



# Resilience and alternative successional trajectories in temperate forests exposed to two large herbivores

Edward K. Faison<sup>a,\*</sup>, Stephen DeStefano<sup>b,1</sup>, Kiana Koenen<sup>c,1</sup>

<sup>a</sup> Highstead Foundation, 127 Lonetown Road, Redding, CT 06896, USA

<sup>b</sup> U. S. Geological Survey, Massachusetts Cooperative Fish and Wildlife Research Unit, University of Massachusetts, Amherst, MA, USA

<sup>c</sup> Department of Conservation and Recreation-Division of Water Supply Protection, 485 Ware Road, Belchertown, MA 01007, USA

## ARTICLE INFO

### Keywords:

Alternative successional trajectory  
Browsing  
Forest structure  
Moose  
Resilience  
White-tailed deer

## ABSTRACT

Ungulate browsing is a key disturbance process influencing forest structure and composition, with the potential to alter forest resilience following canopy disturbance. We examined the effects of 15 years of white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces americana*) browsing in regenerating temperate forests of the northeastern U.S. We tested the alternative hypotheses that woody vegetation is (1) *resilient* to browsing, with structure and composition similar after stems have grown above the browser trap or (2) *altered* by browsing, resulting in long-term legacy effects. Three browser treatments—ungulate exclusion, deer, and deer + moose—were established in seven clear-cut stands. Basal area and species diversity did not differ significantly among treatments after 15 years, indicating resilience, whereas the abundance of two tree species was altered: pin cherry (*Prunus pensylvanica*) was lower by 3-fold in deer + moose plots, while white pine (*Pinus strobus*) was greater by over 5-fold. Forb cover was half as abundant in deer + moose plots compared to ungulate exclusion, while forb richness remained unaffected. Our results suggest that ungulate browsing during stand initiation can alter successional trajectories while still being compatible with long-term forest resilience; however, there are potential trade-offs between woody plant resilience and the vigor of the herbaceous layer when large herbivores are present. With relatively small long-term effects on structure and diversity and by accelerating succession towards longer-lived tree species, deer + moose browsing in northern temperate forests may be less of a management concern than is generally assumed.

## 1. Introduction

Mammalian browsing is an important natural disturbance process and a powerful driver of terrestrial plant populations through space and time (Bakker et al., 2016; Hanberry and Faison, 2023). In forests following canopy disturbance, large herbivores can delay regrowth and temporarily maintain vegetation in a woodland or shrubland state (Bergquist et al., 1999; Faison et al., 2016a; MacSween et al., 2019). Delayed forest regrowth lengthens recovery times, which directly affects forest resilience (Forzieri et al., 2022). Resilience is the ability of forests to withstand and recover from environmental perturbations, which is particularly important amidst increasing frequency and intensity of disturbances related to climate change, as well as increasing management in response to these novel disturbances (D'Amato et al., 2011; Forzieri et al., 2022).

An important question with respect to ungulate browsing, canopy disturbance, and forest resilience is to what extent woody vegetation that passes through the browser trap (i.e., the height zone in which browsers can reach the vegetation) is altered over longer time frames (Gill, 2006). Long-term legacy effects of white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces americana*) browsing have been documented in temperate and boreal forests (McInnes et al., 1992; Reed et al., 2022), including reductions in diversity and structural features and increases in horizontal heterogeneity (i.e., gaps) and canopy complexity in areas exposed to higher levels of browsing. In general, large herbivores tend to increase the spatial heterogeneity of vegetation cover and biomass, while at the same time reducing the mean amounts of both (Trepel et al., 2024).

Ungulate browsing can also result in sustained, compositional shifts – aka alternative successional trajectories (AST) – during forest

\* Corresponding author.

E-mail addresses: [efaison@highstead.net](mailto:efaison@highstead.net) (E.K. Faison), [sdestef@eco.umass.edu](mailto:sdestef@eco.umass.edu) (S. DeStefano), [kiana.ki@gmail.com](mailto:kiana.ki@gmail.com) (K. Koenen).

