Modelling white-tailed deer impacts on forest regeneration to inform deer management options at landscape scales

Mark R. Lesser[a,*], Martin Dovciak[a], Rachel Wheat[a,1], Paul Curtis[b], Peter Smallidge[b], Jeremy Hurst[c], David Kramer[c], Margaret Roberts[a], Jaqueline Frair[a]

[a] State University of New York, College of Environmental Science and Forestry, Department of Environmental and Forest Biology, Syracuse, NY 13210, United States
[b] Cornell University, Department of Natural Resources, Ithaca, NY 14853, United States
[c] New York State Department of Environmental Conservation, Albany, NY 12233, United States

ABSTRACT

Long-term continuity of forest cover in eastern North America may be threatened in part by white-tailed deer (*Odocoileus virginianus*), but effectively managing that threat requires greater understanding of the multi-scale nature of deer browsing pressure and other forces affecting forest regeneration. We isolated the effects of white-tailed deer on the regeneration of ten ecologically and commercially important tree species across the state of New York by fitting forest regeneration models with variables representing fine-scale plant competition, stand-scale seed dispersal, and region-wide patterns of climate, land-use, and deer abundance. Deer effects were not consistent across species or space. Increasing deer abundance was associated with declining seedling abundance for six species (*Acer rubrum, Picea rubens, Pinus strobus, Tsuga canadensis, Prunus serotina, and Abies balsamea*), and nonlinear changes (peaking at intermediate deer abundance) for four species (*Acer saccharum, Betula alleghaniensis, Fagus grandifolia, Fraxinus americana*). Models further indicated: (1) in many areas, meaningful increases in tree seedling abundance may not be achievable by reducing deer abundance alone; (2) in some areas, modest reductions in deer abundance may improve forest regeneration—these would be of high deer management priority; and (3) in some areas, the magnitude of deer population reductions required to achieve meaningful improvement in forest regeneration may be too large to be practical. Predicting forest regeneration across heterogeneous landscapes is complex, and isolating the effects of deer requires greater understanding of multiple potentially limiting and interacting factors (e.g., land-use, climate, forest characteristics). Our approach, based on readily available spatial data, may help prioritize areas, define management goals, and lay a foundation for adaptive management of deer to improve forest regeneration.

1. Introduction

Understanding how tree seedlings establish, grow and recruit into forest canopies is a central theme in forest ecology with applications to forest management and conservation (e.g., Runkle, 1981; Pacala et al., 1993; Urgenson et al., 2013). Forest regeneration is the ultimate driver of future forest composition and thus a key aspect of forest sustainability and health (Nyland, 2016). However, advanced forest regeneration may be too low to reliably secure ecologically or economically desirable future forest canopy characteristics over large areas in many regions, including the northeastern United States (Connelly et al.,

2010; Mcwilliams et al., 1995; Nuttle et al., 2013; Ward et al., 2013). While studies have explored how forest regeneration can be affected by multiple ecological drivers, including abiotic factors (e.g., light, soil, or changing climate) and competing vegetation (Pacala et al., 1994; Dovčiak et al., 2003; Torssonen et al., 2015), herbivory by large mammalian browsers has been increasingly highlighted as one of the main factors suppressing forest regeneration and exacerbating regeneration failure at landscape scales (Augustine and McNaughton, 1998; Frelich et al., 2012; Rhodes et al., 2018; Russell et al., 2017).

In eastern North America and elsewhere, sustained high population densities of white-tailed deer (*Odocoileus virginianus*) exert major effects

on forest ecosystems (Côté et al., 2004; Rooney and Waller, 2003). Browsing by white-tailed deer (hereafter deer) exerts strong influences on plant community diversity and composition (Frerker et al., 2014; Gill and Beardall, 2001; Horsley et al., 2003; Knapp and Wiegand, 2014), and can facilitate invasions by non-native plant species (Averill et al., 2018; Kalisz et al., 2014). Importantly, deer effects on forest ecosystems are not restricted only to vegetation as they can cascade throughout multiple trophic levels—affecting soil nutrients, mycorrhizae, animal populations, and overall ecosystem functioning (Shelton et al., 2014). Consequently, resource management agencies have increasingly considered the interdependency of forest health conditions and deer population management (NYSDEC, 2012; Rosenberry et al., 2009). However, isolating the impacts of deer on forest regeneration at the broad spatial scales relevant for deer management (e.g., wildlife management units) is a non-trivial endeavor that requires integrating information across dramatically different spatial scales and trophic levels—ranging from fine-scale, stand-specific information on forest regeneration to coarse-scale, management unit-specific information on deer abundance.

