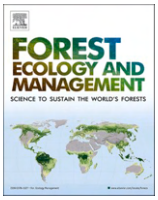
Forest Ecology and Management 593 (2025) 122906

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Effects of browsing by white-tailed deer on tree regeneration vary by ontogeny and palatability in forests of the northeastern USA

Lucas B. Harris [a,*], Melissa A. Pastore [b], Anthony W. D'Amato [a]

[a] Rubenstein School of Environment and Natural Resources, University of Vermont, 81 Carrigan Drive, Burlington, VT 05405, USA
[b] USDA Forest Service, Northern Research Station, Forest Inventory & Analysis, 1992 Folwell Ave., St. Paul, MN 55108, USA

ARTICLE INFO

Keywords:
Tree regeneration
Herbivory
White-tailed deer
Forest inventory
Northern temperate and boreal forest

ABSTRACT

Tree regeneration in northern temperate and southern boreal forests is threatened by multiple factors, including over-browsing by ungulates such as white-tailed deer (*Odocoileus virginiana*). However, characterizing the effects of deer browse on tree regeneration at regional scales has been challenging due to (a) the lack of reliable indicators of browsing intensity and (b) the fact that browsing impacts are likely to vary by seedling size yet coarse metrics are often used to capture this seedling attribute. To address these challenges, we modeled effects of white-tailed deer browse and other biotic and abiotic factors on tree seedlings of different sizes for 12 common species across the northeastern USA by leveraging the Forest Inventory and Analysis (FIA) program's Regeneration Indicator (RI) dataset, which assesses seedling abundance across six height classes. We developed four potential proxies for deer browse intensity, including town-level harvest records, and compared these with field-estimated browse intensity. Highly palatable species experienced moderate to strong negative browse impacts, especially for medium to large seedling sizes, while less palatable species either showed no impact or experienced modest benefits. *Acer saccharum* displayed the strongest negative relationships with browsing intensity and was also affected at smaller size classes than other species, whereas impacts on *Acer rubrum* and *Betula alleghaniensis* were limited to one larger ($\geq$ 0.9 m tall) seedling size class. Collectively, these results underscore the pervasive impacts of deer browse on regeneration dynamics in northeastern forests and the opportunities for adaptive strategies to recruit species beyond vulnerable size classes.

1. Introduction

Overabundance of white-tailed deer (*Odocoileus virginianus*) and other ungulates strongly influences juvenile tree (i.e., seedling and sapling) abundance at regional scales in temperate forests, causing declines in abundance and compositional shifts away from the most palatable species (Bödeker et al., 2023; Miller and McGill, 2019; Russell et al., 2017; Vickers et al., 2019). Over time, these effects propagate into the canopy tree layer, affecting forest composition (Bradshaw and Waller, 2016; White, 2012) and therefore ecosystem functions and services including wildlife habitat, carbon stocks and resilience to climate change (Harris et al., 2024a; Knott et al., 2023). Characterizing the influence of deer browse on tree regeneration at regional scales is particularly important given broader concerns about tree regeneration in temperate forests due to climate change, non-native pests and pathogens and altered disturbance regimes (Dey et al., 2019). A substantial "regeneration debt", or the potential for regeneration failure combined with compositional mismatch between understory and overstory, has been observed in eastern USA forests (Miller and McGill, 2019; Vickers et al., 2019). Deer browse is a strong predictor of this regeneration debt (Miller et al., 2023; Vickers et al., 2019), suggesting (1) that mitigating deer browse impacts could help alleviate existing regeneration debt and (2) that regeneration debt might intensify in the future to the extent that warmer and less snowy winters allow white-tailed deer populations to increase (Contosta et al., 2019; Laurent et al., 2021).

Impacts of ungulate browsing on tree seedlings likely vary by ontogeny and species palatability. Limited evidence from localized studies, often using deer exclosures or enclosures, suggest that the impacts of deer browsing have a unimodal (hump-shaped) relationship with juvenile tree size (Fig. 1a) (Kelly, 2019; Kupferschmid et al., 2020; Rooney, 2001). During initial seedling growth, browse impact may increase with height as seedlings become more conspicuous to deer (Kelly, 2019; Rooney et al., 2000). As juvenile trees approach ~2 m in height, they start to grow beyond the reach of deer and browse impact declines

---

* Corresponding author.

E-mail addresses: lucas.harris@uvm.edu (L.B. Harris), Melissa.Pastore@usda.gov (M.A. Pastore), awdamato@uvm.edu (A.W. D'Amato).

https://doi.org/10.1016/j.foreco.2025.122906
Received 24 March 2025; Received in revised form 2 June 2025; Accepted 3 June 2025

(Walters et al., 2020). For more palatable species, browse impacts may be greater in magnitude and perhaps shifted toward smaller size classes to the extent that deer preferentially seek out these species (Fig. 1a). For less palatable species, browse may primarily affect the most conspicuous, large-sized seedlings, and these species may even benefit from reduced competition under moderate browsing pressure (Fig. 1a and b). Few studies have tested these relationships because tree regeneration assessments rarely include more than one or two seedling size classes, so further work to assess these patterns, particularly across broader, heterogenous regions is informative.

A key barrier to assessing impacts of browse on tree regeneration at regional scales is that juvenile tree abundance within a particular size class reflects the full set of influences on survival and growth up to that point (e.g., climate, land use, soils, overstory and understory vegetation). For example, three stands might have the same abundance of saplings yet this abundance could arise from limitations on seed availability and establishment in one stand, and survival and growth of small and large-sized seedlings, respectively, in the other two stands. This concept of "demographic inertia" is crucial to understanding and interpreting tree regeneration patterns (Rooney et al., 2000), and it confounds efforts to disentangle influences on juvenile tree growth and survival (Beckage et al., 2005; Harris et al., 2024b). Approaches that isolate browse influences on seedling growth and survival within particular size classes can be used to better characterize the effects of ungulate browsing on regeneration success. Additionally, regional-scale analyses typically rely on coarse proxies for browsing pressure (Walters et al., 2016), which do not capture finer-scale variability in deer populations and behavior that in turn influences tree regeneration (Lesser et al., 2019).

The objective of our study was to assess how the impacts of white-tailed deer browse on tree regeneration vary by ontogeny at a regional scale, using nationwide forest inventory plots within the northeastern USA (Fig. 2). Within this objective, we first investigated species of high and low–moderate palatability as groups to gain broader insights that might be generalizable to other regions and deer species. We then investigated effects by tree species for a more detailed picture of deer browse impacts in the northeastern USA that is applicable to forest management in the region. We predicted that the impact of deer browse would be strongest for seedlings of highly palatable species (Fig. 1a), and that deer browse impacts would peak at seedling heights ranging from 30 cm tall for high palatability species to 100 cm tall for low palatability species. Furthermore, we expected deer browse to have a predominantly negative effect on seedling growth and survival but that increased browsing may also benefit seedlings of less palatable species up to a point due to reduced competition (i.e., unimodal relationships with browsing pressure, Fig. 1b).

To address the role of ontogeny, we used plots that were surveyed using "Regeneration Indicator" (RI) protocols under which tree seedlings are tallied within six height classes on a subset of inventory plots instead of the one size class used in the standard nationwide forest inventory plots (McWilliams et al., 2015). We focused on white-tailed deer, which is the primary cervid impacting tree regeneration across much of eastern North America (Rooney, 2001), although we note that moose (*Alces alces*) can also affect tree regeneration in primarily northern parts of the region (Andreozzi et al., 2014; Wattles and Destefano, 2011). The northeastern USA presents an interesting test case because it spans a climate gradient from areas with low snowpack to areas where deep winter snowpacks currently limit deer populations, but may not do so in the future (Hinton et al., 2022). Moreover, ongoing development and expansion of the wildland-urban interface in the region (Sonti et al., 2023) may drive further increases in white-tailed deer populations and browse impact on tree seedlings. To create improved indicators of browsing pressure, we used town-level white-tailed deer harvest records (Supplemental Figure A1) that have not been previously used in analyses of deer browse impacts on tree regeneration, and also considered snow depth and land cover metrics that provide additional information on deer habitat suitability (Lesser et al., 2019).

2. Methods

2.1. Forest inventory data

The Forest Inventory and Analysis (FIA) program surveys field plots annually across USA forests at a national base intensity of 1 plot per 2428 ha, and plots in the northeastern USA are remeasured at 5–7-year intervals. Beginning in 2012, RI protocols were implemented across 12.5 % of FIA plots in the northeastern and midwestern USA (McWilliams et al., 2015). Six seedling height classes are tallied under RI protocols: 1: 5–15 cm tall, 2: 15–30 cm, 3: 30–91 cm, 4: 91–152 cm, 5: 152–305 cm and 6: > 305 cm (McWilliams et al., 2015). RI plots coincide with assessments of vegetation cover and downed dead wood (Woodall et al., 2019), providing additional measurements not available for the broader pool of FIA plots.

The FIA plot design consists of four circular subplots (168 m each) within which trees (diameter at breast height [DBH] ≥ 12.7 cm) are surveyed (Bechtold and Patterson, 2005). One subplot is located at the

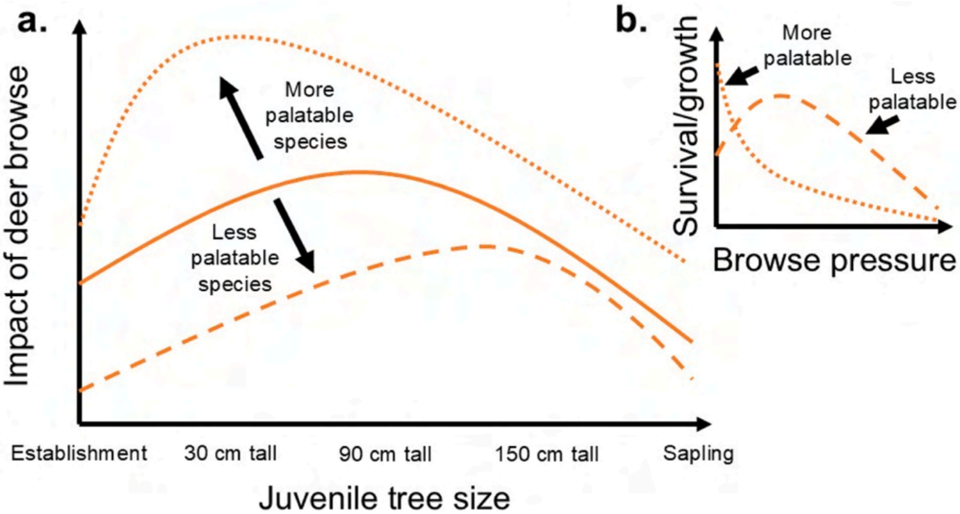


Fig. 1. Hypothesized (a) level of impact of deer browse on juvenile trees by size and species palatability and (b) effect of stand to landscape-scale deer browsing pressure on juvenile tree survival and growth.