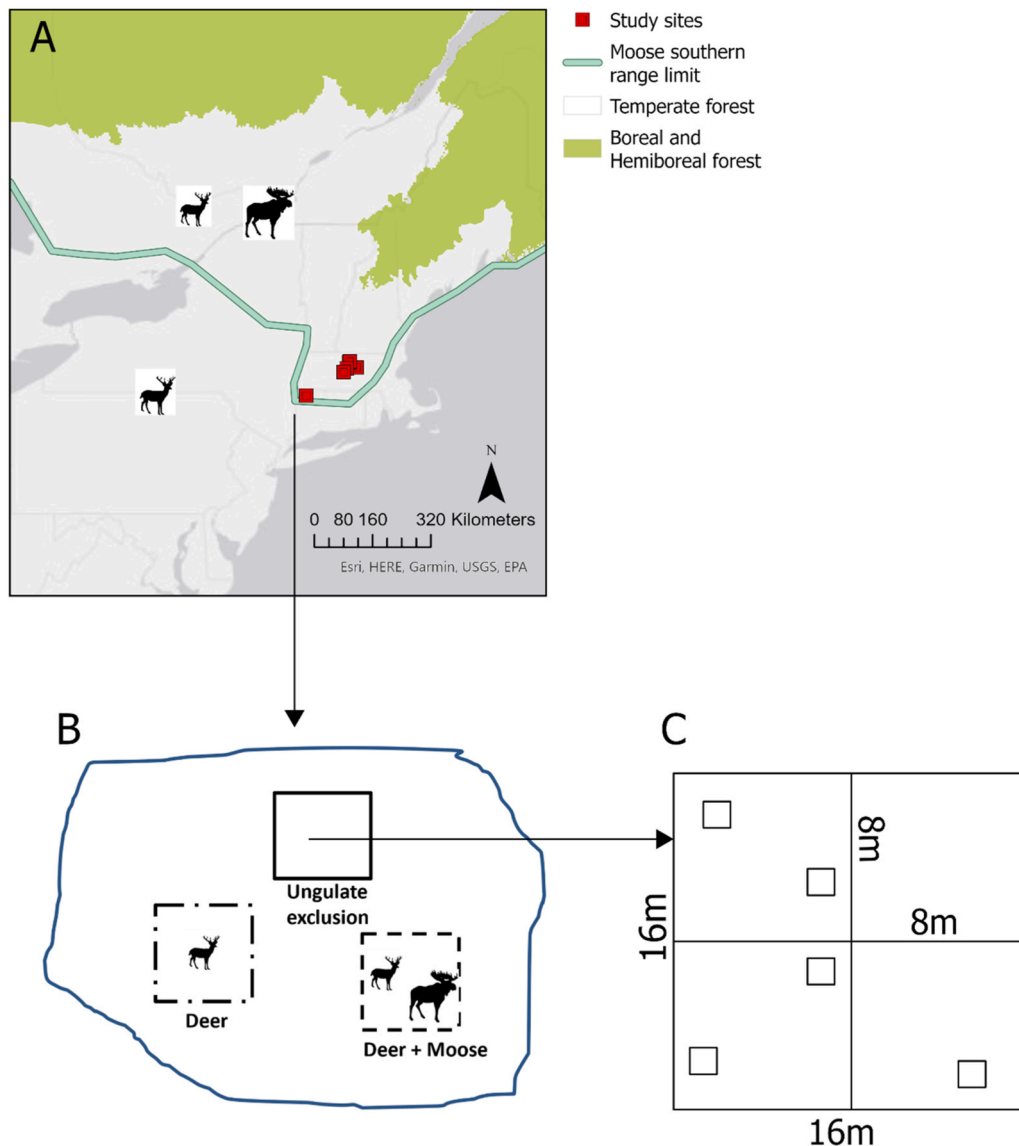
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succession. Selective herbivory can either accelerate, decelerate, or otherwise divert succession, leading to an alternative species composition later in forest development (Pastor et al., 2006; Hidding et al., 2013). However, not all browser impacts result in long-term legacy effects. Composition and structure can also exhibit resilience after woody plants grow above the reach of herbivores during succession (Thompson and Curran, 1993; Hidding et al., 2013; Reed et al., 2022). Because most data on how ungulate browsing shapes forest development are from studies less than 10 years in duration, our understanding of the long-term resilience or alternative successional trajectories of forests exposed to browsers remains limited.

The extent to which resilience occurs in the woody plant layer has implications for the forest floor layer. Reduced height and density of woody plant layers by herbivores following disturbance can result in an increase in diversity and abundance of forest herbs (McInnes et al., 1992; Rojo et al., 2010). However, if woody plant layers recover after growing above the browser trap, herbaceous layers may no longer benefit from reduced competition and be more susceptible to herbivory. Moreover, because herbaceous plants never grow above the browser trap, they may be particularly vulnerable to long-term declines in cover

from sustained herbivory under an intact forest canopy (e.g., Rooney, 2009; Goetsch et al., 2011; Nuttle et al., 2014). At the same time, herbaceous layers may be more apt to display spatial heterogeneity from the effects of sustained herbivory and trampling, which creates more bare ground (Trepel et al., 2024).

Here, we examine the long-term (14–16 years) consequences of browsing by white-tailed deer and moose on succession of oak-pine forests in eastern North America that were formerly clearcut. Specifically, we examine the alternative hypotheses that woody vegetation after passing through the browser trap is (1) *resilient*, with structure and composition similar to areas with reduced or no browsers, or (2) *altered*, with long-term legacy effects including AST and differences in spatial heterogeneity and structure among treatments. We further examine the abundance, diversity, and spatial heterogeneity of the herbaceous layer in the context of resilient or altered woody plant layers. Lastly, we examine how different numbers of browser species affect vegetation structure and composition.