The effects of deer browse on forest vegetation have traditionally been evaluated using exclosure studies in which an artificial "no browse" (or "no deer") state is compared to an uncontrolled and variable level of deer browsing pressure outside the exclosure (Frerker et al., 2014). In contrast, deer enclosure studies incorporate varying known deer densities, and in some cases exclosures and enclosures have been coupled with experimental manipulation of multiple habitat types (e.g., young *vs.* mature forest) and land-use or forest management patterns (Côté et al., 2004; Horsley et al., 2003; Sage et al., 2003; Tremblay et al., 2007) to better isolate deer impacts. While exclosure and enclosure studies provide powerful research tools at local stand scales (*ca.* 1 ha to 1 km^2), they cannot fully encompass the range of forest conditions (e.g., climate, forest composition, topography, land-use patterns) that affect both forest regeneration (Price et al., 2001; Walck et al., 2011; Wason and Dovciak, 2017) and deer browsing behavior (and thus impacts) at the broad landscape scales (≥ 200 km^2) relevant for deer management (Collard et al., 2010; Hurley et al., 2012; Barrett and Schmitz, 2013).

Across broad-spatial scales, landscape heterogeneity influences deer habitat use and resulting browsing pressure depending on dietary preferences and forage abundance (Hurley et al., 2012; Nuttle et al., 2013; Royo et al., 2017; Senft et al., 1987) and non-dietary factors (e.g., thermal cover, Barrett and Schmitz, 2013). Moreover, deer can exhibit density-dependent movement and browsing behavior (Kie and Bowyer, 1999; Patterson and Power, 2002) that result in higher impacts in areas such as small forest fragments surrounded by habitats providing abundant favored forage (e.g., agricultural crops, meadows; Augustine and DeCalesta, 2003). Importantly, models that incorporate landscape-scale heterogeneous browsing effects have been shown to better simulate observed patterns of forest regeneration than those that do not (De Jager et al., 2017). In the mixed agricultural-forested landscape of central New York, any given deer home range (usually ≤ 2 km in radius) may include variable amounts of forest, agricultural, and meadow cover types (with a 2:1:1 ratio on average; Williams et al., 2011), with deer impacts on forest regeneration likely to be positively correlated with the total amount of suitable foraging habitat. Understanding the linkages between coarse-scale (regional) deer abundance and finer-scale variation in deer habitat is a critical step in predicting and managing deer impacts on forest regeneration (Felix et al., 2007).

Our overarching goal was to better understand and predict deer impacts on scales relevant to, and using data readily available to, wildlife managers. Specific objectives were to:

(1) Model the additive and interactive effects of deer abundance and ecological drivers operating at site-, stand- (e.g., forest type, seed source, stand age, light availability; Russell et al., 2001) and landscape-levels (e.g., climate; Thuiller et al., 2005) on

regeneration for common tree species across New York State. We hypothesized that (*i*) the magnitude of deer impacts would be related to deer browse preferences (e.g., sugar maple; *Acer saccharum* more impacted than beech; *Fagus grandifolia*), and (*ii*) deer abundance would be a major driver on regeneration success; potentially equally or more important than stand-level and climate-related drivers, whereas landscape-level factors (e.g., proportion of forage versus forest area, and forest type) would interact with deer abundance to influence local regeneration patterns.

(2) Apply our models to simulate reductions in deer abundance and identify areas where targeted deer management alone may meaningfully improve forest regeneration (cf. Sage et al., 2003; deCalesta, 2010; Stout et al., 2013).

Importantly, intentional use of readily available and regularly updated (e.g., every five to ten years) spatial data on forest structure (U.S. Forest Inventory and Analysis—FIA database; Burkman, 2005) enabled us to evaluate changes in forest regeneration in order to provide feedback for adaptive deer management. Ultimately, this information will allow wildlife and forest managers to more efficiently and effectively accomplish their goals for forest regeneration and ecosystem services (NYSDEC, 2012; PA DCNR, 2013).

2. Methods

2.1. Study area and scope

The study area encompassed the private and public forest lands of New York State in the northeastern United States (Widmann et al., 2015) covering *ca.* 7.66 million ha and 60% of the state (NYSDEC, 2005). Most of this forested area is dominated by second growth forest because 85% of the state was used for agriculture in the 1890s (NYSDEC, 2005). Hardwood forests represent 90% of the forested land, of which maple-beech-birch and oak-hickory forest types are most common, while spruce-fir conifer forests represent a significant portion of forested lands in the northern areas of the state (Widmann et al., 2015).