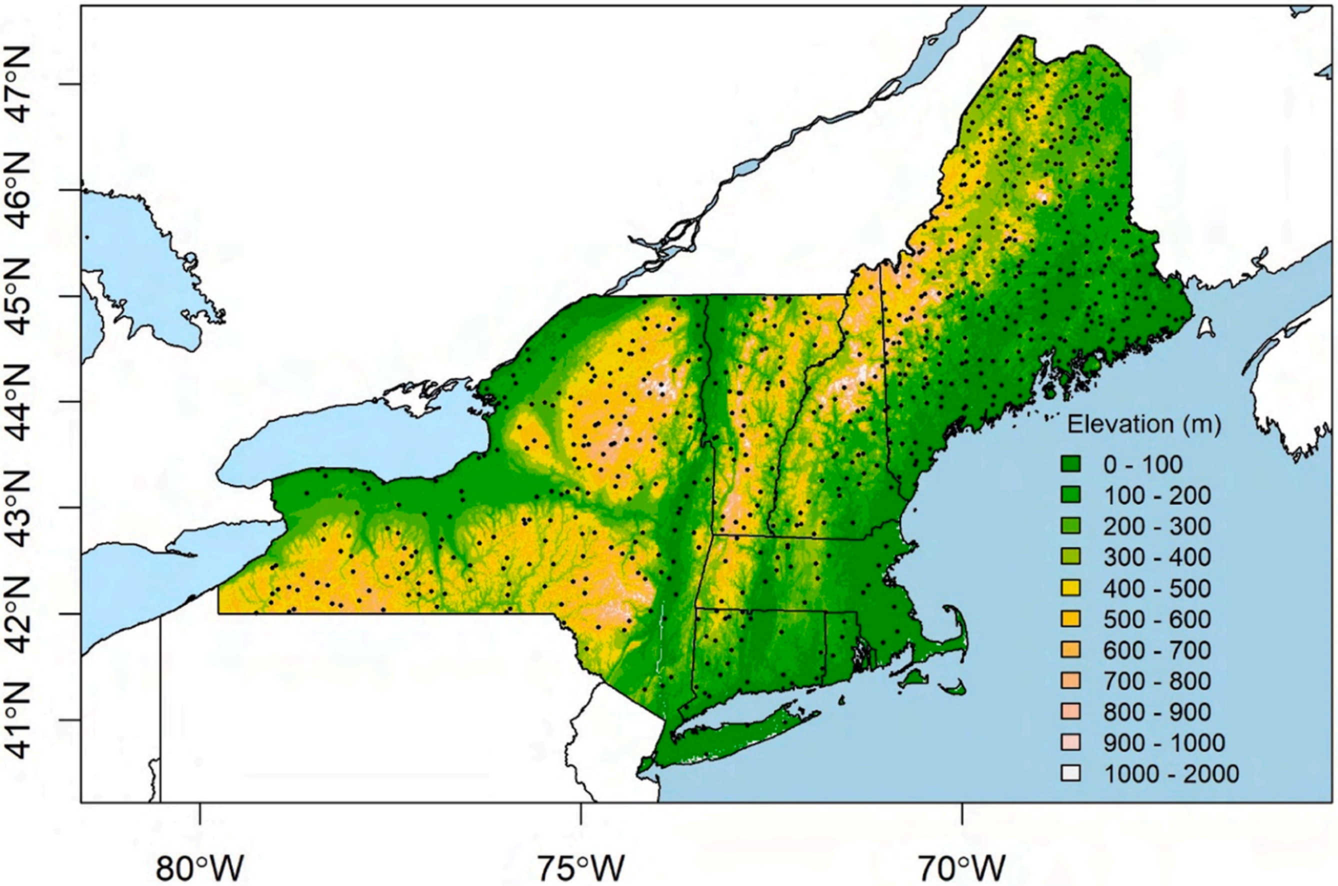


Fig. 2. Study area map showing elevation and the locations of regeneration indicator plots (n = 750) meeting the study criteria within the northeastern USA. Note that plot locations are approximate.

plot center and the others are centered 36.6 m from plot center at azimuths of 0°, 120°, and 240°. Seedlings (<2.5 cm DBH) and saplings (2.5–12.6 cm DBH) are tallied in one circular microplot (13.5 m) nested within each subplot.

We analyzed subplots within the northeastern USA that (a) were surveyed at least twice using RI protocols, (b) lay entirely on accessible forest land and (c) did not show evidence of artificial regeneration (n = 2642 subplots from 750 plots meeting these criteria). The most common forest type in the study is northern hardwood forest dominated by *Acer saccharum*, *Fagus grandifolia* and *Betula alleghaniensis* (46 % of subplots analyzed), with spruce-fir forest in northern and high-elevation areas (21 %) and oak-hickory forests (11 %) common in southern areas. Seedling abundance by species and RI height class were extracted, and we also obtained subplot-level characteristics including elevation; cover of shrubs, grasses and forbs; and total live tree density and basal area (BA) (Table 1). Some FIA attributes are provided at the level of condition classes, or relatively homogenous units by forest type, land use, etc. within a plot (Bechtold and Patterson, 2005). In these cases (see Table 1), attributes were extracted based on the condition class noted at the center of each microplot to obtain the condition class most relevant to observed tree regeneration. Note that subplots were allowed to contain more than one condition class per our selection criteria, but that all of these conditions had to be accessible forest land on which trees were measured. Ancillary data were also extracted to FIA plot locations including terrain indices, growing-season precipitation and soil characteristics (Table 1).

We used the plot locations publicly provided by FIA, which are randomly perturbed by up to 1.6 km (although usually <0.8 km) and sometimes swapped with other nearby plot locations to protect landowner privacy (Burrill et al., 2024). In preliminary work, FIA co-author Pastore ran our analysis using both the exact and fuzzed plot locations and found that use of exact locations did not improve model accuracy on average. FIA data were acquired October 22, 2024 from v2.1.0 of the FIA database (https://apps.fs.usda.gov/fia/datamart/datamart.html).

2.2. Indicators of deer browsing pressure

We developed four potential proxies of white-tailed deer browse intensity from independent datasets: (1) deer harvest records, (2) mean winter snow depth, (3) proportion of non-forest in the 1 km around each plot, and (4) proportion of developed land in the 1 km around each plot.

White-tailed deer harvest records are often used to estimate and map deer populations (Hanberry and Hanberry, 2020; Walters et al., 2016) and as a potential proxy for browsing pressure on tree seedlings (Lesser et al., 2019; Russell et al., 2017) given that population estimates from more accurate techniques such as aerial surveys are not available at a regional scale. To create maps of deer harvest density, annual records of white-tailed deer harvests were gathered from state agencies. Town-level total harvest (including both males and females) was used for every state except Massachusetts (Supplemental Table A1). Town-level records were not available for Massachusetts, so harvest data were instead compiled by wildlife management zone (n = 15). Connecticut records contained extra categories (cropkill, roadkill and other) that were not included in other state records, so totals within these categories were subtracted from town-level totals. Annual averages were calculated from all publicly available years of data between 2007 and 2023 for each state. The beginning year of 2007 was chosen based on being 5 years prior to the beginning of RI measurements in 2012. The land area of each town (or wildlife management zone) was calculated from state-level boundary layers by masking out perennial water bodies

Table 1
Variables considered in models of seedling gain and sapling recruitment.

Category	Variable(s)	Source*	Details
Response	Seedling gain or sapling recruitment	FIA: Seedling Regeneration, Tree	For seedlings of a given size class and species, whether or not Time 2 (most recent) abundance > Time 1 abundance. For saplings, presence of new sapling recruitment in Time 2.
Browse indicator	Proportion non-forest	2021 National Land Cover Database	Proportion of vegetated land that is non-forest in 1-km window, including agricultural land, shrubland and meadow but excluding developed areas, water and barren land
Browse indicator	Proportion developed	2021 National Land Cover Database	Proportion of developed land in 1-km window
Browse indicator	White-tailed deer harvest	State-level harvest reports	Expressed in mean annual density (deer km^{-2})
Browse indicator	Mean December-March snow depth	Snow Depth Assimilation System (National Operational Hydrologic Remote Sensing Center, 2004)	~1 km grid cell, annual means from 5 years preceding each plot measurement
Abiotic	Mean total May-October precipitation	Daly et al. (2008)	~4 km grid cell
Abiotic	Topographic Position Index	30-m Digital Elevation Model (DEM)	difference between focal pixel elevation and mean elevation within a 1-km window
Abiotic	Terrain complexity	30-m DEM	standard deviation of elevation within 1-km window
Abiotic	Topographic Wetness Index	30-m DEM	using "r.topidx" function in GRASS GIS (Neteler et al., 2012)
Abiotic	Elevation, slope and aspect	FIA: Subplot	
Tree	Tree basal area (BA) and density	FIA: Tree	Totals across species
Understory vegetation	Shrub cover, grass cover and forb cover	FIA: Phase 2 Vegetation Subplot Structure	
Seedling abundance	Conspecific seedling density	FIA: Seedling Regeneration	By height class, considering only classes smaller than the response class (e.g., Class 1 and Class 2 density when predicting Class 3)
Seedling abundance	Heterospecific seedling density	FIA: Seedling Regeneration	By height class, all classes included in all models
Abiotic	Volume of Coarse Woody Material	FIA: Condition Down Woody Material Calculation	
Abiotic	Mean litter depth and duff depth	FIA: Condition Down Woody Material Calculation	
Abiotic	Soil Organic Carbon	FIA: Condition	Modeled condition-level estimates (Domke et al., 2017)
Abiotic	Sand, silt, and clay content	SoilGrids 2.0 (Poggio et al. 2021)	5–15 cm depth
Abiotic	Soil pH	SoilGrids 2.0 (Poggio et al. 2021)	5–15 cm depth
Abiotic	Nitrogen	SoilGrids 2.0 (Poggio et al. 2021)	5–15 cm depth

[*] Table name is given for field data from the Forest Inventory and Analysis (FIA) database.

> 10 ha from the National Hydrography Dataset (https://nhd.usgs.gov/), and was used to calculate mean annual harvest density (Supplemental Figure A1). Harvest density was estimated at FIA plot locations using inverse distance weighted interpolation considering values from the five nearest towns, implemented with the “gstat” R package (Gräler et al., 2016).

A deep winter snowpack has been suggested to limit the density of white-tailed deer, especially above mean winter snow depth of ~25–50 cm, corresponding to northern and high-elevation portions of the study area (Hinton et al., 2022; Laurent et al., 2021). Winter snow depth was therefore considered as a potential proxy for deer browse intensity (Supplemental Figure A2). Daily snow depth estimates were acquired at 1-km resolution from the Snow Depth Assimilation System (SNODAS) (National Operational Hydrologic Remote Sensing Center, 2004), and mean December–March snow depth was calculated for the five winters preceding each FIA plot measurement (e.g., 2014–2019 for a 2019 measurement).

Land cover characteristics may influence white-tailed deer abundance and browse intensity including a potential positive effect of non-forest vegetation that offers perennial forage (Hanberry, 2021; Hinton et al., 2022; Hurley et al., 2012; Roseberry and Woolf, 1998). First, we calculated the proportion of vegetated land that was non-forested from the 2021 National Land Cover Database (Dewitz, 2023) in the area surrounding each plot to represent areas of high perennial forage habitat that may support higher deer populations (Table 1). A similar “forage area” metric was suggested as an indicator of deer habitat suitability that may improve characterization of local browse intensity (Lesser et al., 2019). We considered window sizes of 1 km and 2 km, and proceeded with a 1-km window because it more effectively distinguished between browse impact assessed within RI plots (see next paragraph) and because it was more often retained in models of seedling gain and sapling recruitment (see Subsection 2.4). Second, we calculated the proportion of developed land within a 1-km window as a metric of fragmentation and forest edge habitat that may indicate plots at the wildland-urban interface with potentially higher browse intensity (Sonti et al., 2023). The two metrics are complementary because developed land was excluded from calculations of non-forested vegetation.

Plot-level browse impact scores are evaluated in the field as part of the RI protocols. Under these protocols, field crews examine tree seedlings and understory vegetation across all subplots and assign a plot-level impact score: “very low” is an exclosure; “low” is no browsing evidence and abundant seedlings; “medium” is some evidence of browsing and some seedlings present; and “high” and “very high” indicate common to very common browsing of preferred plant species, some browsing of non-preferred plants, and few tree seedlings (McWilliams et al., 2018, 2015). Only two plots were categorized as “very high”, so these were combined with the “high” category. We did not use these scores as a predictor of seedling gain or sapling recruitment, because the abundance of seedlings of preferred browse species is one of the criteria used to generate these scores (i.e., seedling abundance and the browse impact scores are not fully independent) (McWilliams et al., 2018). However, the RI browse impact scores are well-suited to evaluating geospatial proxies of browse intensity (Patton et al., 2018). We used Kruskal-Wallis tests with post-hoc Dunn’s tests to assess how well the four proxies of browse intensity corresponded with the RI browse impact scores at the plot level.

2.3. *Response variables*

To isolate the influence of white-tailed deer browse and other factors on regeneration success within particular seedling height classes, we extended an existing statistical modeling framework (Harris et al., 2024a, 2022) by predicting presence of sapling recruitment in Time 2 (i.e., the most recent RI subplot measurement) as well as *gains in abundance* (as opposed to loss or no change) between Time 1 (the prior measurement) and Time 2 for each seedling height class. The two tallest height classes were combined into a single large seedling category ($\geq$152 cm tall) because seedlings may attain sapling size ($\geq$2.5 cm DBH) from either of the two largest height classes, and therefore attaining the tallest height class ($>$ 305 cm tall) is not a prerequisite for sapling recruitment.

