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Native tree species prosper while exotics falter during gap-phase regeneration, but only where deer densities are near historical levels

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Abstract

Throughout eastern North America, chronic white-tailed deer overbrowsing and widespread exotic plant invasions degrade native plant diversity and abundance. However, because deer densities are high across entire regions, it is challenging to find large areas where deer have been at low density for long periods. We predicted native plant diversity and abundance would be significantly higher during gap-phase regeneration where deer have been maintained at low densities (~7 deer/km²) compared to where deer have been chronically overabundant. Simultaneously, we predicted that exotic plant diversity and abundance would be lower in gaps where deer have been maintained at low versus high densities. We also evaluated whether deer density interacts with gap age, gap size, and gaps in dry versus more mesic forest patches. We studied 41 gaps throughout an 88 km^2 fenced military post where deer were maintained near pre-European-settlement densities for 67 years and in nearby forests where deer have been overabundant for decades. Native species richness, diversity, and cover were 37–65% higher, and exotic species cover was 80% lower in canopy gaps at low relative to high deer density. Stem height and density of multiple native canopy tree species (e.g., two *Quercus* spp.) were 5-20-fold higher within canopy gaps at low deer density. Moreover, 10 native woody species were indicators of low deer density, including three *Quercus* species, whereas no native woody species were indicators of high deer density. Deer were the primary filter underlying these different patterns in diversity, abundance, and plant height. Our findings demonstrate that gaps develop a vigorous and diverse native sapling layer, with far fewer exotics, in areas of low deer density without a history of chronic overbrowsing. We propose that military posts may be conservation and native plant regeneration hotspots wherever they regularly cull deer.

Keywords Oak (*Quercus*) regeneration · Gap-phase dynamics · Historic deer density · Native plant diversity · Exotic establishment · Canopy tree recruitment

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Introduction

In eastern North American forests, canopy gaps typically increase plant diversity and abundance whereas chronic overbrowsing causes sharp declines in diversity and abundance (Rooney 2001; Begley-Miller et al. 2014; Dey et al. 2019; Sabo et al. 2019; Burton et al. 2021; VanderMolen and Webster 2021). Gaps increase light availability in forest understories, leading to increases in the diversity and abundance of both shade-intolerant species as well as species intermediate in shade-tolerance (Anderson and Leopold 2002; Coates 2002; Webster and Lorimer 2005; Hart and Grissino-Mayer 2009; Kern et al. 2013; Burton et al. 2014;). Recruitment of shade-intolerant species typically requires large gaps (>250 m^2; Busing and White 1997; Nuttle et al. 2013; Walters et al. 2016). However, deer browsing often reduces native herbaceous and woody plant diversity and abundance in canopy gaps, and this may vary substantially with gap size and age (Holmes and Webster 2011; Zhang et al. 2013; Ramirez et al. 2018; Sabo et al. 2023). In contrast, when deer are at low or moderate levels, deer can promote herbaceous diversity by decreasing the abundance of fast-growing pioneer trees and shrubs (Royo et al. 2010).

Overbrowsing is often associated with an increase in the abundance and diversity of exotic, invasive species (Knight et al. 2009; Abrams and Johnson 2012; Kalisz et al. 2014; Averill et al. 2018; Huebner et al. 2018; but see Gorchov et al. 2021 on declines in exotic woody species abundance with overbrowsing). Excluding deer with fences or culling deer in areas of high deer abundance leads to declines in exotic species abundance (Webster et al. 2008; Bourg et al. 2017; Nuzzo et al. 2017). For example, Kalisz et al. (2014) found that exotic garlic mustard (*Alliaria petiolata*) had a mean geometric population growth rate of 1.33 when deer were present, thus the population was rapidly increasing, but when deer were excluded, it dropped to 0.88, indicating a sharply declining population.

The speed and trajectory of gap-phase regeneration can be mediated by site conditions (e.g., wet versus drier forests; Boerner and Brinkman 1996; Frey et al. 2007; Amatangelo et al. 2011) as well as canopy gap size and age (Valverde and Silvertown 1997; Holmes and Webster 2011). For example, Hoven et al. (2022) found that deer browsing in canopy gaps reduced native seedling diversity in wetter forest but had no effect on native seedling diversity in drier forest. In large gaps, high light availability may also allow some browse-sensitive species to rapidly grow through the deer filter (Walters et al. 2016; Spicer et al. 2023). Finally, it is unclear whether gap-phase regeneration interacts with browsing as canopy gaps age. Overall, few studies have examined the relationship between deer browsing and gap size and gap age (Clinton et al. 1994; Webster and VanderMolen 2023).