New York State is characterized by a humid temperate climate with average temperatures ranging from -9 to $1\,°C$ in January and 19 to 25 °C in July (Bailey, 1980; NYSDEC, 2005). Mean annual precipitation is *ca.* 1016 mm per year, with relatively drier conditions in the western regions and moister conditions in the northern regions (particularly the Adirondack Mountains) (NYSDEC, 2005). The topography, geology, soils, and climate are highly variable across the state with ecoregions spanning mountainous areas (e.g., the Adirondack Mountains or the Appalachian uplands) to lowlands (e.g., the Great Lakes ecoregion; NYSDEC, 2005).

2.2. Model variables

We derived response (numbers of seedlings) and predictor (site, stand, and landscape) variables from broadly available, standardized data sets associated with large U.S. national monitoring programs. Deer harvest data are collected annually by state agencies, which makes data on deer abundance over relatively large spatial scales also publicly available. Consequently, our approach is broadly applicable to other states in the U.S. or countries with similar monitoring programs.

Forest regeneration—We calculated seedling abundances for all major tree species (response variables) on 2014 plots of the U.S. Forest Inventory and Analysis (FIA) Program (http://www.fia.fs.fed.us) in New York State (Fig. 1). FIA data are based on periodic field surveys of trees and tree seedlings on plots systematically placed on forest land across the United States. FIA plots are 0.4 ha and contain four circular overstory subplots (7.32 m radius). Nested within each subplot there is a circular microplot (2.07 m radius) where seedlings are identified and measured (Burkman, 2005). The FIA program defines tree seedlings as
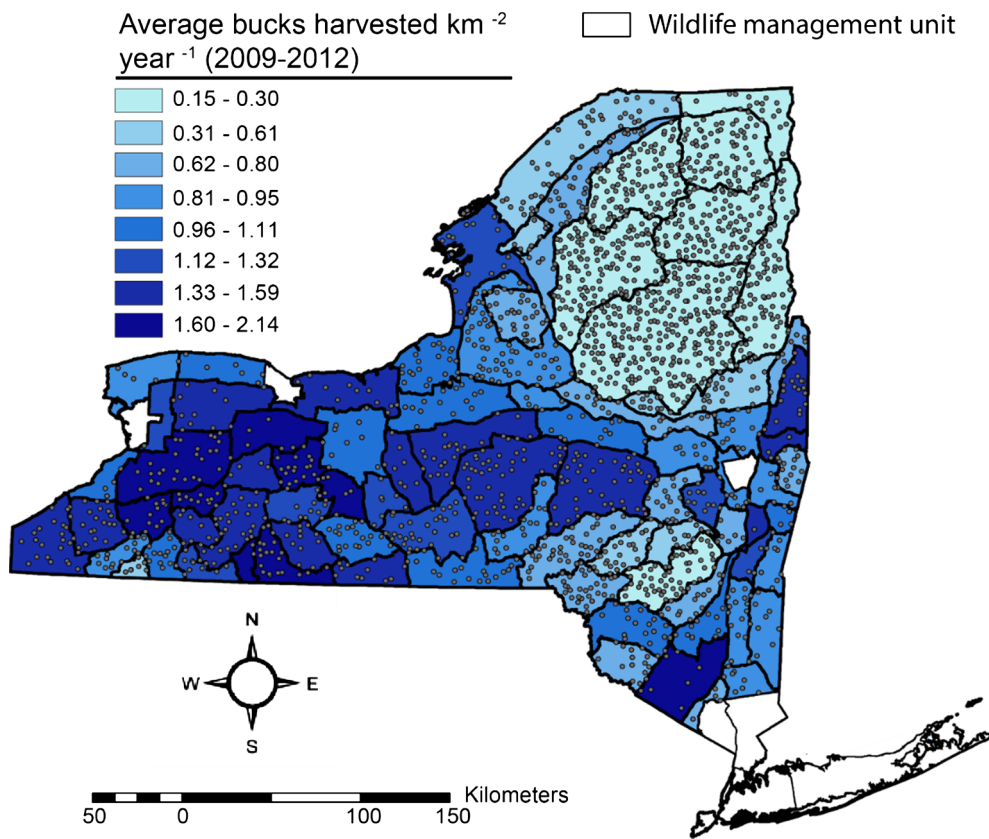
Fig. 1. Map of New York State showing location of 2014 Forest Inventory and Analysis (FIA) plots used in the study (gray dots) and boundaries of wildlife management units (WMUs) (black lines). Shading corresponds to the number of bucks harvested per km² per year (2009–2012 average), used as a proxy of deer abundance (Nesslage and Porter, 2001). White areas indicate WMUs excluded from analysis due to lack of active deer management (and thus data) by the NYSDEC.