Gains in abundance between measurements indicate a positive net balance between ingrowth to a given seedling height class and both mortality and outgrowth from that class. Recruitment within seedling height classes cannot be assessed from RI data because the FIA program, like other national forest inventories, does not track individual seedlings between remeasurements. In using seedling gain as an indicator of regeneration success, we assumed that ingrowth and mortality generally outweighed outgrowth to larger height classes (Canham and Murphy, 2016). Exploratory analysis supported this assumption: change in total seedling abundance between subplot remeasurements within a given height class was in all cases positively correlated (based on Spearman rank correlation coefficient r_s) with abundance of the next largest class ($0.17 \leq r_s \leq 0.23$).

2.4. *Statistical modeling*

We conducted two rounds of statistical modeling. First, we grouped tree species by palatability to white-tailed deer (low–moderate and high), based on characterizations of species available in the literature (Supplemental Table A2). Second, we created individual models for the 12 tree species that had $\geq$ 15 subplots with sapling recruitment in Time 2 (most recent measurement) (Supplemental Table A2). Sample size did not have an impact on model accuracy down to this 15-subplot threshold (Supplemental Figure A3). For each model, only subplots with at least one live individual (seedling, sapling or tree) of that palatability class or species at Time 1 (prior measurement) were considered (Supplemental Table A2) in order to analyze regeneration success within currently occupied stands as opposed to assessing the environmental niche of regeneration across all forests in the study area. Boosted Regression Tree (BRT) models (Elith et al., 2008) were used to generate predictions of seedling gain by seedling height class and sapling recruitment in Time 2 as a function of different biotic and abiotic predictors assessed at Time 1 (Table 1). Note that mean annual temperature was not included as a predictor due to its correlation with harvest density ($r_s = 0.81$) and snow depth ($r_s = -0.91$). We also removed some variables from consideration because preliminary analysis showed that they were removed during variable selection in $>$ 90 % of cases. These variables included stand age, physiographic class, slope, aspect, and conspecific tree basal area and density. Models included the abundance of smaller-sized seedlings of the same palatability class (for the first round of modeling) or conspecific seedlings (for the individual species models) to account for demographic inertia by considering the pool of smaller seedlings that could potentially recruit to the focal height class.

To create parsimonious models, variable selection was performed using the “gbm.simplify” function of the “dismo” R package (Hijmans et al., 2021). BRT models were run using a tree complexity of 4, a learning rate of 0.001 and otherwise default settings. Model accuracy was quantified using the Area Under the receiver operating characteristic Curve (AUC) assessed from tenfold cross-validation. AUC is a commonly used metric in which 0.5 indicates accuracy no better than chance alone and 1 indicates a perfect model fit (Fielding and Bell, 1997). Note that in two cases, both for *Thuja occidentalis*, models could not be produced due to low accuracy. Relationships between predictors and seedling gain and sapling recruitment were assessed using relative influence of individual variables and groups of variables (Table 1) within each model as well as partial dependence plots showing the marginal influence of individual predictors (Friedman, 2001; Greenwell, 2017). Partial dependence values were transformed into z-scores to facilitate comparisons in the shape of relationships across species and size classes.

To broadly highlight spatial variability in the sensitivity of seedlings to deer browse and potential impacts of deer management, we generated maps of predicted change in regeneration under four scenarios: (1) 50 % lower harvest density (i.e., lower deer abundance) with current snow conditions, (2) 50 % higher harvest density (i.e., higher deer abundance) with current snow conditions, (3) 50 % lower harvest density with 50 % lower snow depth, and (4) 50 % higher harvest density with 50 % lower snow depth. While these numbers were arbitrarily chosen to gauge the sensitivity of our models, a 50 % decrease in snow depth is not unrealistic given that snow cover has already declined in the region over the past century, and the percentage of days with deep snow (snow water equivalent $\geq$ 30 mm) is projected to decline 37 % by mid-century and 56 % by late-century under a high-emissions scenario for eastern North America (Burakowski et al., 2022; Contosta et al., 2019). Predictions of seedling gain under these scenarios were compared with predictions under observed conditions. Maps of percentage change in likelihood of seedling gain were generated via IDW interpolation to 5-km grid cells, with the number of observations and the inverse distance power optimized to reduce root mean squared error in 20 % of observations randomly withheld as a test dataset.

3. Results

3.1. *Proxies for white-tailed deer browse intensity*

Comparison with field-assessed browse impact scores suggested that each of the four metrics were useful proxies for browse impact ($p < 0.05$, Kruskal-Wallis test), with harvest density having the strongest relationship with browse impact scores and proportion non-forest the weakest (Fig. 3). Harvest density was negatively correlated with mean snow depth ($r_s = -0.80$), and proportion developed land was correlated with harvest density ($r_s = 0.57$) and snow depth ($r_s = -0.54$), with $|r_s| < 0.5$ for the other sets of proxies.

3.2. *Seedling gain and sapling recruitment by palatability*

Although high-palatability species as a group were more likely to register gains in small ($<$ 30 cm tall) seedling abundance, species with low–moderate palatability were more likely to register gains in large seedling abundance ($\geq$90 cm tall) and had twofold higher sapling recruitment rates than high-palatability species (Fig. 4). Losses in abundance were more common than gains in abundance within each seedling height class for both low–moderate and high-palatability species, indicating overall declines in regeneration (Supplementary Figure A4). Model accuracy generally increased with size class, and the model for high-palatability species outperformed the model for low–moderate-palatability species within each size class (Table 2). Overall, gain in seedlings $<$ 90 cm tall were most strongly influenced by abiotic factors (Fig. 5), with the most frequently chosen variables being soil organic carbon and the topographic position index (Supplemental Table A3). Soil organic carbon was negatively related to seedling gain, whereas topographic position showed negative relationships for high-palatability seedlings and positive relationships for low-palatability seedlings. Gains in seedlings $\geq$ 90 cm tall and saplings were most strongly influenced by prior abundance of smaller-sized seedlings (Fig. 5).

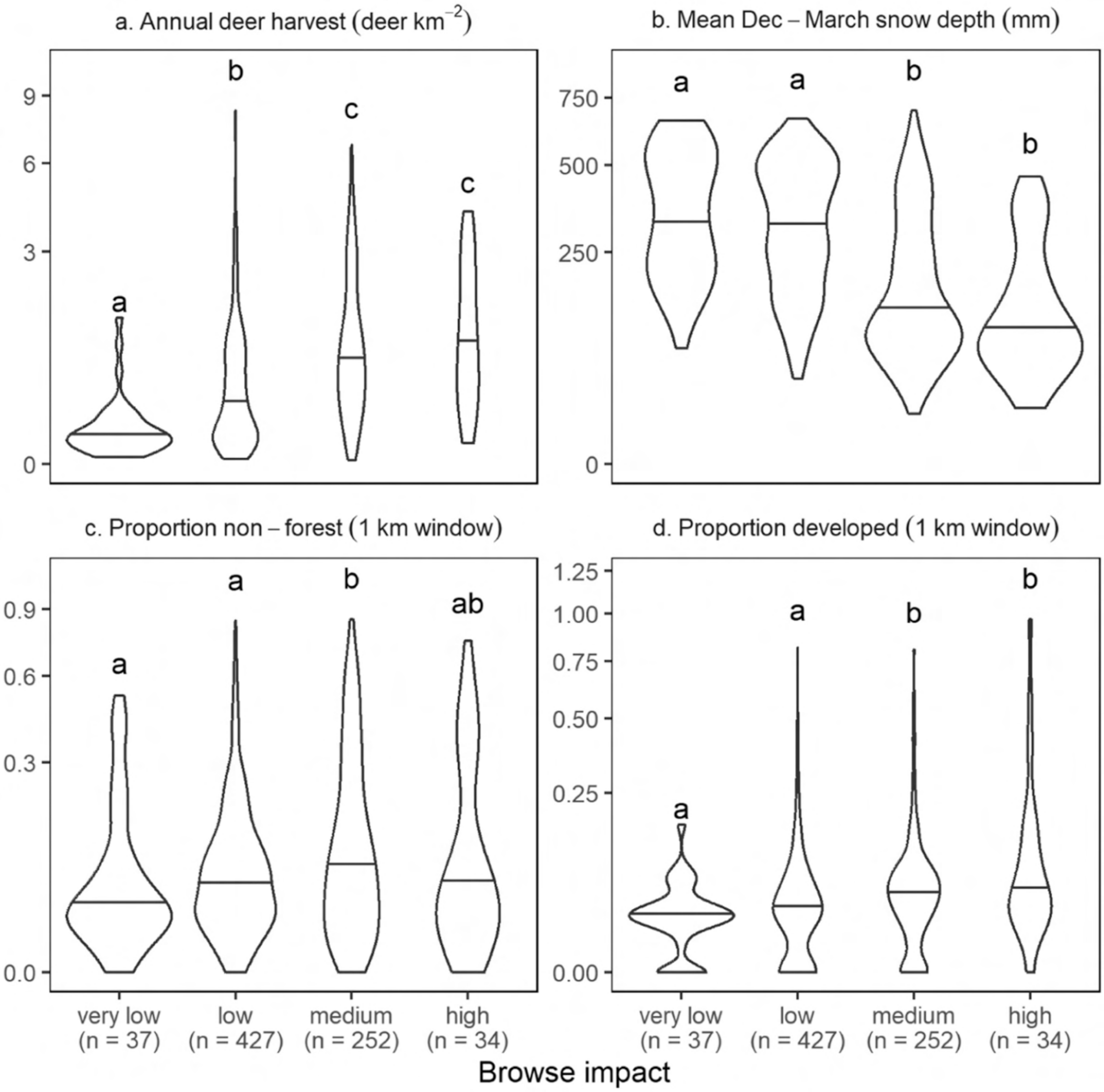


Fig. 3. Violin plots comparing browse impact assessed at the plot level (n = 750) with geospatial proxies of White-tailed deer browsing pressure: (a) mean annual deer harvest density, (b) mean December–March snow depth, and (c) proportion of non-forest vegetation, and (d) proportion of developed land within the 1 km surrounding each plot location. Horizontal lines indicate median values. Letters indicate significant differences among browse impact categories ($p < 0.05$ from Dunn's tests with a Holm correction). the number of plots within each category is shown below the category labels. Note that values are shown on a square-root scale for visibility.

Proxies for white-tailed deer browse had moderate influence (10–34 %) on gain of high-palatability seedlings across all seedling height classes, but only influenced gain of seedlings < 15 cm tall for low–moderate-palatability species (Fig. 5). Deer harvest density was the most influential browsing proxy (Fig. 5), and was negatively related to seedling gain for high-palatability seedlings ≥ 30 cm tall (Fig. 6). For high-palatability seedlings < 30 cm tall, seedling gain initially decreased with harvest density but then increased at high values of > 1.5 deer km^{-2} yr^{-1} (Fig. 6). Small (<15 cm tall) seedlings of low–moderate palatability had a mostly negative relationship with harvest density, although the relationship was positive at very low densities (Fig. 6). Proportion of non-forest was unimodally related to gain in small (<15 cm tall) seedlings and positively related to gain in seedlings > 150 cm tall for high-palatability species (Supplemental Figure A5). Snow depth and proportion of developed land were retained for one model each: snow depth was positively related to gain of high-palatability seedlings 15–30 cm tall, and proportion developed was negatively related to gain of low-palatability seedlings < 15 cm tall. Notably, the two sapling recruitment models were nearly identical in terms of relative influence (Supplemental Table A3), retaining just two variables: abundance of large seedlings > 152 cm tall and live tree basal area.