A major challenge in studying the interaction between canopy gaps and browsing is that nearly all studies have occurred where deer have been overabundant over vast regions for nearly a century. Indeed, finding forests not subjected to sustained overbrowsing is difficult and is often confined to small deer refugia (e.g., tall boulders) or deer-free islands (Banta et al. 2005; Comisky et al. 2005; Mudrak et al. 2009; Chollet et al. 2013). Ecologists have also used exclosures to study browsing but these studies sometimes fail to find substantial responses to browsing manipulations, particularly in short-term studies (e.g., <3 years; see Nuttle et al. 2013 and Habeck and Schultz 2015 for good long-term studies). Lack of exclosure effects is also common in sites that suffer from legacy effects, whereby fences are constructed where chronic overbrowsing had already created impoverished forests region-wide, including soil seed banks (Kain et al. 2011; Goetsch et al. 2011; Royo and Carson

2022; Webster and VanderMolen 2023). For example, Knauer et al. (2023) did not detect an increase in diversity or richness in exclosures that were maintained for nearly 20 years in a region where deer had been overabundant for nearly a century (Royo and Carson 2022).

One solution to overcome the problem of region-wide, chronic deer overabundance is to find large areas where deer have been maintained at low densities for long periods and focus research efforts in forest regeneration hotspots, specifically canopy gaps. Here, we studied gap-phase regeneration within an 88 km^2 area where deer have been maintained at low densities (~ 7 deer/km^2) for nearly seven decades versus canopy gaps in nearby forest stands where deer are at least four times more abundant. We tested the hypothesis that deer abundance regulates the diversity and abundance of native tree species as well as the diversity and abundance of exotic plant species during gap-phase regeneration. This hypothesis makes the following predictions: (1) The diversity, abundance, and height of native tree species will be substantially higher in gaps where deer are at lower densities and this will vary depending on gap age and gap size. (2) The diversity, richness, and abundance of exotic species will be substantially lower in gaps where deer are at low densities and this will vary depending on gap age and gap size. (3) The composition of the regenerating tree community will be distinct in gaps in areas of low versus high deer density. (4) Gap-phase regeneration will be distinct in wet versus drier forest, regardless of deer density. To evaluate our predictions, we studied 20 gaps where deer were at high density and 21 gaps where deer were at low density. All gaps were studied in mature second-growth forest in eastern Ohio, USA. To our knowledge, this is the first study of gap-phase regeneration in sites subjected to decades of persistently high versus persistently low deer density.

Materials and methods

Study sites

We studied 21 canopy gaps in an approximately 80-year-old forest at Camp James A. Garfield, a fenced military post (87.8 km^2) located in northeast Ohio, USA (41.1 N, 81.1 W). This forest was historically part of the beech-maple association of the Eastern Deciduous Forest Biome (Vankat 1979). A subset of these 21 gaps occurred in wetter, hydric, seasonally flooded soils (n = 14 gaps; ODNR 1991) dominated by swamp white oak (*Quercus bicolor*) and pin oak (*Q. palustris*). The other subset occurred in drier, more upland forest (n = 7 gaps; ODNR 1991) which was dominated by northern red oak (*Q. rubra*), American beech (*Fagus grandifolia*), and shagbark hickory (*Carya ovata*). We also surveyed 20 gaps in nearby forest outside Camp Garfield in continuous closed-canopy wet (n = 8 gaps) and dry mature forest (n = 12 gaps) with similar age, structure, and canopy composition (41.1 N, 80.4 W). We were careful to avoid small stands, younger stands, and forests that were dominated by other canopy species or, for the upland sites, dominated by only one or two canopy species. The abundance of exotic species played no role in gap selection. Our only other criteria for gap selection were that a range of gap age and size was represented inside and outside of Camp Garfield, and that gaps were far apart from each other. The median distance between plots inside of Camp Garfield was 240 m (range: 72 – 2,060 m), median distance between plots outside of Camp Garfield was 420 m (range: 240–2,600 m), and median distance between plots inside versus outside of Camp Garfield was 11.3 km. Importantly, fire has not occurred at Camp Garfield since it was founded in 1942 (Brian P. Riley, Natural Resource Manager of Camp Garfield). Similarly, outside Camp Garfield, if fires do occur, they are rapidly extinguished by fast-responding, proactive local fire departments.

Estimating canopy gap age and size

We identified canopy gaps in wet and drier upland forests through satellite images with extensive ground truthing and entered gap coordinates into ArcGIS-Pro (Esri Inc. 2021). We determined gap age by visually identifying gaps using time-series satellite images from the National Agriculture Imagery Program and Google Earth (USDA 2022a; Google Earth V. 7.3). For example, if a gap was present in 2010, absent in 2008, and no image was available in 2009, we concluded the gap formed the first year there was an image of the gap (i.e., in 2010). We placed markers around the edges of each gap in ArcGIS-Pro to estimate gap area. We identified 41 gaps ranging in age from 2 to 14 years and size from 83 to 522 m^2 (median size: $230m^2$).