**Fig. 1.** (A) Location of seven study sites in northeastern North America. Extent of boreal and hemiboreal forest from Brandt (2009). Moose southern range limit from (Esri, 2025). (B) Experimental design with three treatment levels of ungulate browsers in patch cut harvests. (C) Sampling plot dimensions for woody stems (16 x 16 m, divided into four, 8x8m quadrants) and herbaceous vegetation (five, 1x1m quadrants).

## 2. Materials and methods

### 2.1. Study site and design

Our study area included seven blocks located in Central New England, USA at the southern range limit for moose in eastern North America (Fig. 1 A). The study area represents a relatively narrow band of temperate mixed deciduous forest where moose and white-tailed deer ranges overlap south of the boreal and hemiboreal forest zone (Boer, 1997; Brandt, 2009; Wattles and DeStefano, 2011). We established each block between 2007 and 2010 in mixed conifer-deciduous stands that had been clear-cut within the past 3–6 months. Blocks were at least 700 m apart. Four sites were former conifer plantations (larch [*Larix* spp.], red pine [*Pinus resinosa*] or spruce [*Picea* spp.]) with mixed native hardwoods, and three were naturally grown red oak (*Quercus rubra*)–white pine (*Pinus strobus*)-dominated stands with red maple (*Acer rubrum*) and black birch (*Betula lenta*) in the understory (Table 1). The herbaceous layer is dominated by Canada mayflower (*Maianthemum canadense*), with lesser amounts of hay-scented fern (*Dennstaedtia punctilobula*), wild sarsaparilla (*Aralia nudicaulis*), and starflower (*Lysimachia borealis*). Additionally, there are locally abundant patches of blue-bead lily (*Clintonia borealis*), Pennsylvania sedge (*Carex pennsylvanica*), evergreen wood fern (*Dryopteris intermedia*), and fringed bindweed (*Fallopia ciliinoides*). Each block included three treatment levels of large herbivores – ungulate exclusion (full enclosure), deer-only (partial enclosure), and deer + moose (control; Fig. 1B). Enclosure fences varied slightly in size, with four blocks having fences 20 × 20 m in size and three blocks with fences 23 × 23 m in size. Full and partial enclosure fences were always the same size within an individual block. The 2.5-m-tall enclosures were made of high-tension wire game fence with 15-cm grid mesh, which enabled small mammals including lagomorphs and rodents to access the plots. Full enclosures were fenced to the ground; partial enclosures had a 60-cm opening between the bottom of the fence and the ground surface that excluded moose but allowed access to deer and all other wildlife; and control plots were unfenced and open to both browsers (Faison et al., 2016a,b). Treatment plots were located at least 10 m apart within a block. At the start of the experiment, no residual trees > 1.4 m in height were present in the three treatments. Within the first year after the enclosures were built, we sampled

**Table 1**  
Characteristics of study site blocks in patch cut harvests.

Site	Location	Previous overstory composition	Opening size (ha)	Year stand cut and enclosures built
Dana	Quabbin Reservation Forest, MA	<i>Quercus</i> , <i>Acer rubrum</i> , <i>Betula lenta</i>	0.4	2007
Fisher	Harvard Forest, MA	<i>Pinus resinosa</i> , <i>P. strobus</i> , <i>Acer rubrum</i> , <i>Betula lenta</i>	1.4	2008
GMF	Great Mountain Forest, CT	<i>Pinus strobus</i> , <i>Quercus rubra</i> , <i>Betula lenta</i> , <i>Acer rubrum</i>	1.0	2010
Locust	Harvard Forest, MA	<i>Pinus resinosa</i> , <i>Acer rubrum</i> , <i>Quercus rubra</i>	3.3	2008
Prescott	Quabbin Reservation Forest, MA	<i>Quercus</i> , <i>Acer rubrum</i> , <i>Betula lenta</i>	0.3	2007
Prospect	Harvard Forest, MA	<i>Picea</i> , <i>Prunus serotina</i> , <i>Acer rubrum</i>	6.2	2008
Ware	Ware River Reservation Forest, MA	<i>Pinus</i> , <i>Larix</i> , hardwoods	2.1	2007

regeneration ( $\geq 30$  cm in height) in 25, 4 m<sup>2</sup> subplots in each treatment plot (spring 2008–2009 at the Massachusetts sites and spring 2010 at the GMF site). Stem densities already showed a browser effect in the first year of the experiment, with densities greater in ungulate exclusion plots than in deer or deer + moose plots (Table 2). No significant differences in individual species abundance were detected in this initial sampling, although white pine was notably low in abundance in deer + moose plots (Table 2).