3.3. *Seedling gain and sapling recruitment by species*

Accuracy of individual species models increased with juvenile tree size class, and varied more by size class than species (Table 3). In general, the influence of abiotic factors decreased with size class and the influence of live tree basal area/density and abundance of smaller-sized seedlings increased (Fig. 7). The most frequently selected abiotic variables were soil organic carbon, duff depth, soil nitrogen, coarse woody material and the Topographic Position and Topographic Wetness indices (Supplemental Figure A6), and the shape of relationships with these influences varied considerably by species (Supplemental Figures A7–A12). Live tree basal area had a strong and consistently negative relationship with gain of seedlings > 91 cm tall and sapling

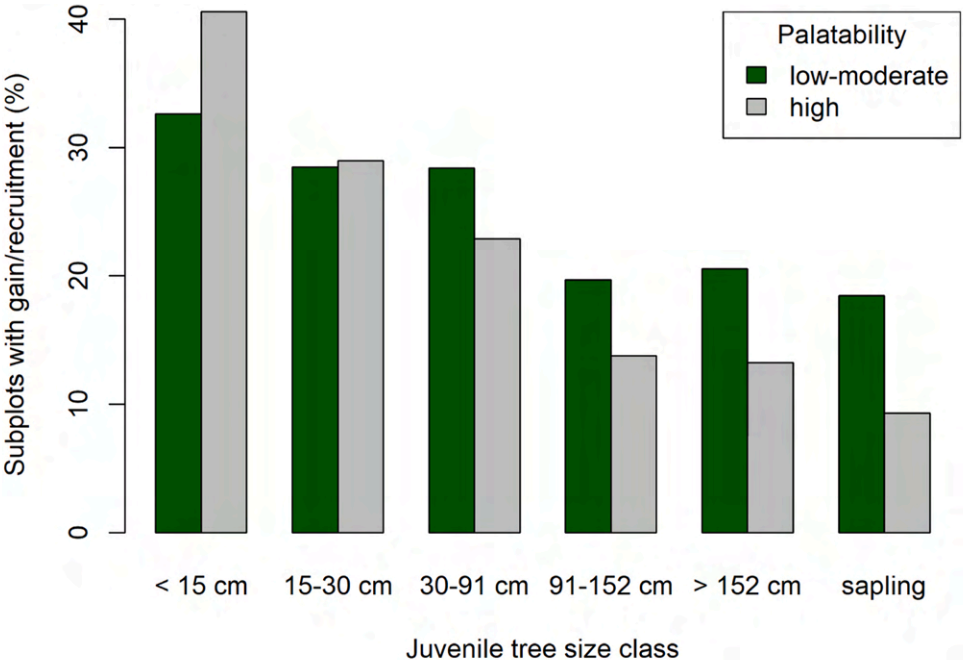


Fig. 4. Percentage of subplots for which gains in seedling abundance or sapling recruitment were observed between measurements by juvenile tree size class and tree species palatability to White-tailed deer. Saplings are 2.5–12.6 cm diameter at breast height [DBH], while seedlings are < 2.5 cm DBH. Species within each palatability class are shown in table A2.

Table 2
Model accuracy (Area Under the receiver operating characteristic Curve, mean and standard error) from models of seedling gain and sapling recruitment for species with low–moderate and high palatability to White-tailed deer.

Size class	Low-moderate	High
< 15 cm	0.65 (0.01)	0.69 (0.01)
15–30 cm	0.61 (0.01)	0.64 (0.01)
30–90 cm	0.63 (0.01)	0.69 (0.01)
90–150 cm	0.71 (0.02)	0.80 (0.01)
> 150 cm	0.75 (0.01)	0.86 (0.01)
sapling	0.84 (0.01)	0.88 (0.02)

recruitment (Supplementary Figure A13). Proxies for deer browse tended to be moderately influential for gains in seedlings < 152 cm tall, with both the degree of influence and the size class at which browsing influence peaked varying by species (Fig. 7). While proportion of non-forest and of developed land were each retained in at least one model for the majority of tree species, the shape of these relationships varied considerably and rarely displayed the negative relationship that would be consistent with a response to browsing (Supplementary Figures A13 and A14).

Of the eight low–moderate palatability species, six were influenced by harvest density for at least one juvenile tree size class and each of these relationships were broadly unimodal except for a positive relationship with *A. pensylvanicum* sapling recruitment and a bimodal relationship with gain of 30–91 cm *Pinus strobus* seedlings (Fig. 8). Species of low–moderate palatability had variable relationships with snow depth, in contrast with the consistently positive relationship seen with highly palatable species (Fig. 9).

Among the four species considered highly palatable, *Acer saccharum* was most strongly influenced by browsing proxies including a negative relationship with harvest density for seedlings 15–152 cm tall and a positive relationship with snow cover for seedlings 15–91 cm tall. Meanwhile, *Acer rubrum* and *Betula alleghaniensis* each had one height class at which browsing primarily appeared to limit seedling gains: 91–152 cm tall for *A. rubrum* and > 152 cm tall for *B. alleghaniensis*. In each case, a negative relationship with harvest density and a positive relationship with snow cover were observed. Despite being considered a highly palatable species, *Fraxinus americana* showed a generally positive relationship with harvest density for seedlings < 30 cm tall, although a largely negative relationship for seedlings 91–152 cm tall (Fig. 8). In some cases, likelihood of seedling gain increased at the highest harvest density values (>4 deer km^{-2} yr^{-1}), which were found almost exclusively in westernmost portion of the study area (Supplementary Figure A1).

3.4. Predicted change in regeneration

Predictions for *Acer rubrum, Acer saccharum* and *Betula alleghaniensis* under scenarios of reduced and increased browsing pressure suggested widespread benefits for reduced browse intensity, including the southern portion of the study area, and potential for reduced regeneration particularly in northern areas in a future with increased browse pressure and decreased snowpack (Fig. 10). Projected decreases in regeneration were particularly acute for *A. saccharum* under a combination of greater deer density and lower snow depth, although predictions for *A. saccharum* under increased deer density alone were mixed (Fig. 10, Supplementary Figure A16).

4. Discussion

Consistent with our expectations, we found that white-tailed deer browse had a stronger influence on seedlings of high-palatability species, and that impacts were strongest at intermediate height classes. We had expected browse impact to peak at the 30–90 cm height class based on prior work in eastern USA forests, rather than the 91–152 cm height class as we observed (Henry et al., 2021; Kelly, 2019; Larouche et al., 2010; Rooney, 2001; Rooney et al., 2000; Walters et al., 2020). However, our results are consistent with research from Europe demonstrating that browsing of both foliage and bark tend to be most intense at shoulder height of deer (Konôpka et al., 2022; Renaud et al., 2003). We also found that the species most strongly influenced by browsing overall (*Acer saccharum*, sugar maple) was affected at smaller size classes than species less strongly influenced by browsing, supporting the idea that

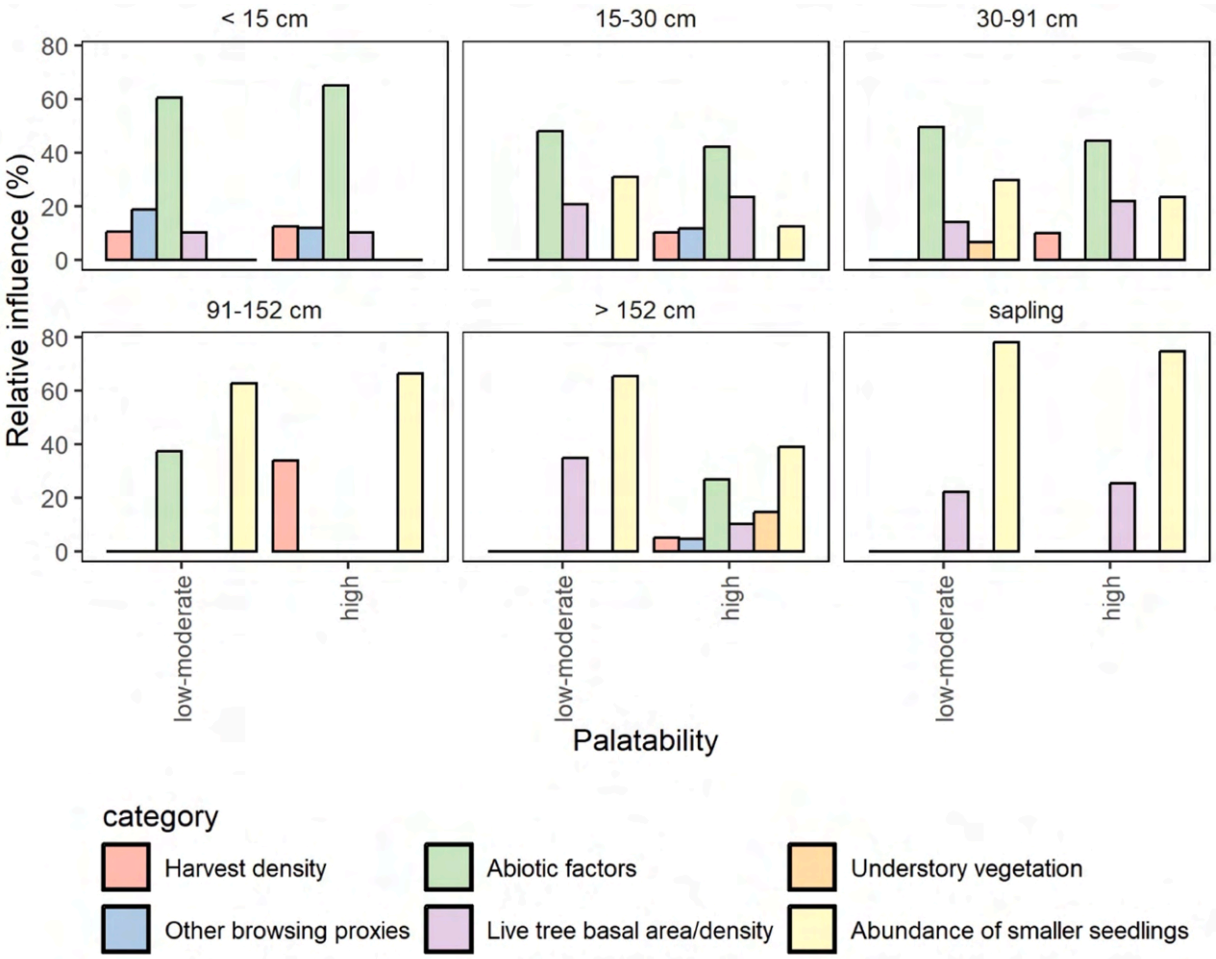


Fig. 5. Relative influence from models of seedling gain by height class or sapling recruitment for tree species with low–moderate and high palatability, by category of variables (Table 1). saplings are 2.5–12.6 cm diameter at breast height [DBH], while seedlings are < 2.5 cm DBH. Species within each palatability class are shown in table A2.

the most palatable species are preferentially browsed at smaller size classes.

We had also expected to see negative effects of browsing on high-palatability species and unimodal effects on the least palatable species to the extent that they benefit from reduced competition under moderate browsing pressure. Indeed, some less palatable species including *Fagus grandifolia* (American beech) and *Acer pensylvanicum* (striped maple) appeared to benefit from increased browsing up to a point, although this threshold varied considerably from a peak at < 0.2 to > 3.0 deer harvested per km^2 per year depending on species and size class. These species are known to benefit from deer browse, and may suppress regeneration of other species when abundant in the understory (Nyland et al., 2006).

4.1. Deer browse and juvenile tree size

Influences on seedling gains varied considerably for small seedlings (<30 cm tall) and medium–large seedlings (≥ 30 cm tall). Gains in small seedling abundance (<30 cm tall) were challenging to predict and more strongly influenced than larger seedlings by abiotic factors including soil properties, terrain, litter and duff depths and downed dead wood. These relationships appear to reflect species-level differences in site and microsite preferences for small seedlings. The only abiotic influence on small seedling gains that was consistent across low and high-palatability groups was soil organic carbon, which was negatively related to small seedling gains particularly for the three maple (*Acer*) species and *Fraxinus americana* (white ash). This relationship was surprising and merits further investigation. High soil organic carbon could indicate productive environments with dense undergrowth, closed-canopy forests with limited light availability, acidic soils or cold environments, or deep leaf litter that could impair regeneration for these species. Yet, we note that these characteristics were also represented in our models by understory plant cover, tree basal area, soil pH, snow depth and litter depth variables, respectively.