Deer density estimates

Annual deer hunts have occurred on Camp Garfield since 1955, along with detailed hunt data (e.g., hunter days and total deer harvested). We quantified deer densities using 13 annual post-hunt winter aerial surveys (2002–2003, 2006–2010, 2012–2016, and 2021) as well as annual data from deer harvests that date back to 1955. We used the aerial deer surveys of Camp Garfield to estimate deer density from 1955 to 2021. Specifically, we estimated an annual pre-hunt population (*PHP)* by adding the post-hunt aerial count to the total number of deer harvested each year. To estimate annual deer density, we performed linear regressions using these pre-hunt population estimates (*PHP)* and the total number of hunter days (*HD*) within those same years. From this linear regression, we generated the equation: $PHP_t = 0.45(HD_t)+421$, where PHP_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 and 2021, which was divided by 87.8 km^2, the area of Camp Garfield. Because aerial surveys represent post-hunt populations, we calculated the difference between our pre-hunt estimates from 1955 to 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 conducted a two-tailed paired *t*-test to compare the deer density estimated from aerial counts and our post-hunt estimates within the same year. No difference between aerial counts and post-hunt estimates was detected ($p=0.977$), indicating our estimates accurately reflect post-hunt populations (Fig. 1). Estimated deer density averaged 6.6 deer/km^2 since 1955, and averaged 7.5 deer/km^2 over the last 14 years (Fig. 1).

We did not estimate deer density outside Camp Garfield. Nonetheless, deer in this region of Ohio, western Pennsylvania, and throughout much of the eastern United States are well known to be quite high (>30 deer/km2) and this has been true for decades (see references in Fig. 1). Moreover, the understory vegetation outside Camp Garfield is dominated by unpalatable and browse-tolerant native and non-native species, which is indicative of high deer density (Tilghman 1989; Horsley et al. 2003; Rossell et al. 2005; Rooney 2009; Morrison 2017; Averill et al. 2018).

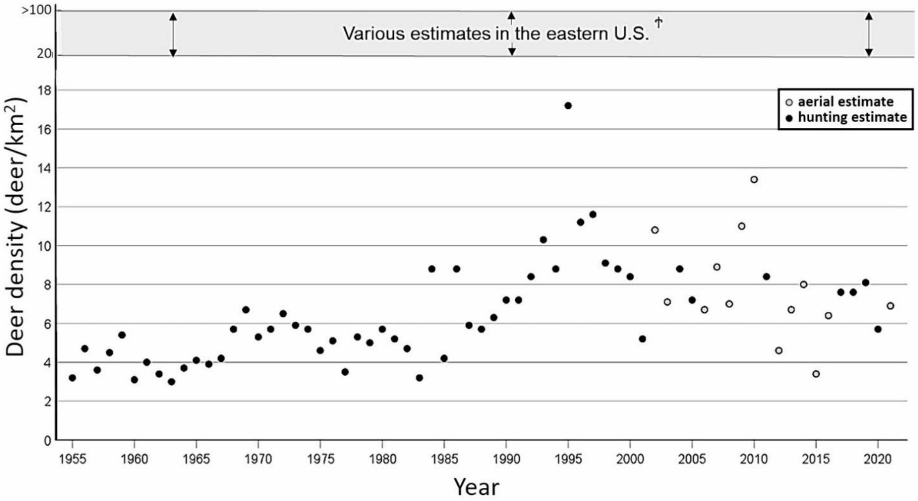


Fig. 1 White-tailed deer density estimates within Camp Garfield from 1955–2021 using our post-hunt population estimates, represented by solid points, and post-hunt aerial counts from 2002–2003, 2006–2010, 2012–2016, and 2021, shown as gray points. Estimates of deer densities throughout the eastern U.S. are also shown (Anderson and Loucks 1979; Scott and Townsend 1985; Witham and Jones 1990; Boerner and Brinkman 1996; Shafer-Nolan 1997; Iverson and Iverson 1999; Wallingford 2000; Russell et al. 2001; Rossell et al. 2005; Asnani et al. 2006; Long et al. 2007; Rooney 2009; Urbanek and Nielsen 2013; DiTommaso et al. 2014; Kalisz et al. 2014; Pendergast et al. 2016; Morrison 2017; Averill et al. 2018; Adams et al. 2020; Adams and Villarreal 2020). We note that deer densities throughout much of eastern North America have not been constant between 1955–2020 but have generally increased throughout this interval, in some cases, dramatically (references above; also see Kelly 2019 and Derico 2023)

Vegetation sampling

In 2020–2021, we established a 3×9 m plot (three 3×3 m subplots) at gap-center in 21 gaps inside Camp Garfield and 20 gaps outside. In April and early May 2021–2022, we visually estimated the cover of only herbaceous species in each subplot from 0 to 2 m tall (browse zone). In September and early October 2020–2021, we re-censused the plots, but also visually estimated the cover of all woody species. The same two people recorded all data together to minimize observer bias. We used the USDA (2022b) PLANTS database to assign species as native or exotic. For each species, we also quantified woody stem density as well as the height of the tallest woody individual (in each subplot) up to 10 m in height as an indicator of browsing pressure (see Rawinski 2018). Each 3×9 m plot was our unit of replication. We calculated a mean for each species by summing the cover of each species in each of the 3×3 m subplots and dividing by three. Here, we evaluate our predictions using primarily the responses of tree species. However, we incorporated herbaceous and shrub species into our estimates of species richness, diversity, and total cover as well as into our indicator species analysis.