Timber harvesting is the dominant disturbance process in the Northeastern US, with exotic forest insects, and pathogens and meteorological events (ice and windstorms) also prevalent and increasing (Cohen et al., 2016; Thompson et al., 2017). Deer densities – based on data collected from check stations, hunter surveys, and pellet counts – are estimated to be 4–7 km<sup>-2</sup> (Massachusetts Division of Fisheries and Wildlife, 2025; Great Mountain Forest pers. comm.). Densities appear to have increased marginally in Massachusetts from 2 to 7 deer km<sup>-2</sup> at the start of the experiment to 4–7 deer today (McDonald et al., 2007). In northwestern CT, harvested deer numbers declined by about 35 % from the start of the experiment (2010–2012) and have stabilized over the past 10 years (2013–2023; Connecticut Department of Energy and Environmental Protection, 2014; Connecticut Department of Energy and Environmental Protection, 2023). Moose densities are estimated to be 0.3–0.8 km<sup>-2</sup> (Koenen et al., 2016; Great Mountain Forest pers. comm.). Independent abundance indices (e.g., sighting data, road mortalities) indicate that moose reached peak abundance in the mid-2000s. Numbers of moose declined after the mid-2000s and currently are stable or declining slightly during the early 2020 s (USGS Massachusetts Cooperative Research Unit, unpublished data; Great Mountain Forest pers. comm.).

#### 2.1.1. Vegetation sampling

In 2024, we established a 16 × 16 m sampling area in the center of each treatment plot with four, 8 × 8 m quadrants (Fig. 1C). In each quadrant, we recorded species and DBH of all woody stems  $\geq 5$  cm diameter. This diameter threshold reflects the size at which tree stems have largely escaped the browser trap (i.e., when moose can no longer pull down and break tree stems to browse the leading shoots; Telfer and Cairns, 1978). For herbaceous plants, we sampled 5, 1 m<sup>2</sup> subplots randomly selected from a systematic grid of 25 subplot locations that were established in each treatment plot at the start of the experiment (Fig. 1C). At each 1 × 1 m subplot, we recorded all vascular (woody and herbaceous) plants < 1.37 m in height and estimated percent cover abundance for each species in one of 7 cover classes (1 = <1 %, 2 = 1–5 %, 3 = 6–15 %, 4 = 16–25 %, 5 = 26–50 %, 6 = 51–75 %, 7 = 76–100 %). Grasses and sedges were generally identified to genus or

**Table 2**

Density and composition of tree regeneration ( $\geq 30$  cm in hgt.) in three ungulate browser treatments in 2008–2010. Data reflect conditions < 1 year after fences were established at each site. N = 7 blocks. Values are means with standard errors in parentheses.

Variable	Ungulate Exclusion	Deer	Deer + Moose	Likelihood Ratio Test
Tree stem density $\geq 30$ cm in hgt. (no./ha)	4986 (1050)	2529 (692)	2629 (469)	$X^2 = 6.8$ ; df = 2; P = 0.03
<i>Acer rubrum</i> (% abundance)	58.5 (8.2)	41.9 (10.9)	51.7 (8.4)	$X^2 = 3.3$ ; df = 2; P = 0.19
<i>Betula</i> spp. (% abundance)	6.7 (4.9)	7.5 (3.7)	4.0 (2.0)	$X^2 = 0.68$ ; df = 2; P = 0.71
<i>Pinus strobus</i> (% abundance)	9.6 (4.3)	9.5 (7.1)	1.1(1.1)	$X^2 = 4.28$ ; df = 2; P = 0.12
<i>Prunus</i> spp. (% abundance)	12.6 (6.2)	14.9 (6.6)	17.1 (7.2)	$X^2 = 0.43$ ; df = 2; P = 0.81
<i>Quercus</i> spp. (% abundance)	6.3 (2.8)	16.4 (11.9)	14.5 (7.5)	$X^2 = 2.71$ ; df = 2; P = 0.26

family rather than to species.

### 2.1.2. Data analysis

We converted woody stem densities in each plot to no./ha and stem basal area to m<sup>2</sup>/ha. For individual woody species abundance, we used relative basal area. For woody species diversity we used the PIE index (probability of an interspecific encounter) without correction factor – aka the Gini coefficient (Gotelli and Ellison, 2013). The PIE index, unlike species richness or the Shannon diversity index, is not sensitive to sample size (Gotelli and Ellison, 2013). For structural complexity metrics, we used tree diameter size class diversity and the percentage of basal area in larger diameter (>12.9 cm DBH) trees (Keeton, 2006; D'Amato et al., 2011). Tree diameter size class diversity was calculated as the relative basal area of 2.5 cm DBH classes (5.1–7.6...,20.7–23.2; >23.2) using the Shannon Diversity Index (D'Amato et al., 2011; Faison et al., 2023). For spatial heterogeneity of woody stems, we calculated the standard deviation (SD) of basal area among the four 8×8 m quadrants in each plot. Greater SD values would reflect increased heterogeneity of stem growth within each plot.

