85	58.61	22.62	1.31	0.253
	High	6.10	12.51	19.30		
Rhamnus frangula Stem Count	Low	3.29	5.00	24.38	4.20	0.040
	High	0.70	1.53	17.45		
Rhamnus frangula Max height	Low	101.12	131.56	24.43	4.29	0.038
	High	21.34	46.49	17.40		
Lonicera spp. Stem count	Low	0.29	1.10	18.93	2.69	0.101
	High	0.90	1.77	23.18		
Lonicera spp. Max height	Low	7.26	29.95	18.83	2.95	0.086
	High	37.34	60.05	23.28		