We found some counterintuitive bimodal relationships with harvest density for small seedlings, indicating that areas with the highest deer populations in our study area are favorable sites for small seedlings in ways that are not otherwise accounted for in our analysis. This bimodal response was seen for small *A. saccharum* seedlings, generating counterintuitive predictions that small *A. saccharum* seedlings would benefit from greater browse impact in some parts of the study area. We did not account for seed predation and seedling herbivory by small mammals, which may strongly influence tree seedling establishment and early survival and interact with other factors including tree composition, downed dead wood and snow depth (Connolly et al., 2024; Guiden et al., 2019; Schnurr et al., 2004). Another possibility is that soil properties, which may strongly influence seedling establishment and growth in the study region (Tourville et al., 2023), were not adequately characterized by the gridded data and modeled values that we used (Domke et al., 2017; Poggio et al., 2021). Unexpected positive relationships with harvest density for small seedlings of *Fraxinus americana* (white ash) may be an artifact of the invasive emerald ash borer, which is not known to kill

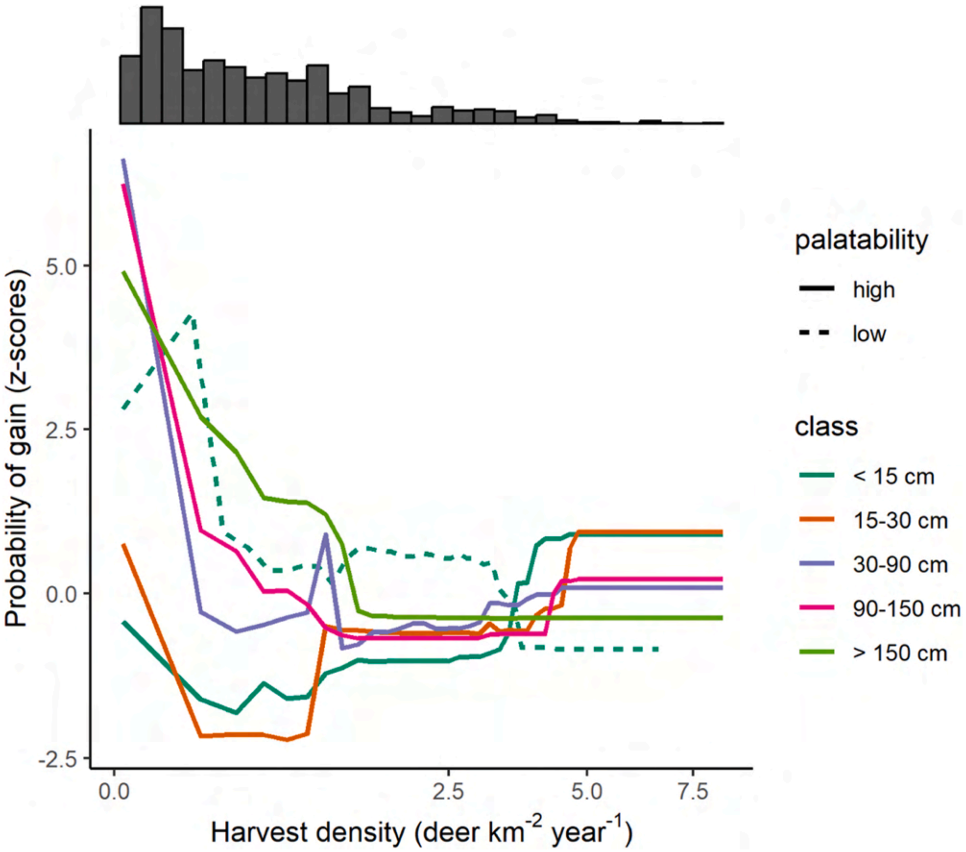


Fig. 6. Partial dependence plot showing the relationships between gains in seedling abundance by height class and White-tailed deer harvest density for species of low–moderate and high palatability. Probability of seedling gain is transformed into z-scores to visualize the shape of relationships across models. The histogram shows the distribution of deer harvest density values among the subplots used for analysis. Species within each palatability class are shown in table A2.

Table 3
Model accuracy (Area Under the receiver operating characteristic Curve) for models of gains in seedling abundance and sapling recruitment by juvenile tree size class and species.

Species	< 15 cm	15–30 cm	30–91 cm	91–152 cm	> 152 cm	sapling
Abies balsamea	0.71 (0.02)	0.69 (0.02)	0.75 (0.02)	0.75 (0.02)	0.80 (0.02)	0.89 (0.02)
Fagus grandifolia	0.61 (0.02)	0.66 (0.02)	0.68 (0.03)	0.70 (0.03)	0.83 (0.02)	0.85 (0.02)
Acer rubrum	0.71 (0.01)	0.67 (0.01)	0.73 (0.01)	0.82 (0.01)	0.84 (0.01)	0.91 (0.02)
Picea rubens	0.72 (0.05)	0.71 (0.04)	0.73 (0.04)	0.78 (0.03)	0.81 (0.04)	0.89 (0.01)
Acer pensylvanicum	0.62 (0.02)	0.64 (0.02)	0.63 (0.03)	0.81 (0.02)	0.75 (0.03)	0.87 (0.03)
Betula alleghaniensis	0.60 (0.04)	0.64 (0.06)	0.68 (0.03)	0.80 (0.03)	0.88 (0.02)	0.92 (0.02)
Acer saccharum	0.69 (0.04)	0.67 (0.03)	0.72 (0.03)	0.83 (0.02)	0.87 (0.02)	0.86 (0.04)
Fraxinus americana	0.73 (0.03)	0.60 (0.03)	0.71 (0.02)	0.74 (0.05)	0.78 (0.03)	0.83 (0.05)
Thuja occidentalis		0.63 (0.06)		0.64 (0.06)	0.88 (0.03)	0.90 (0.04)
Pinus strobus	0.69 (0.03)	0.73 (0.02)	0.79 (0.04)	0.77 (0.04)	0.85 (0.02)	0.94 (0.02)
Tsuga canadensis	0.67 (0.03)	0.65 (0.04)	0.77 (0.05)	0.76 (0.05)	0.78 (0.07)	0.95 (0.02)
Ostrya virginiana	0.72 (0.05)	0.73 (0.05)	0.74 (0.04)	0.77 (0.07)	0.65 (0.10)	0.96 (0.02)

seedlings $<$ 2.5 cm DBH yet has strongly affected seedling establishment due to extensive overstory mortality of ash trees (Klooster et al., 2014). The complexity of small seedling dynamics may help to explain sometimes-unexpected relationships between abundance of medium–large seedlings and browsing pressure uncovered in previous work (Lesser et al., 2019), and underscores the utility of further work on dynamics of seedlings $<$ 30 cm tall that are often excluded from forest inventories and ecological studies.

In contrast with small-sized seedlings, gains in medium–large seedlings were predicted with greater accuracy and browse intensity had a consistent negative influence on high-palatability (but not low-palatability) species. Our results are in line with observations from the eastern USA region that forests with high browsing pressure may still have abundant small-sized seedlings of palatable species, yet abundance of large seedlings and saplings is typically low (Henry et al., 2021; Kelly, 2019; Rooney, 2001; Walters et al., 2020). This pattern has also been observed in European temperate forests subject to moderate to high deer browsing pressure (Borowski et al., 2021; Götmark et al., 2005; Kupferschmid et al., 2020). It is also possible that deer at very high densities may forage less selectively in terms of both species and seedling height, causing differences in browse intensity among species and height classes to diminish (Borowski et al., 2021). However, we did not find strong evidence to support this idea (e.g., negative effects of white-tailed deer on less palatable species at high deer densities).

Sapling recruitment over the 5–7-year window that was studied was not influenced by deer browse but rather by a combination of large seedling abundance and light availability, which is consistent with prior work on sapling recruitment (Harris et al., 2024a) and supports the idea

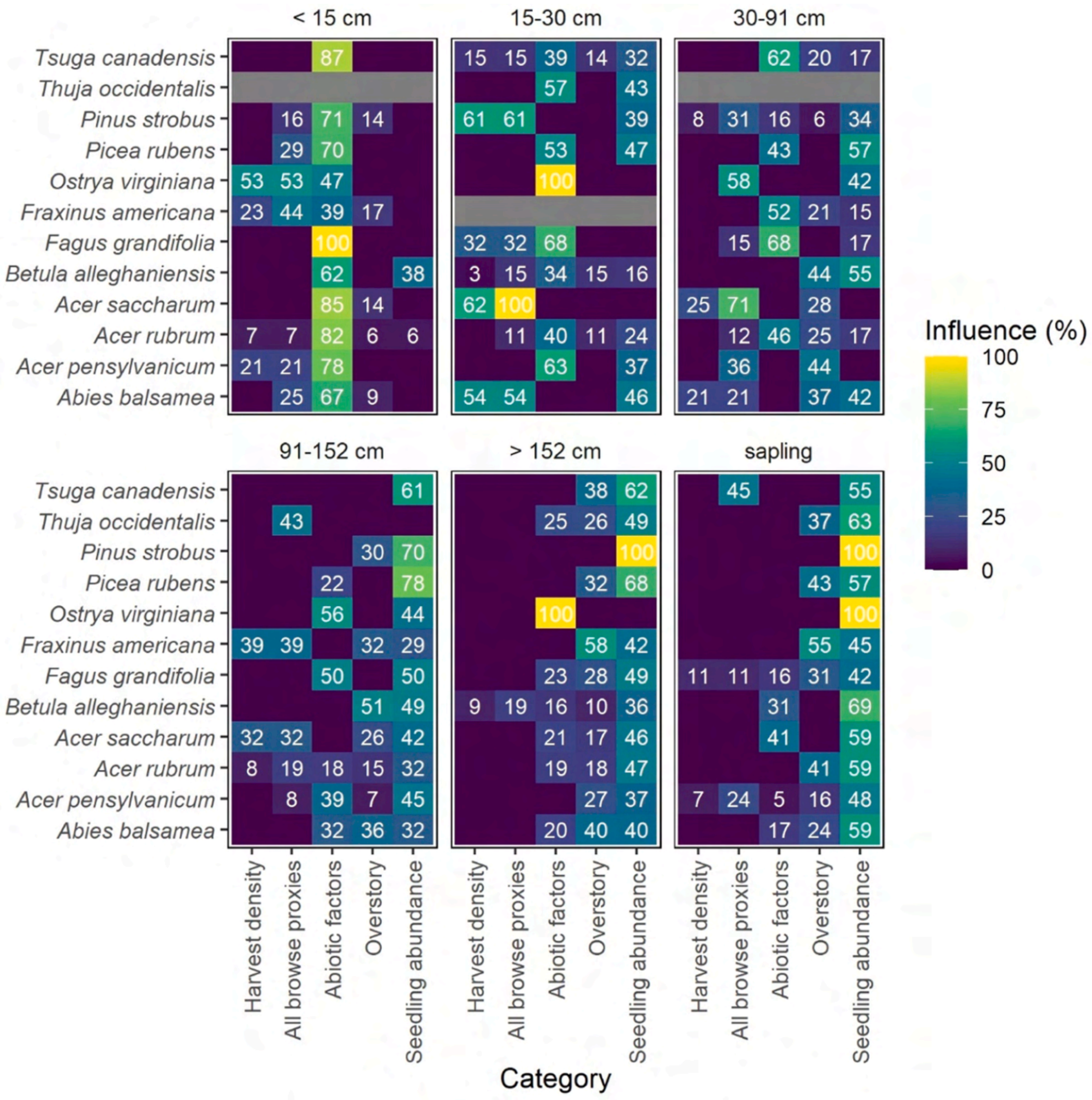


Fig. 7. Relative influence of different categories of variables on seedling gain/sapling recruitment by tree species and juvenile tree size class, with non-zero values shown in each cell. "Overstory" refers to total live tree basal area and/or density. See table 1 for variables within each of these categories. Saplings are 2.5–12.6 cm diameter at breast height [DBH], while seedlings are < 2.5 cm DBH. Species considered highly palatable are *Acercer rubrum*, *Acercer saccharum*, *Betulabetula alleghaniensis, Fraxinusfraxinus americana* and *Thujathuja occidentalis*.

that browse impact wanes as seedlings approach sapling size and start to grow beyond the reach of deer (Walters et al., 2020).

Model accuracy varied considerably by juvenile tree size, from typically good to excellent accuracy (AUC ≥ 0.8) for sapling recruitment and gains in abundance of large seedlings (> 91 cm tall) to much lower accuracy for the three smallest size classes. We expected populations of small-sized seedlings to be more stochastic and therefore difficult to predict due to greater influence of interannual variability in seed production and predation, pests and pathogens, and climate. Prior regional analyses of seedling abundance in eastern USA forests using standard (one size class) FIA seedling tallies have obtained relatively low model accuracy, which speaks to the difficulty of predicting tree seedling dynamics (Lesser et al., 2019; Miller and McGill, 2019; Russell et al., 2017).