For herbaceous plant data, we used percent cover as a measure of vegetation abundance. We first converted cover classes to percent cover midpoints, and then calculated the mean percent cover for species and growth form groups (i.e., ferns, forbs, graminoids) across the 5, 1 × 1 m subplots in each plot. We examined species richness for forest forbs at the subplot scale (mean number of species in 5, 1 m<sup>2</sup> quadrats). Although these measurements are technically species density (Gotelli and Ellison, 2013), we hereafter refer to species density as “species richness” for the sake of clarity. We examined spatial heterogeneity of total herbaceous plant (forbs, fern, graminoids) cover as the standard deviation of total herbaceous cover among the five quadrats in each plot.

We used generalized linear mixed-effects models (package glmmTMB; the R Foundation for Statistical Computing, 2024; R version 4.4.1) with ungulate treatment as fixed effect and block as random effect to analyze the effect of treatment on woody vegetation structure and composition and herbaceous layer abundance and forb diversity. We used either a normal, log normal or Tweedie with log link error distribution for all response variables after examining the residuals of models to determine the best fit. The Tweedie distribution is appropriate for zero-inflated data and mixed data types (Foster and Bravington, 2013), which characterized a number of the variables in our dataset. We then performed likelihood ratio tests to determine significant effects of treatment. For variables in which there was a significant effect of treatment, we performed pairwise comparisons between treatment pairs using Tukey's multiple comparisons with the package “emmeans.”

## 3. Results

### 3.1. Woody plant structure and diversity

Stem density and basal area did not differ significantly among treatments (Table 3), although both metrics were marginally higher in ungulate exclusion plots (P = 0.06, P = 0.095 respectively). Tree species diversity as identified by the PIE index (without correction factor) did not vary by treatment (P = 0.69) nor did diameter size class diversity (P = 0.41; Table 3). Percentage of basal area in larger diameter size classes (stems >12.9 cm dia.) was marginally higher in deer + moose plots (P = 0.08), while spatial heterogeneity of biomass (basal area) did not vary by treatment (P = 0.12; Table 3).

#### 3.1.1. Tree species composition

Pin cherry (*Prunus pensylvanica*) relative basal area varied by treatment (LRT  $X^2 = 9.15$ ; df = 2; P = 0.01; Fig. 2) and was over three times greater in ungulate exclusion (P = 0.01) and deer plots (P = 0.006) than in deer + moose plots. There was no difference in pin cherry abundance between ungulate exclusion and deer plots. White pine relative basal area also varied by treatment (LRT  $X^2 = 8.7$ ; df = 2; P = 0.01) and was

**Table 3**

Structural and diversity attributes of woody and herbaceous vegetation in three ungulate browser treatments. N = 7 blocks. Values are means with standard errors in parentheses.

Variable	Ungulate Exclusion	Deer	Deer + Moose	Likelihood Ratio Test
<b>Woody vegetation (stems ≥5 cm DBH)</b>				
Stem density (no./ha)	3615 (116.8)	3571 (138.4)	3019 (287.0)	$X^2 = 5.54$ ; df = 2; P = 0.06
Basal area (m <sup>2</sup> /ha)	18.4 (1.6)	17.1 (1.1)	15.2 (1.9)	$X^2 = 4.7$ ; df = 2; P = 0.095
Tree species diversity (PIE index)	0.62 (0.08)	0.56 (0.06)	0.55 (0.08)	$X^2 = 0.75$ ; df = 2; P = 0.69
Diameter size class diversity (Shannon Diversity Index)	1.16 (0.07)	1.08 (0.07)	1.21 (0.11)	$X^2 = 1.76$ ; df = 2; P = 0.41
Percentage of basal area in larger diameter trees (>12.9 cm DBH)	9.3 (0.04)	4.3 (0.01)	15.6 (0.05)	$X^2 = 4.97$ ; df = 2; P = 0.083
Spatial heterogeneity of biomass (SD of basal area in four, 8×8 m quadrants)	1.27 (0.2)	0.87 (0.08)	0.91 (0.18)	$X^2 = 4.25$ ; df = 2; P = 0.12
<b>Herbaceous vegetation</b>				
Total herbaceous cover (%)	37.5 (7.5)	35.5 (8.8)	30.0 (7.9)	$X^2 = 2.12$ ; df = 2; P = 0.345
Spatial heterogeneity of herbaceous cover (SD of 5, 1 m <sup>2</sup> quadrants)	23.9 (4.6)	15.2 (3.9)	20.0 (5.5)	$X^2 = 3.54$ ; df = 2; P = 0.17
Forb richness (no. species/m <sup>2</sup> )	1.94 (0.26)	2.37 (0.29)	2.14 (0.27)	$X^2 = 3.67$ ; df = 2; P = 0.16