Table 1

The 10 tree species selected for analysis, ranked by general deer browse preference* and shade tolerance (Horsley et al., 2003, Latham et al., 2005). Species with the highest seedling abundance were selected, representing > 70% of all seedlings on the 2014 FIA plots meeting our selection criteria (see section *Model variables—Forest regeneration* for details) in New York State.

Species	Common name	Species code	Deer browse preference	Shade tolerance	% of total seedling abundance
Betula alleghaniensis	Yellow birch	BEAL	High	Intermediate	3.68
Fraxinus americana	White ash	FRAM	High	Intermediate	12.72
Acer rubrum	Red maple	ACRU	High	Tolerant	5.92
Acer saccharum	Sugar maple	ACSA	High	Very tolerant	8.98
Tsuga canadensis	Eastern hemlock	TSCA	Moderate	Very tolerant	1.53
Prunus serotina	Black cherry	PRSE	Low	Intolerant	4.4
Pinus strobus	Eastern white pine	PIST	Low	Intermediate	1.99
Picea rubens	Red spruce	PIRU	Low	Tolerant	5.13
Abies balsamea	Balsam fir	ABBA	Low	Very tolerant	8.89
Fagus grandifolia	American beech	FAGR	Low	Very tolerant	19.25

Notes: * Deer browse preferences may vary to some degree across sites depending on food availability, alternative forage sources, disturbance history, snow cover, and other regional and site-specific factors (Horsley et al., 2003, Latham et al., 2005).

individuals < 2.54 cm in diameter at breast height (DBH, 1.3 m height) that are either ≥15.24 cm tall for hardwood species or ≥30.48 cm tall for conifer species (Burkman, 2005). We used the complete FIA inventory for New York State spanning the period between 2008 and 2013. All plots were sampled once during this timeframe. We selected plots following Shirer and Zimmerman (2010) that were (1) fully forested (all four subplots categorized as forested), (2) of natural origin (not a plantation), (3) without human disturbance within the past 5 years, (4) mature or maturing rather than young post-harvest forests (i.e., containing live trees with DBH > 12.7 cm), and (5) with live stocking between 20 and 100%. In addition, plots had to be located in Wildlife Management Units (WMUs; delineated by NYSDEC for deer management purposes) that were open to deer harvest and thus for which we had a measure of deer abundance (see below). The ten ecologically- and commercially-important target species accounted for > 70% of all tree seedlings on the selected plots (Table 1).

Deer abundance index—Formal estimates of deer abundance are rarely available, especially at large extents such as the entirely of a state. Accordingly, we used a deer abundance index (DAI) based on harvest data, specifically the number of bucks harvested in each WMU per year and km². DAI has been shown to correlate well with deer abundance in New York State (Nesslage and Porter, 2001; Sage et al., 1983), and large mammal abundance elsewhere (Ueno et al., 2014), despite natural variation caused by varying hunting effort (e.g., due to local differences in doe harvest or site access). DAI was calculated from New York State Department of Environmental Conservation (NYSDEC) data on annual deer harvest. The 92 WMUs in New York State range in size from 238 to 7892 km² (average size of 1373 km²; NYSDEC, 2012). We excluded six WMUs that occurred in largely urban or suburban areas where deer harvest records are not considered to be a reliable indicator of deer abundance due to hunting restrictions (Buffalo, Rochester, New York City and surroundings, Long Island; Fig. 1). We

averaged the annual deer harvest data for the 2009–2012 period to reduce potential year-to-year variation in deer abundance and hunting regulations.