4.2. Indicators of deer browse

Like other regional-scale studies of deer browse impacts, we used geospatial proxies for browsing pressure that each have their own strengths and weaknesses (Lesser et al., 2019; Russell et al., 2017). We found that deer harvest density was the strongest indicator of browsing pressure, and our use of town-level harvest records provided a finer-resolution indicator than estimates at the level of wildlife management units or zones that have been used in past work (Lesser et al., 2019; Miller and McGill, 2019; Russell et al., 2017). However, the assumption that deer harvest density is an indicator of deer abundance is unlikely to be true in suburban and exurban forests with lower hunting pressure. Differences in state-level hunting regulations, reporting and data availability could all generate differences in deer harvest densities among states that are not reflective of differences in deer populations. Overall, our results suggest that town-level harvest records do have value as a proxy for deer browsing pressure on tree seedlings, particularly when used with other complementary proxies.

We found positive relationships between snow depth and regeneration of high-palatability species that are consistent with deep snowpacks limiting deer populations. In fact, the differences between the response

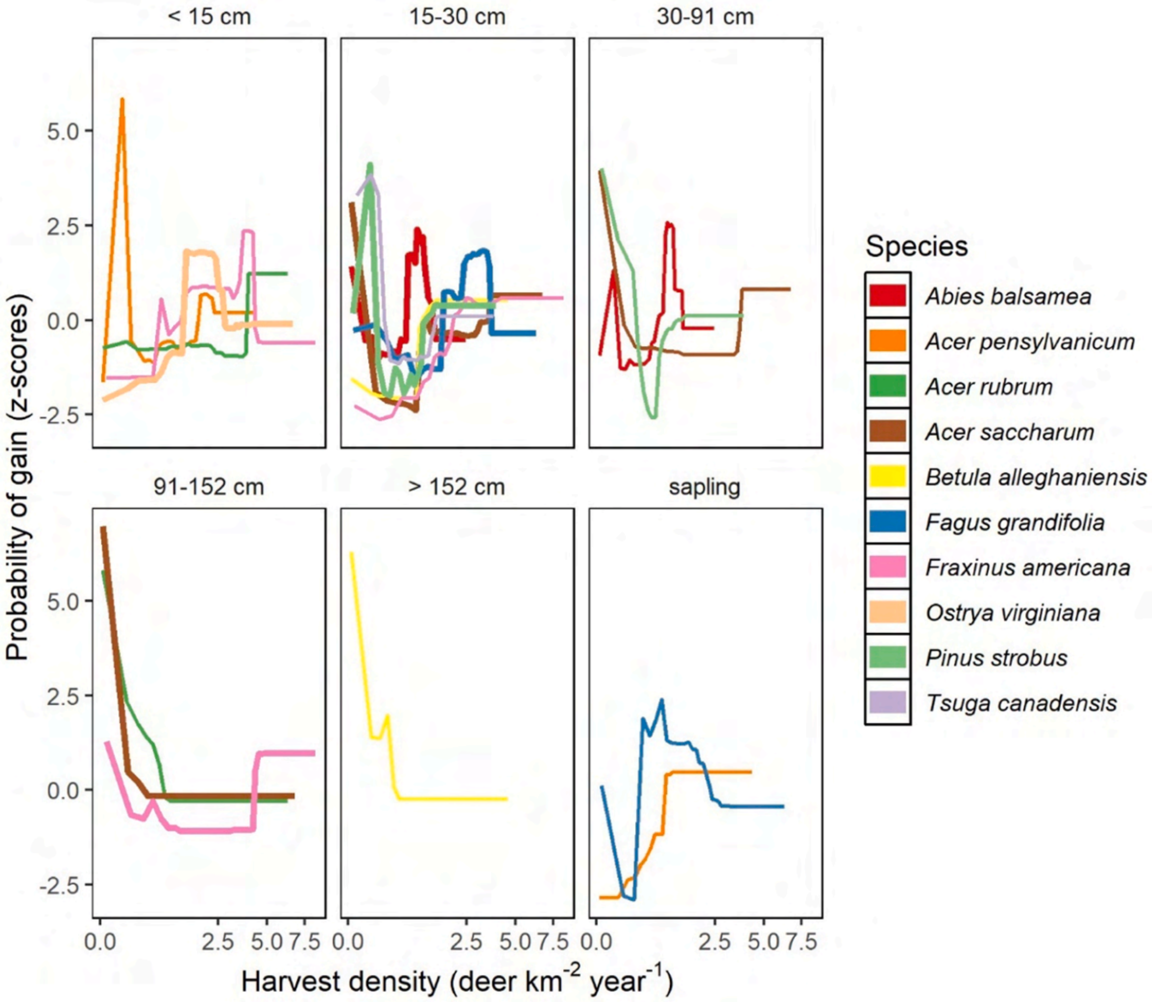


Fig. 8. Partial dependence plots showing the relationships between gains in juvenile tree abundance by size class and White-tailed deer harvest density for individual tree species. Thick (thin) lines represent relative influence ≥ 25 % (<25 %). saplings are 2.5–12.6 cm diameter at breast height [DBH], while seedlings are < 2.5 cm DBH. Species considered highly palatable are *rubrum*, *Acer saccharum*, *Betula alleghaniensis* and *Fraxinus americana*.

of high and low–moderate-palatability seedlings to snow depth were striking (consistently positive and highly variable, respectively). Yet, snowpack dynamics also have direct impacts on tree seedling growth and survival (Henne et al., 2007) that cannot be teased apart from indirect effects of snowpack on deer in the context of our analysis. For example, loss of snow may subject seedlings to more freeze-thaw cycles that cause root damage (Sanders-DeMott et al., 2018). In addition, areas with deeper snowpacks are likely to have higher populations of moose (*Alces alces*), which were not considered in our analysis.

The land cover metrics that we considered, proportion of non-forest and of developed land, were less effective proxies for deer browse impact than harvest density or snow depth. To the extent that these metrics indicate deer browsing pressure, they should be negatively related to regeneration of palatable species. Yet, relationships with land cover were unimodal or positive in the majority of cases, suggesting that these metrics are indicating other aspects of land use and development that may influence regeneration such as light availability, invasive plant species abundance, and differences in forest management practices at the wildland-urban interface (Sonti et al., 2023). Land cover characterization could potentially be improved in future work by considering area of non-forested vegetation instead of proportion non-forested (Lesser et al., 2019), quantifying the spatial arrangement of habitat types (Hurley et al., 2012), or separating non-forest vegetation into components including shrub land and crop land.

4.3. *Implications for future management*

Prior work suggests widespread tree regeneration debt in eastern USA forests south of 43°N and especially south of 42°N (i.e., southern New England and the Mid-Atlantic region) due in part to deer browse, whereas forests farther north currently have more robust regeneration (Miller and McGill, 2019). However, ongoing declines in winter snowpack and severe cold and increased habitat alteration from development will likely lead to further increases in deer populations in the future for northern forests (Contosta et al., 2019; Laurent et al., 2021), potentially leading to the northwards expansion of regeneration challenges. Indeed, our results suggest that a positive feedback between climate change and deer browse may emerge as a key threat to the regeneration of high-palatability tree species in northern temperate and southern boreal forests where deep winter snowpack was previously limiting to deer populations. On the other hand, forests that already have moderate to high browse intensity may represent the greatest near-term opportunity to alleviate regeneration debt through management intervention. For example, our predictions generally suggest that risk to seedlings from future increases in deer browse are most acute in the northern portion of our study area, whereas the benefits to seedlings of reducing deer browse are equal or greater in the southern portion. Our analysis focused on the presence or absence of gains in seedling and sapling abundance rather than absolute abundance or the magnitude of change, meaning that we cannot directly link our results to indices of regeneration debt as

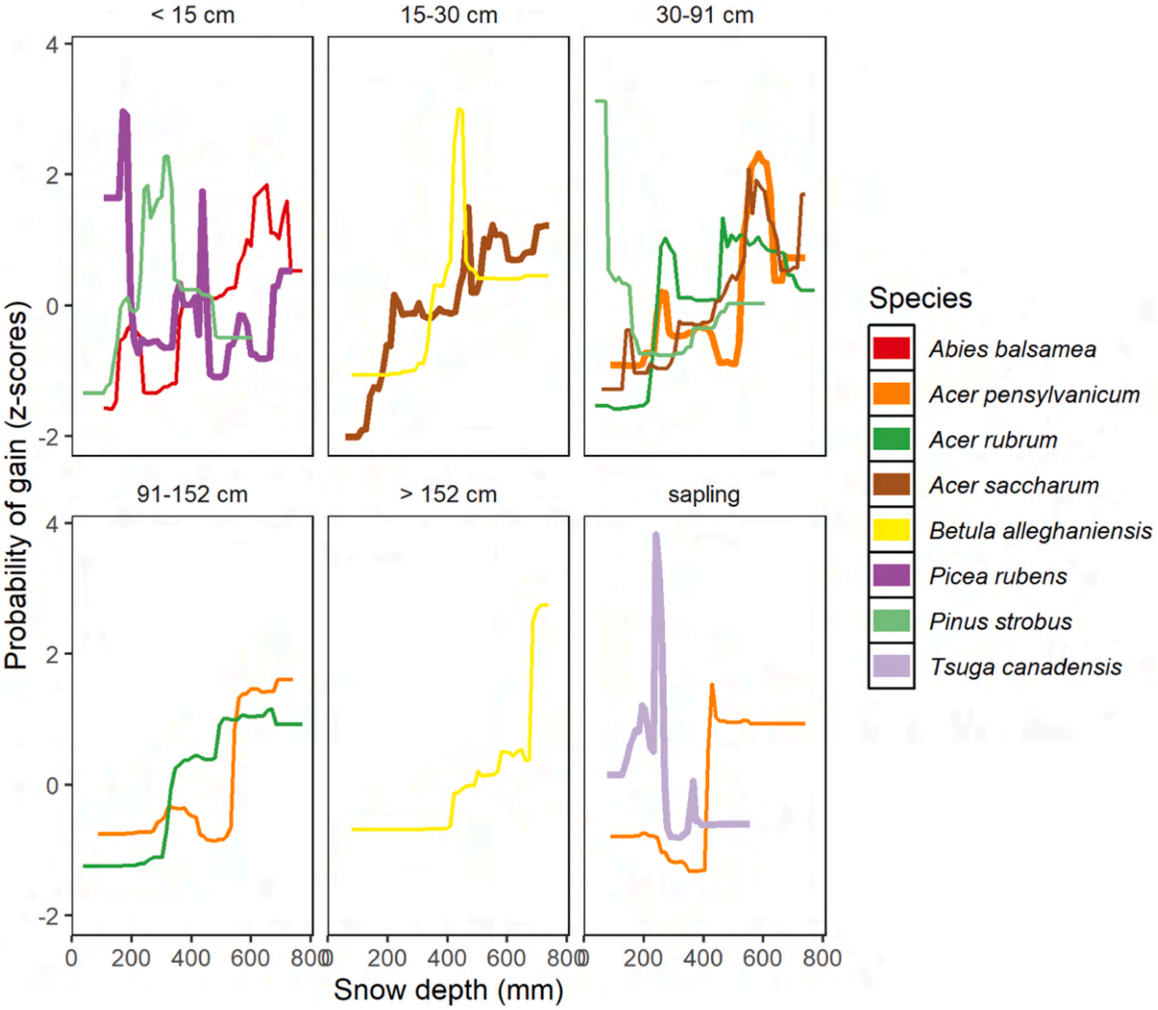


Fig. 9. Partial dependence plots showing relationships between snow depth and probability of seedling gain/sapling recruitment for individual tree species and size classes. Thick (thin) lines represent relative influence ≥ 25 % (<25 %). saplings are 2.5–12.6 cm diameter at breast height [DBH], while seedlings are < 2.5 cm DBH. Species considered highly palatable are *Acer rubrum*, *Acer saccharum* and *Betula alleghaniensis*.

defined by Miller et al. (2023). Making a direct connection to regeneration debt would be useful in future work given the correspondence between deer browse impact and regeneration debt (Miller et al., 2023; Vickers et al., 2019) and the potential for white-tailed deer browse impacts to increase in the future.