over five times greater in deer + moose plots than in ungulate exclusion (P = 0.006) and almost five times greater in deer + moose plots than in deer plots (P = 0.01; Figs. 2 and 3). There was no difference in white pine abundance between ungulate exclusion and deer plots. Black birch (*Betula lenta*; LRT  $X^2 = 0.43$ ; df = 2; P = 0.81), oak (*Quercus* spp.; LRT  $X^2 = 2.9$ ; df = 2; P = 0.23), red maple (LRT  $X^2 = 2.17$ ; df = 2; P = 0.34), paper birch (*Betula papyrifera*; LRT  $X^2 = 5.06$ ; df = 2; P = 0.08) and black cherry (*Prunus serotina*; LRT  $X^2 = 2.82$ ; df = 2; P = 0.24) abundance did not vary by treatment (Fig. 2). Pin cherry was the first ranked species in ungulate exclusion plots, second ranked species in deer plots, and the fourth ranked species in deer + moose plots. White pine was the sixth ranked species in ungulate exclusion, fifth ranked species in deer plots and the third ranked species in deer + moose plots (Fig. 2).

#### 3.1.2. Herbaceous layer

Forb abundance differed significantly by treatment (LRT  $X^2 = 11.56$ ; df = 2; P = 0.003), with abundance greater in both ungulate exclusion (P = 0.002) and deer plots (P = 0.047) than in deer + moose plots (Fig. 4). Other treatment pairs did not differ significantly (Ungulate Exclusion:Deer – P = 0.28). Graminoid (LRT  $X^2 = 2.68$ ; df = 2; P = 0.26) and fern (LRT  $X^2 = 0.2555$ ; df = 2; P = 0.88) abundance did not differ by treatment (Fig. 4). Total herbaceous cover (combined

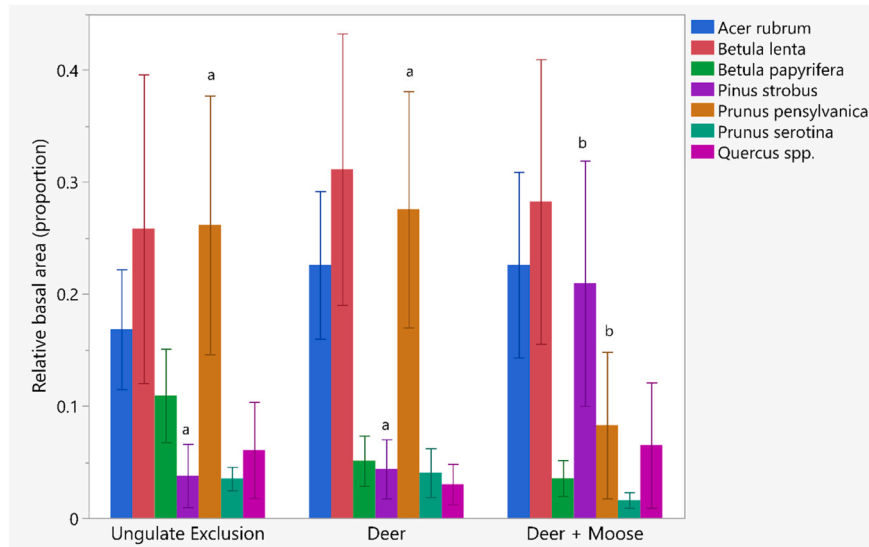


Fig. 2. Relative basal area of seven most abundant tree species by ungulate browser treatment. Treatment means with different letters differed significantly. Taxa without letters did not differ among treatments.  $N = 7$ . Bars represent mean  $\pm$  SE.



Fig. 3. The first author in front of the (A) deer only plot (partial enclosure) and (B) deer + moose plot (unfenced) at the GMF site in Northwestern CT, USA. Note the dominant hardwoods (84 % of basal area above 5 cm dia.) including black birch, red maple, and pin cherry growing behind (inside) the fence posts in picture A compared to the abundant white pine (70 % of basal area  $\geq$  5 cm dia.) growing in picture B. Photos by Timothy Brown.

graminoids, ferns, forbs) did not differ among treatments ( $P = 0.345$ ; Table 3). Forb richness did not differ among treatments ( $P = 0.16$ ) nor did the spatial heterogeneity of herbaceous cover ( $P = 0.17$ ; Table 3).