Statistical analyses – multiple analysis of covariance

We conducted multiple analysis of covariance (MANCOVA) in SPSS (IBM Corp 2021) to evaluate the main and interactive effects of deer density and habitat (wet vs dry) on plant species composition using gap age and gap size as covariates. Our design was a 2×2 factorial, with two levels of deer density (high vs. low) and two levels of habitat type (wet vs. dry). Statistically significant factors from the MANCOVA analysis were then analyzed using analysis of covariance, using gap size and gap age as covariates. Our response variables were native and exotic species richness, mean cover, and diversity (i.e., effective species number, $e^{H'}$). We calculated Shannon indices (H') in the 'BiodiversityR' package in R using mean relative cover (Kindt and Coe 2005; R Core Team 2022). We then converted Shannon indices to effective species number for each plot to avoid comparing nonlinear Shannon indices and retain meaningful comparisons among communities (see Jost 2006). We used estimated marginal means, which calculates covariate-adjusted means for response variables across all treatment combinations, for significant univariate main and interactive effects. We used log transformations to meet the assumption of homogeneity of covariance in both spring and fall (Box's M test, $p \leq 0.003$) and statistics are based on log-transformed data. However, we present all results using non-transformed data.

Linear regression of covariates and indicator species analysis

We used linear regression analysis in SPSS to evaluate the relationships between covariates and response variables when MANCOVA indicated significant differences. For example, we performed regression analysis using our fall data to quantify the association between canopy gap age and native and exotic abundance in high vs. low deer density areas. We found one outlier that was >3 standard deviations away from its predicted mean and we excluded it from our analyses. We performed indicator species analyses using the 'indicspecies' package in R, which calculates significant species associations to habitats based on abundance data (de Cáceres and Legendre 2009; R Core Team 2022). This was done on spring and fall data to determine if plant species were associated with high versus low deer density, and wet versus dry habitat (de Cáceres et al. 2010).

Evaluating browsing and habitat type on woody species abundance and maximum height

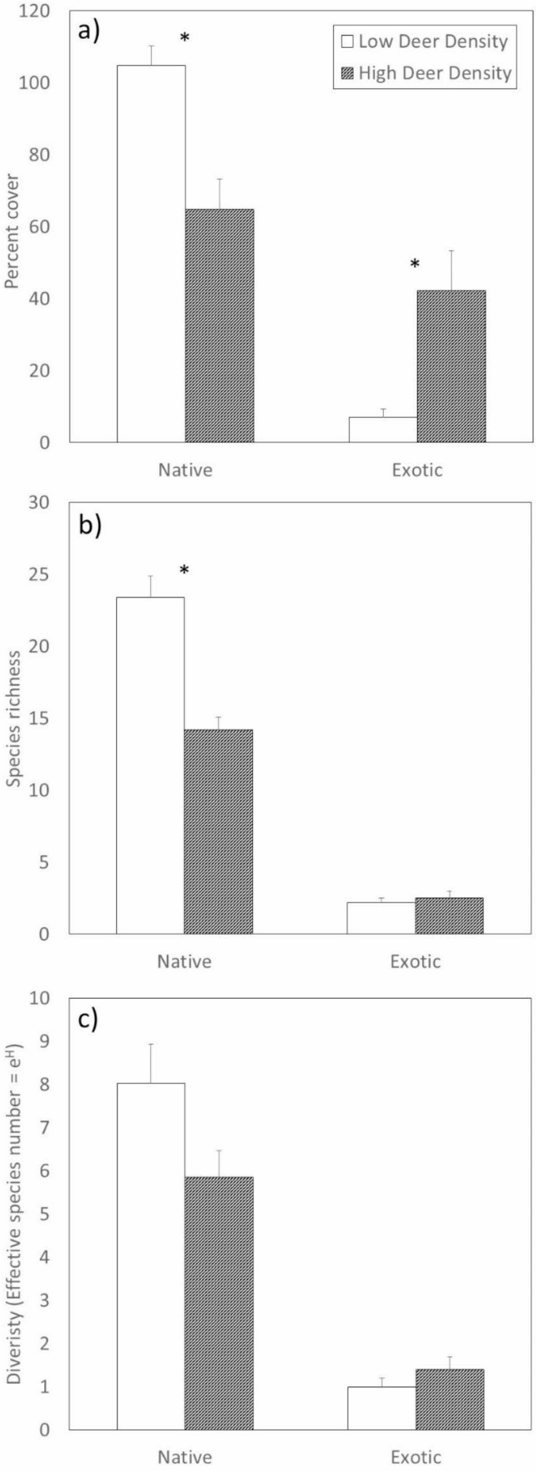
We limited our analyses to species that occurred in ≥20% of our plots to quantify the impact of browsing on woody stem density and maximum height. We then compared these metrics using the Kruskal-Wallis nonparametric independent samples test because Levene's homogeneity of variance test revealed significant between-group heteroscedasticity that was not rectified by log transformation.