Impacts of deer overpopulation on tree regeneration can sometimes be mitigated through strategies including excluding deer using fencing or walls made from slash (Smallidge et al., 2021); reducing deer populations through increased deer harvesting (Bödeker et al., 2023; Tanentzap et al., 2011; Ward and Williams, 2020); using tree cages/tubes to protect individual seedlings; and targeted release of seedlings through overstory harvests, mechanical cleaning, herbicide release or other means to help them grow through vulnerable height classes. These strategies are most valuable and cost-effective when used at locations and times where impacts of deer browse are expected to be greatest based on the size and species composition of seedlings. Our work suggests that the size class at which deer browse has the greatest impact varies substantially among species. For example, regeneration efforts focused on *A. saccharum* may be most effective by targeting smaller height classes (15–152 cm), whereas those targeting *B. alleghaniensis* may benefit from targeting larger height classes (>152 cm). *A. saccharum* deserves special mention as a species with high ecological, economic and cultural value that has been in decline in the sapling layer since the 1980s in the northeastern USA (Bose et al., 2017). Our results suggest both that *A. saccharum* regeneration could be substantially improved at a regional scale if browsing pressure were to be reduced from current levels, and that further declines in *A. saccharum* regeneration are likely if browsing pressure increases in the future.

Our results also highlight potential to increase abundance of small seedlings through silvicultural techniques such as manipulating substrate or understory vegetation, helping to counteract impacts of deer browse on larger seedling height classes. In addition, the strong negative response of seedlings > 91 cm tall to live tree basal area that we observed also speaks to the potential to manipulate canopy gap sizes to allow tree regeneration to succeed despite high browsing pressure (Bödeker et al., 2023).

5. Conclusion

An improved understanding of the factors limiting tree regeneration, including browsing by ungulates, is crucial to making accurate predictions of how forests are likely to change in the future and how to manage for successful regeneration of key species. By isolating the effects of browse intensity on different seedling size classes, we showed how the influence of white-tailed deer browse varies both by ontogeny and palatability in forests of the northeastern USA. Our results highlight how dynamics of small seedlings (< 30 cm tall) are more stochastic and strongly influenced by abiotic factors. In contrast, medium to large seedlings of palatable species had consistent negative relationships with browsing pressure. Negative impacts of deer browse on tree

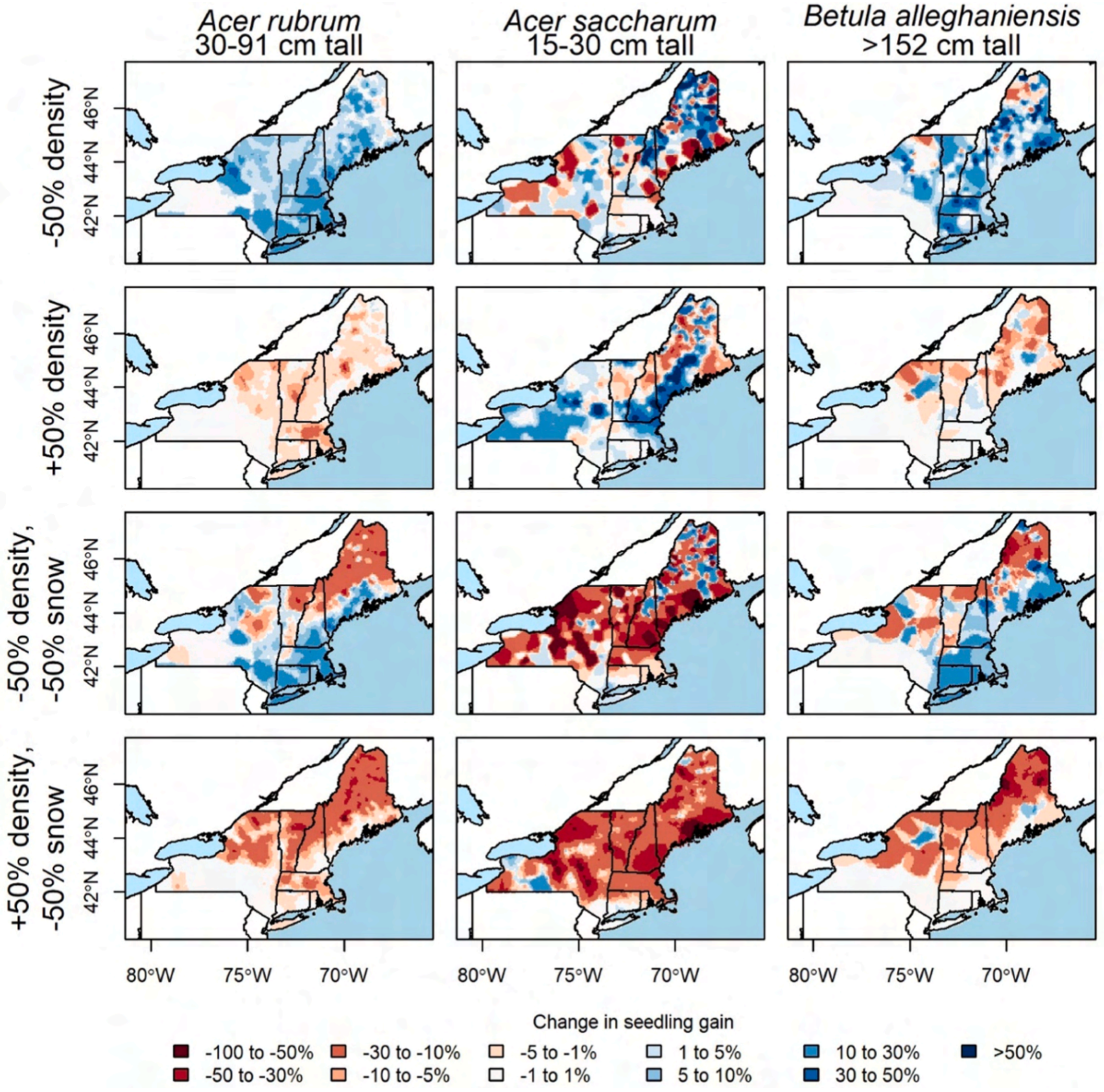


Fig. 10. Predicted change in likelihood of seedling abundance gains for three highly palatable tree species under scenarios representing potential near-term and future changes in browsing pressure: 50 % reduced or increased deer density, using deer harvest density as a proxy; and observed or 50 % reduced snow depths. In each case, the seedling height class is shown at which proxies for browsing pressure had the strongest influence.

regeneration are likely to increase in areas where harsh winters historically limited deer populations, but our results suggest that there is opportunity to mitigate some of these impacts. Targeted management to help cohorts of seedlings grow through the most vulnerable height class could form the basis of management strategies to promote successful regeneration. Deer browse impacts peaked at seedling heights of 91–152 cm for highly palatable species as a group, but we observed variation among species that may be useful when formulating species-specific regeneration strategies.

CRediT authorship contribution statement

Melissa A. Pastore: Writing – review & editing, Methodology, Conceptualization. **Harris Lucas:** Writing – original draft, Methodology, Formal analysis, Conceptualization. **Anthony W. D'Amato:** Writing – review & editing, Methodology, Conceptualization.

Funding sources

This work was supported by the Northeastern States Research Cooperative (grant number 23DG11242311–020).

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.

Acknowledgements

We thank the field crews of the UDSA Forest Service Forest Inventory and Analysis program, who made this work possible through their hard work and dedication. This project was supported by the Northeastern States Research Cooperative through funding made available by the USDA Forest Service. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122906.

Data availability

Data will be made available on request.

References

Andreozzi, H.A., Pekins, P.J., Langlais, M.L., 2014. Impact of moose browsing on forest regeneration in northeast vermont. Alces 50, 67–79.

Bechtold, W.A., Patterson, P.L. (Eds.), 2005. The Enhanced Forest Inventory and Analysis Program — National Sampling Design and Estimation Procedures. USDA Forest Service Southern Research Station General Technical Report SRS-80, Asheville, NC, USA.

Beckage, B., Lavine, M., Clark, J.S., 2005. Survival of tree seedlings across space and time: estimates from long-term count data. J. Ecol. 93, 1177–1184. https://doi.org/10.1111/j.1365-2745.2005.01053.x.

Bödeker, K., Jordan-Fragstein, C., Vor, T., Ammer, C., Knoke, T., 2023. Abrupt height growth setbacks show overbrowsing of tree saplings, which can be reduced by raising deer harvest. Sci. Rep. 13. https://doi.org/10.1038/s41598-023-38951-8.

Borowski, Z., Gil, W., Bartoń, K., Zajączkowski, G., Łukaszewicz, J., Tittenbrun, A., Radliński, B., 2021. Density-related effect of red deer browsing on palatable and unpalatable tree species and forest regeneration dynamics. Ecol. Manag. 496. https://doi.org/10.1016/j.foreco.2021.119442.

Bose, A.K., Weiskittel, A., Wagner, R.G., 2017. A three decade assessment of climate-associated changes in forest composition across the north-eastern USA. J. Appl. Ecol. 54, 1592–1604. https://doi.org/10.1111/1365-2664.12917.

Bradshaw, L., Waller, D.M., 2016. Impacts of White-tailed deer on regional patterns of forest tree recruitment. Ecol. Manag. 375, 1–11. https://doi.org/10.1016/j.foreco.2016.05.019.

Burakowski, E.A., Contosta, A.R., Grogan, D., Nelson, S.J., Garlick, S., Casson, N., 2022. Future of winter in northeastern North America: climate indicators portray warming and snow loss that will impact ecosystems and communities. Northeast Nat. (Steuben) 28, 180–207. https://doi.org/10.1656/045.028.s1112.

Burrill, E.A., Christensen, G.A., Conkling, B.L., DiTommaso, A., Kralicek, K.M., Lepine, L. C., Perry, C.J., Pugh, S.A., Turner, J.A., Walker, D.M., 2024. Forest Inventory and Analysis Database, FIADB user guides, volume: database description (version 9.3), nationwide forest inventory (NFI).

Canham, C.D., Murphy, L., 2016. The demography of tree species response to climate: seedling recruitment and survival. Ecosphere 8, 1–16. https://doi.org/10.1002/ecs2.1701.

Connolly, B., Zirbel, C., Orrock, J., 2024. Rodent-mediated seed limitation affects woody seedling establishment more than invasive shrubs and downed woody debris. Can. J. For. Res. 54, 421–430. https://doi.org/10.1139/cjfr-2023-0131.

Contosta, A.R., Casson, N.J., Garlick, S., Nelson, S.J., Ayres, M.P., Burakowski, E.A., Campbell, J., Creed, I., Eimers, C., Evans, C., Fernandez, I., Fuss, C., Huntington, T., Patel, K., Sanders-DeMott, R., Son, K., Templer, P., Thornbrugh, C., 2019. Northern forest winters have lost cold, snowy conditions that are important for ecosystems and human communities. Ecol. Appl. 29, 1–24. https://doi.org/10.1002/eap.1974.

Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., Pasteris, P.P., 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. Int. J. Climatol. 28, 2031–2064. https://doi.org/10.1002/joc.

Dewitz, J., 2023. National land cover database (NLCD) 2021 products. U.S. Geological Survey data release. https://doi.org/10.5066/P9JZ7AO3.

Dey, D.C., Knapp, B.O., Battaglia, M.A., Deal, R.L., Hart, J.L., O'Hara, K.L., Schweitzer, C. J., Schuler, T.M., 2019. Barriers to natural regeneration in temperate forests across the USA. N. (Dordr.) 50, 11–40. https://doi.org/10.1007/s11056-018-09694-6.

Domke, G.M., Perry, C.H., Walters, B.F., Nave, L.E., Woodall, C.W., Swanston, C.W., 2017. Toward inventory-based estimates of soil organic carbon in forests of the United States. Ecol. Appl. 27, 1223–1235. https://doi.org/10.1002/eap.1516.

Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77, 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence / absence models. Environ. Conserv 24, 38–49. https://doi.org/10.1017/S0376892997000088.

Friedman, J.H., 2001. Greedy function approximation: a gradient boosting machine. Ann. Stat. 29, 1189–1232.

Götmark, F., Berglund, Å., Wiklander, K., 2005. Browsing damage on broadleaved trees in semi-natural temperate forest in Sweden, with a focus on oak regeneration. Scand. J. Res 20, 223–234. https://doi.org/10.1080/02827580510008383.

Gräler, B., Pebesma, E., Heuvelink, G., 2016. Spatio-Temporal interpolation using gstat. R. J. 8, 204–218. https://doi.org/10.32614/RJ-2016-014.

Greenwell, B.M., 2017. Pdp: an r package for constructing partial dependence plots. R. J. 9, 421–436.

Guiden, P.W., Connolly, B.M., Orrock, J.L., 2019. Seedling responses to decreased snow depend on canopy composition and small-mammal herbivore presence. Ecography 42, 780–790. https://doi.org/10.1111/ecog.03948.