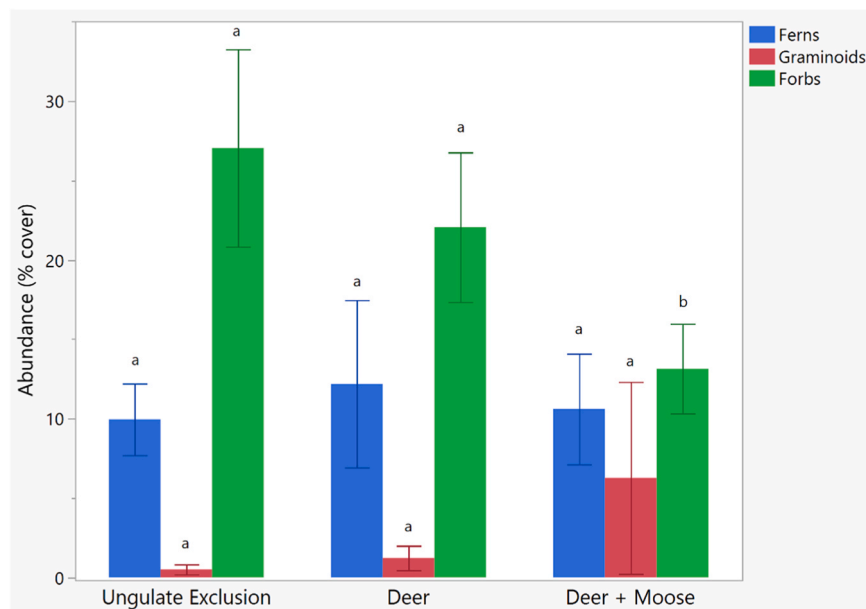
#### 4. Discussion

Fifteen years of succession in mixed temperate forests exposed to three levels of ungulate browsers provided support for both the *resilient* and *altered* hypotheses, depending on the attributes in question. In support of the resilient hypothesis, ungulate browsing had little effect on the diversity of trees able to grow above the browser trap ( $\geq 5$  cm dia.), while stem density and basal area trended higher (though not significantly) with increasing protection from browsers. Additionally, we detected no significant effects of browsing on spatial heterogeneity or structural complexity of trees, although there was a non-significant trend toward an increasing proportion of basal area in larger diameter size classes in deer + moose plots. Overall, these results suggest relatively small long-term impacts on structural and diversity characteristics by large herbivores in these northern temperate forest stands.

Our results on the long-term resilience of woody plant structure and diversity differed to some extent from those reported in temperate deciduous forests of Pennsylvania, USA where moose are absent. There, stands experimentally exposed to 25 deer  $\text{km}^{-2}$  (1613  $\text{kg km}^{-2}$ ) for 10 years supported lower basal area, tree density and tree species diversity – as well as greater structural complexity and spatial heterogeneity – than stands exposed to 4 deer  $\text{km}^{-2}$  (258  $\text{kg km}^{-2}$ ), three decades after the experiment ended (Reed et al., 2022). However, our results were more similar to the comparison of stands formerly exposed to 15 deer  $\text{km}^{-2}$  (968  $\text{kg km}^{-2}$ ) with those formerly exposed to 4 deer  $\text{km}^{-2}$ . Vegetation exposed to these two deer densities did not differ in structural and diversity attributes, with the exception of the higher deer density areas supporting greater canopy complexity (Reed et al., 2022).

Our results also differed from those reported in the boreal forests of Isle Royale, Michigan. McInnes et al. (1992) reported long-term reductions in tree biomass in areas browsed by moose, 40 years following disturbance by fire. The persistent effect by moose on tree biomass in this study likely reflects the roughly 2-fold greater ungulate densities on Isle Royale (1237  $\text{kg moose}/\text{km}^2$ ) compared to our study area (580  $\text{kg moose} + \text{deer}/\text{km}^2$ ; McInnes et al., 1992; Jones et al., 2009; Koenen et al., 2016) combined with slower growth rates of trees in the boreal forest compared to the temperate zone (Cook-Patton et al., 2020). Slower growth rates maintain woody vegetation within the browser trap for a longer period of time.

In support of the altered hypothesis, we observed ASTs related to the abundance of pin cherry and white pine. The relative basal area of pin cherry growing above the browser trap ( $\geq 5$  cm dia.) was significantly



**Fig. 4.** Herbaceous plant abundance by ungulate browser treatment. Treatment means with the same letter do not differ significantly.  $N = 7$ . Bars represent mean  $\pm$  SE.

reduced in plots browsed by deer + moose compared to ungulate exclusion and deer plots. Pin cherry, a shade-intolerant and fast-growing species, appears to be particularly susceptible to the interactive effects of browsing and shading (e.g., Gill, 2006). When shade-intolerant species are reduced in height by browsing, they quickly succumb to the shade of other neighboring tree species, whereas more shade-tolerant tree species such as red maple, black birch, and oaks are more resilient to being reduced in height and enduring shade (Pastor et al., 2006). For instance, oak saplings above 2 m in height were greatly reduced in number in 2014 by deer + moose (Faison et al., 2016b), but in 2024, oak basal area  $\geq 5$  cm dia. was virtually identical in deer + moose and ungulate exclusion plots. Thus, although herbivores can greatly reduce the density of oak saplings in the short term (Gill, 2006, Nuttle et al., 2013), oaks may be resilient to moderate levels of herbivory over longer periods of time.

As pin cherry declined sharply in deer + moose plots, white pine diverged in the opposite direction. Relative basal area of this unpalatable and light demanding conifer was about five times greater in deer + moose plots compared to ungulate exclusion and deer plots. In fact, white pines growing in deer + moose plots achieved the largest diameter of any tree species in our study plots in 2024. In ungulate exclusion and deer plots, white pine saplings were frequently overtopped by deciduous species, causing the pines to grow more slowly or to die.