Results

Community-level responses to deer density, gap size and age, and habitat type

At high deer density (outside Camp Garfield), the mean total cover of exotic species was nearly six times higher ($F_{1,35}$ =16.34, $p < 0.001$), and the mean total cover of native species was 40% lower, than at low deer density within Camp Garfield ($F_{1,35}$=12.68, $p = 0.001$, Fig. 2a). Also, at high deer densities, native species richness was 39% lower ($F_{1,35}$= 26.81,

Fig. 2 Whole plant community (i.e., woody and herbaceous species) native versus non-native: **a** percent cover, **b** species richness, and **c** diversity, during fall vegetation surveying of low (inside Camp Garfield) and high deer density sites (outside Camp Garfield). Data presented as means ± standard errors among sites. Diversity is presented as “effective species number”, i.e. $e^{H'}$. Note that all metrics for native plant species were higher under low deer abundance. In contrast, percent cover of non-native plants was higher under high deer density. Significance is indicated by * ($p \leq 0.001$)



$p<0.001$, Fig. 2b) and native diversity was 27% lower, although this was not statistically significant ($F_{1,35}$ =2.57, $p=0.118$, Fig. 2c). At high deer density, exotic cover marginally increased ($r^2=0.169$, $p=0.080$) as gaps aged but exotic cover did not significantly increase in older gaps at low deer density (Fig. 3). In fact, at high deer density, exotic cover in 9-12-year old gaps was more than twice as high compared to same-aged gaps at low deer density (Table 1; Fig. 3). Gap age did not affect any other metric of richness, diversity, or abundance ($F_{1,35}\leq1.76$, $p>0.190$). Similarly, habitat type and gap size did not affect any metric of richness, diversity, or abundance (Table 1).

Species-level responses to deer density, gap size and age, and habitat type

Stem densities of red oak, pin oak, and red maple (*Acer rubrum*) were respectively 8-, 20-, and 22-fold higher at low versus high deer density ($p<0.05$, Fig. 4a). Total stem density of these two oak species was 13 times higher at low deer density. While not significant, the density of all other tree species was substantially higher at low deer density, with one exception (Fig. 4a). Specifically, black cherry was 95% more abundant at *high deer density*. Total stem density of all native canopy tree species combined was 130% higher at low deer density ($p<0.05$, Fig. 4a). Only one exotic species, buckthorn (*Rhamnus frangula*), had 4-fold higher stem density at low deer density ($p<0.05$). Mean maximum stem heights of red oak, pin oak, tuliptree (*Liriodendron tulipifera*), red maple, and ash (*Fraxinus* spp.) were 3-, 48-, 37-, 4.5- and 4-fold higher, respectively, at low deer density versus high deer density

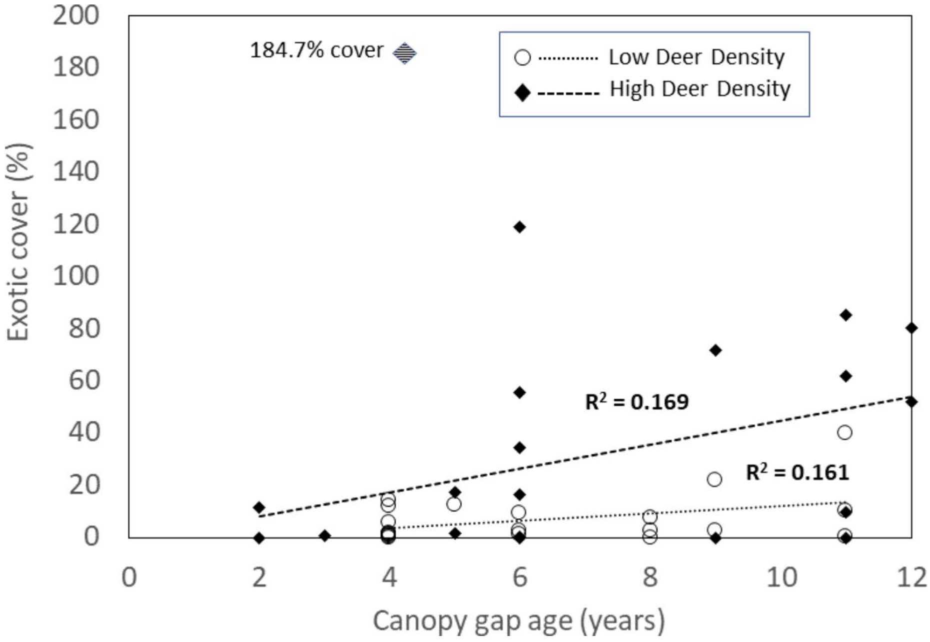


Fig. 3 Percent cover by exotic plant species regressed on canopy gap age, for low deer and high deer density sites. The very high cover case, which occurred at high deer density, was excluded from analysis because it was >3 standard deviations away from its predicted mean. Regressions were marginally significant (p–values of 0.071 and 0.080 for low and high deer density sites, respectively)