Hanberry, B., Hanberry, P., 2020. Rapid digitization to reclaim thematic maps of White-tailed deer density from 1982 and 2003 in the conterminous US. PeerJ, e8262. https://doi.org/10.7717/peerj.8262.

Hanberry, B.B., 2021. Addressing regional relationships between White-tailed deer densities and land classes. Ecol. Evol. 11, 13570–13578. https://doi.org/10.1002/ece3.8084.

Harris, L.B., Woodall, C.W., D'Amato, A.W., 2022. Increasing the utility of tree regeneration inventories: linking seedling abundance to sapling recruitment. Ecol. Indic. 145, 109654. https://doi.org/10.1016/j.ecolind.2022.109654.

Harris, L.B., Woodall, C.W., D'Amato, A.W., 2024a. Sapling recruitment as an indicator of carbon resiliency in forests of the Northern USA. Ecol. Evol. 14, e70077. https://doi.org/10.1002/ece3.70077.

Harris, L.B., Woodall, C.W., D'Amato, A.W., 2024b. Relationships between juvenile tree survival and tree density, shrub cover and temperature vary by size class based on ratios of abundance. Can. J. For. Res. 54, 122–133. https://doi.org/10.1139/cjfr-2023-0097.

Henne, P.D., Hu, F.S., Cleland, D.T., 2007. Lake-effect snow as the dominant control of mesic-forest distribution in michigan, USA. J. Ecol. 95, 517–529. https://doi.org/10.1111/j.1365-2745.2007.01220.x.

Henry, C.R., Walters, M.B., Finley, A.O., Roloff, G.J., Farinosi, E.J., 2021. Complex drivers of sugar maple (*acer saccharum*) regeneration reveal challenges to long-term sustainability of managed Northern hardwood forests. Ecol. Manag. 479, 118541. https://doi.org/10.1016/j.foreco.2020.118541.

Hijmans, R.J., Phillips, S., Leathwick, R., Elith, J, J., 2021. dismo Species Distrib. Model. (https://doi.org/https://cran.r-project.org/web/packages/dismo/index.html).

Hinton, J.W., Hurst, J.E., Kramer, D.W., Stickles, J.H., Frair, J.L., 2022. A model-based estimate of winter distribution and abundance of White-tailed deer in the adirondack park. PLoS One 17, 1–18. https://doi.org/10.1371/journal.pone.0273707.

Hurley, P.M., Webster, C.R., Flaspohler, D.J., Parker, G.R., 2012. Untangling the landscape of deer overabundance: reserve size versus landscape context in the agricultural midwest. Biol. Conserv 146, 62–71. https://doi.org/10.1016/j.biocon.2011.10.034.

Kelly, J.F., 2019. Regional changes to forest understories since the mid-Twentieth century: effects of overabundant deer and other factors in Northern new jersey. Ecol. Manag. 444, 151–162. https://doi.org/10.1016/j.foreco.2019.04.050.

Klooster, W.S., Herms, D.A., Knight, K.S., Herms, C.P., McCullough, D.G., Smith, A., Gandhi, K.J.K., Cardina, J., 2014. Ash (*fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*agrilus planipennis*). Biol. Invasions 16, 859–873. https://doi.org/10.1007/s10530-013-0543-7.

Knott, J., Domke, G., Woodall, C.W., Walters, B., Jenkins, M., Fei, S., 2023. Shifting forests and carbon: linking community composition and aboveground carbon attributes. Ecosystems 26, 412–427. https://doi.org/10.1007/s10021-022-00765-6.

Konôpka, B., Šebeň, V., Pajtík, J., Shipley, L.A., 2022. Influence of tree species and size on bark browsing by large wild herbivores. Plants 11. https://doi.org/10.3390/plants11212925.

Kupferschmid, A.D., Bütikofer, L., Hothorn, T., Schwyzer, A., Brang, P., 2020. Ungulate species and abundance as well as environmental factors determine the probability of terminal shoot browsing on temperate forest trees. Forests 11. https://doi.org/10.3390/F11070764.

Larouche, C., Kenefic, L.S., Ruel, J.C., 2010. Northern White-cedar regeneration dynamics on the penobscot experimental forest in maine: 40-year results. North. J. Appl. For. 27, 5–12. https://doi.org/10.1093/njaf/27.1.5.

Laurent, M., Dickie, M., Becker, M., Serrouya, R., Boutin, S., 2021. Evaluating the mechanisms of landscape change on White-tailed deer populations. J. Wildl. Manag. 85, 340–353. https://doi.org/10.1002/jwmg.21979.

Lesser, M.R., Dovciak, M., Wheat, R., Curtis, P., Smallidge, P., Hurst, J., Kramer, D., Roberts, M., Frair, J., 2019. Modelling White-tailed deer impacts on forest regeneration to inform deer management options at landscape scales. Ecol. Manag. 448, 395–408. https://doi.org/10.1016/j.foreco.2019.06.013.

McWilliams, W.H., Westfall, J.A., Brose, P.H., Dey, D.C., Hatfield, M., Johnson, K., Laustsen, K.M., Lehman, S.L., Morin, R.S., Nelson, M.D., Ristau, T.E., Royo, A.A., Stout, S.L., Willard, T., Woodall, C.W., 2015. A regeneration indicator for forest inventory and analysis: history, sampling, estimation, analytics, and potential use in the Midwest and Northeast United States. U.S. Department of Agriculture, Forest Service, General Technical report NRS-148 1–74.

McWilliams, W.H., Westfall, J.A., Brose, P.H., Dey, D.C., D'Amato, A.W., Dickinson, Y.L., Fajvan, M.A., Kenefic, L.S., Kern, C.C., Laustsen, K.M., Lehman, S.L., Morin, R.S., Ristau, T.E., Royo, A.A., Stoltman, A.M., Stout, S.L., 2018. Subcontinental-scale patterns of large-ungulate herbivory and synoptic review of restoration management implications for midwestern and northeastern forests. Usda forest service Northern research station general technical report NRS-182. Newtown Square, Pennsylvania, USA.

Miller, K.M., McGill, B.J., 2019. Compounding human stressors cause major regeneration debt in over half of eastern US forests. J. Appl. Ecol. 56, 1355–1366. https://doi.org/10.1111/1365-2664.13375.

Miller, K.M., Perles, S.J., Schmit, J.P., Matthews, E.R., Weed, A.S., Comiskey, J.A., Marshall, M.R., Nelson, P., Fisichelli, N., 2023. Overabundant deer and invasive plants drive widespread regeneration debt in eastern United States national parks. Ecol. Appl., e2837 https://doi.org/10.1002/eap.2837.

National Operational Hydrologic Remote Sensing Center, 2004. Snow data assimilation system (SNODAS) data products at NSIDC. Version 1.

Neteler, M., Bowman, M.H., Landa, M., Metz, M., 2012. GRASS GIS: a multi-purpose open source GIS. Environ. Model. Softw. 31, 124–130. https://doi.org/10.1016/j.envsoft.2011.11.014.

Nyland, R.D., Bashant, A.L., Bohn, K.K., Verostek, J.M., 2006. Interference to hardwood regeneration in northeastern North America: controlling effects of American beech, striped maple, and hobblebush. North. J. Appl. For. 23, 122–132. https://doi.org/10.1093/njaf/23.2.122.

Patton, S.R., Russell, M.B., Windmuller-Campione, M.A., Frelich, L.E., 2018. Quantifying impacts of White-tailed deer (*odocoileus virginianus* Zimmerman) browse using forest inventory and socio-environmental datasets. PLoS One 13, 1–16. https://doi.org/10.1371/journal.pone.0201334.

Poggio, L., De Sousa, L.M., Batjes, N.H., Heuvelink, G.B.M., Kempen, B., Ribeiro, E., Rossiter, D., 2021. SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. SOIL 7, 217–240. https://doi.org/10.5194/soil-7-217-2021.

Renaud, P.C., Verheyden-Tixier, H., Dumont, B., 2003. Damage to saplings by red deer (*cervus elaphus*): effect of foliage height and structure. Ecol. Manag. 181, 31–37. https://doi.org/10.1016/S0378-1127(03)00126-9.

Rooney, T.P., 2001. Deer impacts on forest ecosystems: a north American perspective. Forestry 74, 201–208. https://doi.org/10.1093/forestry/74.3.201.

Rooney, T.P., McCormick, R.J., Solheim, S.L., Waller, D.M., 2000. Regional variation in recruitment of hemlock seedlings and saplings in the upper great lakes, USA. Ecol. Appl. 10, 1119–1132. https://doi.org/10.1890/1051-0761(2000)010[1119:RVIROH]2.0.CO;2.

Roseberry, J.L., Woolf, A., 1998. Habitat-population density relationships for White-tailed deer in Illinois. Wildl. Soc. Bull. 26, 252–258.

Russell, M.B., Woodall, C.W., Potter, K.M., Walters, B.F., Domke, G.M., Oswalt, C.M., 2017. Interactions between White-tailed deer density and the composition of forest understories in the Northern United States. Ecol. Manag. 384, 26–33. https://doi.org/10.1016/j.foreco.2016.10.038.

Sanders-DeMott, R., McNellis, R., Jabouri, M., Templer, P.H., 2018. Snow depth, soil temperature and plant–herbivore interactions mediate plant response to climate change. J. Ecol. 106, 1508–1519. https://doi.org/10.1111/1365-2745.12912.

Schnurr, J.L., Canham, C.D., Ostfeld, R.S., Inouye, R.S., 2004. Neighborhood analyses of small-mammal dynamics: impacts on seed predation and seedling establishment. Ecology 85, 741–755. https://doi.org/10.1890/02-0644.

Smallidge, P.J., Chedzoy, B., Curtis, P., Sims, K., 2021. Evaluating the construction and effectiveness of slash walls at the perimeter of regeneration harvests to exclude deer. Ecol. Manag. 497. https://doi.org/10.1016/j.foreco.2021.119529.

Sonti, N.F., Riemann, R., Mockrin, M.H., Domke, G.M., 2023. Expanding wildland-urban interface alters forest structure and landscape context in the Northern United States. Environ. Res. Lett. 18. https://doi.org/10.1088/1748-9326/aca77b.

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.

Tourville, J.C., Zarfos, M.R., Lawrence, G.B., McDonnell, T.C., Sullivan, T.J., Dovčiak, M., 2023. Soil biotic and abiotic thresholds in sugar maple and American beech seedling establishment in forests of the northeastern United States. Plant Soil 491, 387–400. https://doi.org/10.1007/s11104-023-06123-2.

Vickers, L.A., McWilliams, W.H., Knapp, B.O., D'Amato, A.W., Dey, D.C., Dickinson, Y.L., Kabrick, J.M., Kenefic, L.S., Kern, C.C., Larsen, D.R., Royo, A.A., Saunders, M.R., Shifley, S.R., Westfall, J.A., 2019. Are current seedling demographics poised to regenerate Northern US forests? J 117, 592–612. https://doi.org/10.1093/jofore/fvz046.

Walters, B.F., Woodall, C.W., Russell, M.B., 2016. White-tailed deer density estimates across the eastern United States, 2008. https://doi.org/10.13020/D6G014.

Walters, M.B., Farinosi, E.J., Willis, J.L., 2020. Deer browsing and shrub competition set sapling recruitment height and interact with light to shape recruitment niches for temperate forest tree species. Ecol. Manag. 467, 118134. https://doi.org/10.1016/j.foreco.2020.118134.

Ward, J.S., Williams, S.C., 2020. Influence of deer hunting and residual stand structure on tree regeneration in deciduous forests. Wildl. Soc. Bull. 44, 519–530. https://doi.org/10.1002/wsb.1120.

Wattles, D.W., Destefano, S., 2011. Status and management of moose in the northeastern United States. Alces 47, 53–68.

White, M.A., 2012. Long-term effects of deer browsing: composition, structure and productivity in a northeastern minnesota old-growth forest. Ecol. Manag. 269, 222–228. https://doi.org/10.1016/j.foreco.2011.12.043.

Woodall, C.W., Monleon, V.J., Fraver, S., Russell, M.B., Hatfield, M.H., Campbell, J.L., Domke, G.M., 2019. Data descriptor: the downed and dead wood inventory of forests in the United States. Sci. Data 6, 1–13. https://doi.org/10.1038/sdata.2018.303.