This AST away from pin cherry and towards white pine in deer + moose plots suggests an acceleration of succession through the stand initiation phase – which is frequently dominated by pin cherry in northeastern forests for 25–30 years following canopy disturbance (Marks, 1974; Oliver and Larson, 1996; Anderson, 2004). Variation in number of browser species (and browsing intensity) had a large effect on these successional trajectories, as deer browsing alone had little effect on altering white pine and pin cherry abundance. A compositional shift from early successional deciduous species towards a later successional conifer shows parallels to the boreal forest where selective and heavy browsing by moose and deer on early successional paper birch and aspen accelerated succession toward late successional spruce (McInnes et al., 1992; Thompson et al., 1992; Hidding et al., 2013).

#### 4.1. Herbaceous layer

In the herbaceous layer, forb cover was more than twice as abundant

in ungulate exclusion plots compared to deer + moose plots, and spatial heterogeneity was not significantly affected. Deer alone did not significantly reduce forb abundance compared to ungulate exclusion, suggesting that additional trampling and grazing on herbs by moose (and possibly greater deer activity in deer + moose plots) may have been an important contributing factor in reducing forb cover (Kolstad et al., 2018). Forb species richness did not differ among treatments, which was consistent with the general trend of large herbivores reducing vegetation cover but having little effect on alpha diversity (Trepel et al., 2024).

Forb diversity and abundance can be indirectly promoted by browsers when woody plant layers are reduced in height and/or density by browsers (Royo et al., 2010; Webster, 2016). However, when this competitive advantage to the herb layer is missing, through resilient woody plant growth, the direct effects of herbivory and trampling may shift to negative impacts on forb cover and neutral effects on diversity (Royo et al., 2010; Kolstad et al., 2018).

Forb cover under an intact canopy can decline from herbivore densities as low as 4 deer  $\text{km}^2$  (Alverson et al., 1988), which is equivalent to estimated deer densities for pre-European settlement forests (4–6 deer/ $\text{km}^2$ ; Callan et al., 2013). Additionally, differences in forb cover from herbivory can occur in forested landscapes that include top predators such as wolves (*Canis lupus*), as a result of variation in predator densities across the landscape (Callan et al., 2013). Thus, herbivore-mediated declines (and increases) in forb abundance are likely to be long-standing and naturally occurring dynamics in eastern deciduous forests.

## 5. Conclusions and management implications

Our 15-year study revealed that the structure and particularly the diversity of northern temperate forests are generally resilient to the browser trap imposed by moderate densities of two large herbivores during stand initiation. However, the resilience of the tree layer combined with reduced cover in the forb layer suggests an inverse relationship between woody plant resilience and herbaceous cover when large herbivores are present. Deer and moose may continue to reduce forb cover under an intact canopy until the next canopy-opening disturbance interacts with browsers to potentially rejuvenate the herb layer (e.g., Royo et al., 2010).

Alternative successional trajectories in the woody plant layer

imposed by browsing resulted in an acceleration of succession towards a species composition (white pine, black birch, red maple) with potentially greater ecosystem services (timber value and perhaps larger diameter trees) compared to ungulate exclusion and deer plots where pin cherry may continue to dominate along with black birch and lesser amounts of red maple and paper birch for the next 10–12 years (Marks, 1974; Anderson, 2004). Stem deformities and crown irregularities (e.g., broken or multi-apical forms, dead tops and eventually tree cavities) associated with ungulate browsing could offset timber value to some extent (Andreozzi et al., 2014; Olmsted et al., 2021; Cacciatori et al., 2025); however, these changes in tree physiognomy ultimately enhance stand complexity and wildlife habitat (DeGraaf et al., 2006; Donato et al., 2012). Ungulate browsing during stand initiation may be less of a management concern with respect to protecting forest resilience, diversity, and ecosystem services than is generally assumed.

### CRedit authorship contribution statement

**DeStefano Stephen:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Faison Edward:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Koenen Kiana:** Writing – review & editing, Resources, Project administration, Investigation.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Acknowledgments

We thank Dan Clark for providing access to and maintaining the Ware, Dana, and Prescott enclosures in the Quabbin and Ware River Watershed Forests. We also thank the Harvard Forest Woods Crew for maintaining the Fisher, Locust, and Prescott enclosures. Lastly, we are grateful to Michael Zarfos and Matt Gallagher for continued access to the Great Mountain Forest site. Kelly Sempreb provided helpful field assistance and data entry. Funding was provided by the Highstead Foundation, the Massachusetts Department of Conservation and Recreation, and by HFR NSF Grant # DEB 1832210, DEB 0620443, and DEB 1237491. Additional financial and logistical support was provided by the Massachusetts Division of Fisheries and Wildlife.

### Data availability

The data will be stored and available in the Harvard Forest data archives (<https://harvardforest.fas.harvard.edu/data-archives>) by May 2026.

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