Table 1 Statistics from multiple analysis of covariance (MANCOVA) using fall data. Statistically significant factors from the MANCOVA analysis were then analyzed using analysis of covariance, using gap size and gap age as covariates. All significant values and variables are bolded ($p \leq 0.05$)

MANCOVA

Test	Variable	F-value	p-value	partial η²
Multivariate				
	Gap age	$F_{8,28}$= 2.07	0.074	0.371
	Gap size	$F_{8,28}$= 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				
Gap age	Native richness	$F_{1,35}$= 1.76	0.193	0.048
	Exotic richness	$F_{1,35}$= 1.37	0.249	0.038
	Native cover	$F_{1,35}$= 1.61	0.212	0.044
	Exotic cover	**$F_{1,35}$= 4.74**	**0.036**	**0.119**
	Native diversity ($e^{H'}$)	$F_{1,35}$= 0.055	0.816	0.002
	Exotic diversity ($e^{H'}$)	$F_{1,35}$= 1.33	0.256	0.037
Deer density	**Native richness**	**$F_{1,35}$= 26.8**	**<0.001**	**0.434**
	Exotic richness	$F_{1,35}$= 0.005	0.944	0.000
	Native cover	**$F_{1,35}$= 16.3**	**<0.001**	**0.318**
	Exotic cover	**$F_{1,35}$= 4.57**	**0.040**	**0.115**
	Native diversity ($e^{H'}$)	$F_{1,35}$= 2.57	0.118	0.068
	Exotic diversity ($e^{H'}$)	$F_{1,35}$= 0.159	0.692	0.005

($p < 0.05$, Fig. 4b). The mean height of the exotic buckthorn was three times higher at low versus high deer density ($p < 0.05$).

Indicator species analysis

Seven native canopy tree species were indicators of low deer density, including three different species of oak, as well as one native sub-canopy tree (*Cornus florida*) and two native shrubs ($p < 0.05$, *Lindera benzoin* and *Rubus allegheniensis*; Table 2). Seven herbaceous taxa were significantly associated with high deer density, three of which were exotic species ($p < 0.05$). Ten native herbaceous taxa were indicators of low deer density, whereas only one exotic species, the herb *Geum urbanum*, was an indicator of low deer density ($p < 0.05$). Overall, we found that 20 native species were indicators of low deer density and 15 native species were associated with drier sites. No shrubs or trees were associated with high deer densities (Table 2).

Discussion

Here, we evaluated gap-phase forest regeneration where deer had been kept close to pre-European-settlement densities of 3–4 deer/km^2 (McCabe and McCabe 1997) for nearly seven decades compared to nearby forests where deer have been overabundant for a similar

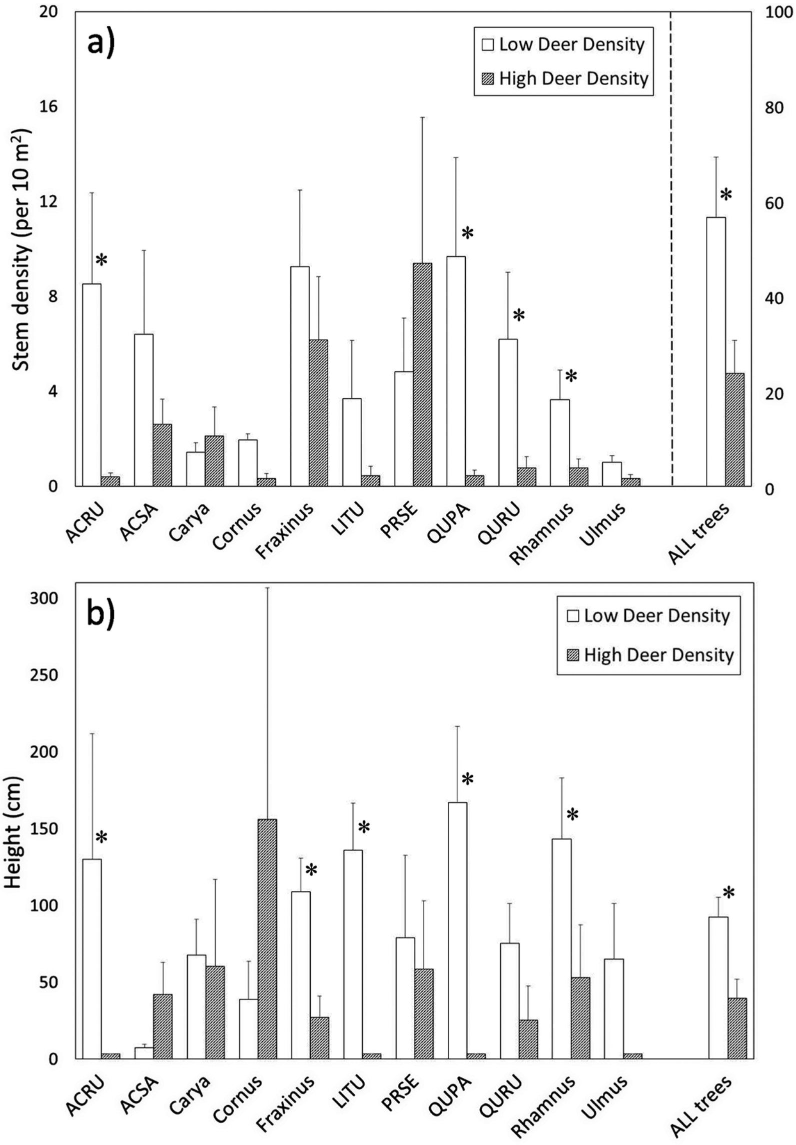


Fig. 4 Abundance and height of tree species under low (Camp Garfield) versus high deer density (near Camp Garfield): **a** stem density per 10 m^2, and **b** height of tallest individual of each species in each 27 m^2 plot. Note that in Fig. 4a, the left and right y-axis changes scale and therefore there is a vertical line on the far right separating all trees versus individual tree species. Data presented as means ± standard errors among sites. Significance is indicated by * ($p<0.05$), as determined by test statistic “H” using Kruskal-Wallis tests. Only the genus is given for trees difficult to identify to species as seedlings/saplings, and when nearby adults did not provide clear evidence of identity. Four-letter codes for genus-species IDs as follows: ACRU=*Acer rubrum* (red maple), ACSA=*Acer saccharum* (sugar maple), LITU=*Liriodendron tulipifera* (tuliptree), PRSE=*Prunus serotina* (black cherry), QUPA=*Quercus palustris* (pin oak), QURU=*Quercus rubra* (northern red oak). All trees here are native except for *Rhamnus* sp. (common buckthorn), which is exotic. Note generally greater densities and heights under low deer density, notably for red maple, tuliptree, and the two oaks

Table 2 Indicator species analysis for spring and fall flora, showing plant species significantly associated in gaps with high or low deer density in mesic or dry forest ($p<0.05$); "*" designates exotic species. (H) = herb, (CT) = canopy tree, (SCT) = sub-canopy tree, and (S) = shrub. Indicator species were determined by using a multi-level pattern analysis which evaluates associations between species relative cover and site characteristics (i.e., deer abundance and habitat type)

Deer density	Habitat type	Species	Corr. Coef.	p-value
Fall				
High	Dry			
(n = 12 gaps)		*Panicum* spp. (H)	0.420	0.0381
High	Wet			
(n = 8 gaps)		*Geum* spp. (H)	0.492	0.0046
		Lycopus uniflorus (H)	0.467	0.0201
		*Lysimachia nummularia** (H)	0.471	0.0076
		*Veronica officinalis** (H)	0.454	0.0082
High	Wet & Dry			
(n = 20 gaps)		*Parthenocissus quinquefolia* (H)	0.408	0.0424
Low	Dry			
(n = 7 gaps)		*Quercus velutina* (CT)	0.433	0.0141
		Quercus rubra (CT)	0.567	0.0008
		Oxydendrum arboreum (CT)	0.550	0.0026
		Liriodendron tulipifera (CT)	0.436	0.0148
		Tilia americana (CT)	0.365	0.0238
		Cornus florida (SCT)	0.521	0.0016
		Rubus allegheniensis (S)	0.529	0.0032
		Mitchella repens (H)	0.479	0.0266
		Rhynchospora spp. (H)	0.355	0.0034
		Carex glaucodea (H)	0.479	0.0245
		Solidago canadensis (H)	0.430	0.0353
		*Geum urbanum** (H)	0.428	0.0133
Low	Wet			
(n = 14 gaps)		*Quercus palustris* (CT)	0.587	0.0009
		Ulmus spp. (CT)	0.427	0.0385
		Lindera benzoin (S)	0.464	0.0230
		Thelypteris noveboracensis (H)	0.586	0.0014
Spring				
High	Wet			
(n = 8 gaps)		*Symplocarpus foetidus* (H)	0.448	0.0275
		*Alliaria petiolata** (H)	0.462	0.0147
Low	Dry			
(n = 7 gaps)		*Fragaria virginiana* (H)	0.486	0.0100
		Carex swanii (H)	0.546	0.0001
		Carex blanda (H)	0.470	0.0114
		Oxalis spp. (H)	0.528	0.0022
Low	Wet			
(n = 14 gaps)		*Arisaema triphyllum* (H)	0.437	0.0283

period. Overall, we only found support for our hypothesis that took deer abundance into account. For example, we found that abundance, richness, and diversity of native herbaceous and woody species were 37–65% higher at low deer density. At low deer density, the average height of tree species was more than double that at high deer density, with three native tree species *more than 10 times taller*. Essentially, at high deer density, tree species were unable to push through the deer filter. Moreover, at low deer density, we found that 11 native species were significantly associated with drier habitats (indicator species analysis), including five canopy tree species, one understory tree, and one understory shrub. Two additional native canopy tree species and one native shrub were associated with wet habitat at low deer density only. *No native canopy tree or shrub species was associated with wet or dry sites at high deer densities*. Moreover, native tree species abundance was always greater at low deer density except for browse-resistant black cherry (*Prunus serotina*), which was more abundant at high deer density. High deer densities often lead to understories dominated by black cherry (Horsley et al. 2003; Royo et al. 2019; Royo and Carson 2022). Collectively, these findings clearly demonstrate that keeping deer density much closer to their pre-European-settlement levels (McCabe and McCabe 1997) leads to gap-phase regeneration dominated by native tree and shrub species.

In contrast, at high deer density, exotic species were much more abundant in gaps, whereas native tree species were short in stature and in low abundance. In fact, woody and herbaceous exotic species were 6-fold more abundant at high deer density (Fig. 2a). Surprisingly, neither gap age nor habitat type (wet vs. dry) had a significant impact on plant diversity, richness, or abundance, except where exotic species were more abundant in older gaps with more deer (Fig. 3). This is a potential threat to biodiversity because it indicates that older gaps experience more exotic species growth during the first 12 years of gap-phase regeneration at high deer density, and high deer density is now the norm across vast regions (Long et al. 2007; Pendergast et al. 2016; Adams and Villarreal 2020). Interestingly, indicator species analysis revealed that an exotic shrub (buckthorn) was significantly associated with low deer density, suggesting that deer browsing may reduce the abundance of this species but this remains speculative. Indeed, Gorchov et al. (2021) documented several cases where deer browsing reduced the abundance of exotic species, particularly vines and shrubs.

We expected that exotic richness and diversity would be higher outside of Camp Garfield because exotic propagule pressure increases substantially with human settlement, extensive public roadways, and hiking trails (Stohlgren et al. 2006; Iannone et al. 2015; Von Der Lippe and Kowarik 2007; Liedtke et al. 2020). Indeed, our gaps outside of Camp Garfield were accessible to the public and were closer to urban and urban-fringe habitats, though they were still in large tracts of continuous forest. It is important to note that exotic richness and diversity did not differ in areas of low versus high deer density (Fig. 2b and c). However, as gaps aged, exotic *cover* increased, suggesting that competition for light and soil resources between native and exotics may have intensified in older gaps. The finding that the richness and diversity of exotics did not differ in gaps within high versus low deer density was surprising. This may relate to the documented paucity of exotic species in the regional species pool that are both highly shade-tolerant and can also persist in closed canopy mature forests prior to gap formation (Martin et al. 2009; Eschtruth and Battles 2011).

On the relevance of our findings to oak regeneration

Across much of the eastern deciduous forest, oaks have poor regeneration due to a combination of overbrowsing, fire suppression, small canopy gap size, and dense recalcitrant understories layers (Rooney and Waller 2003; Royo and Carson 2006; Amatangelo et al. 2011; Nuttle et al. 2013; Thomas-Van Gundy et al. 2014). Nonetheless, our findings demonstrate that where deer were at low density, gaps had a diverse, dense, and robust native sapling layer, which included three species of oak. These saplings reached well into the subcanopy (Fig. 4a and b). Whether understory fires in these fairly mesic forests would further enhance oak regeneration is unknown but fires were likely far less common historically in beech-maple forests relative to other forest types formerly dominated by oaks (Vankat 1979). Indeed, Iverson et al. (2008) found that canopy gap creation coupled with fire was effective in promoting oak regeneration in dry but not mesic sites in southeastern Ohio, USA in forest outside of the Beech-Maple Association.

On the importance of military installments as refugia from overbrowsing

The forests we sampled occurred on lands that were abandoned from farming in 1940. Natural forest regeneration at Camp Garfield and within natural areas outside Camp Garfield occurred at a time when deer densities were beginning to rise dramatically in the eastern US (Leopold et al. 1947; Côté et al. 2004; Fig. 1 references). Thus, Camp Garfield represents an 88 km^2 area that has undergone secondary succession with atypically low deer densities. Based on current trends outside Camp Garfield, the prognosis for the regeneration of many native plant species is poor, but the prognosis for exotic plants is more favorable (Eschtruth and Battles 2009; Knight et al. 2009; Kalisz et al. 2014; Averill et al. 2018). Consequently, military bases and posts with extensive forest cover and aggressive deer management may typically provide important deer refugia for numerous, browse-sensitive, native plant species over large areas. Indeed, the top five largest military bases in the continental U.S. total 5,001 km^2 (mybaseguide.com). The prospect of large-scale refugia for browse-sensitive native plants from deer overbrowsing should be explored for military installments around the U.S. whenever these posts are located in areas of high ungulate density.

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Declarations

Competing interests The authors declare no competing interests.

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