Forest stand indices—We used FIA overstory data to derive key, stand-level covariates likely to affect tree seedling abundance. We calculated total basal area as an index to the understory light environment, and used target species overstory abundance (canopy abundance; the number of trees > 2.54 cm DBH) as an index of species seed rain (cf. Messier et al., 1998). We used stand age to represent forest development stage (cf. Messier et al., 1998). Importantly, we also calculated interaction terms to account for changes in stand structure over time (stand basal area × stand age) and changes in potential seed rain with stand development (canopy abundance × stand age; cf. McEuen and Curran, 2004). We further hypothesized that while increasing canopy abundance would have a positive effect in terms of seed rain, large abundances of conspecifics may have a negative effect on seedling regeneration with respect to resource levels (e.g., light) or accumulation of seed predators and pathogens (cf. the Janzen-Connell model; Clark and Clark, 1984; Hille Ris Lambers et al., 2002), thus we included a second order polynomial term for canopy abundance to accommodate non-linear responses in our models. To account for general environmental differences, we categorized each plot into one of three broad forest types—mixed hardwoods (maple-dominated hardwoods with other deciduous and conifer species), oak-dominated hardwoods, or spruce-fir forests. Finally, we included the abundance of understory beech (individuals < 2.54 cm DBH) as a predictor of understory competition from beech suckers, which have been noted to create highly competitive beech thickets that can suppress other vegetation in our region (cf. Wagner et al., 2010; Giencke et al., 2014). We also expected that the amount of beech, an undesirable browse species, in the understory may also influence deer behavior and browse selection of other species (Champagne et al., 2018).

Climate—Given pronounced climatic gradients across the state, we obtained mean annual precipitation and mean annual temperature from 30-year Climate Normals (1980–2010) quantified at an 800 m resolution (PRISM, 2004). Although mean annual variables may not be the actual climatic factors directly influencing regeneration success, they tend to be highly correlated with potentially more biologically relevant albeit more difficult to quantify climatic variables (e.g., growing season precipitation or growing season length; Hamann and Wang, 2006; Wason and Dovciak, 2017). Importantly, using these more general climatic variables allowed us to readily characterize broad-scale climatic gradients while avoiding the model over-fitting that can result from including multiple correlated variables within the same model.

Land-use—We characterized land cover within a 2-km radius (1257 ha) around each FIA plot using the National Land Cover Database (NLCD; Fry et al., 2011) and ArcGIS (ESRI, 2018). The radius was chosen to incorporate routine deer movements (< 2 km daily) and home-range sizes in central New York State (Williams et al., 2011), and to account for uncertainty in plot locations due to random displacement (≤1 km) of plot coordinates by the FIA program to protect landowner confidentiality (Woudenburg et al., 2011). To minimize model over-parameterization, we excluded open water and barren cover types. We then pooled all non-forested and non-developed cover types into a single category representing foraging area (Table 2). Importantly, we included foraging area as a modifier on deer abundance (foraging area × DAI) to effectively downscale the WMU-level estimate of deer abundance to more localized contexts where deer abundance (and thus impacts) may be higher or lower relative to the overall WMU estimates. For example, forest plots with a large foraging area in their vicinity may experience greater local deer abundance (and browsing pressure) than plots with no nearby foraging areas, irrespective of regional deer abundance (Augustine and DeCalesta, 2003). Finally, we included as covariates the latitude and longitude of the FIA plots to account for other spatial gradients that might exist across the study area.

Table 2
Predictor variables included in models of species seedling abundance. Units, range, and source are given.

Variable	Description	Type and Units	Range	Source
DAI	Deer abundance index	Continuous, Bucks harvested km^{-2}year^{-1}	0.15–2.14	DEC
BA	Basal area of live trees with ≥2.54 cm DBH	Continuous, m^{2}ha^{-1}	29–309	FIA
Canopy abundance	Canopy abundance of target species with DBH ≥2.54 cm	Continuous, stems/FIA plot	0–56	FIA
Age	Stand age	Continuous, years	15–215	FIA
Fortype	Generalized forest type	Categorical, 1 = mixed hardwood, 2 = oak-dominated hardwood, 3 = spruce/fir	1–3	FIA
FAGR understory	Abundance of understory beech with DBH ≥2.54 cm	Continuous, Stems/FIA plot		FIA
Annual precip.	Mean annual precipitation	Continuous, mm	806–1687	Prism 800 m resolution, 1980–2010 normal
Annual temp.	Mean annual temperature	Continuous, °C	2.89–12.03	Prism 800 m resolution, 1980–2010 normal
Forage area	Area of non-forested, non-developed cover types (meadow, shrubland, grassland, row crops, pasture, and herbaceous wetland) within 2-km radius of FIA plot	Continuous, hectares		NLCD 2006
Latitude	EW coordinate of FIA plot	Continuous, degrees		FIA
Longitude	NS coordinate of FIA plot	Continuous, degrees		FIA

Table 3

Predictor variables in species final models for tree seedling abundance across New York State. Variables are labelled with + or − to show their positive or negative effects on seedling abundance. Parentheses indicate variables retained using the AIC selection despite their lower statistical significance ($P > 0.10$). Species codes and variable explanations are in Tables 1 and 2. Coefficient estimates, standard errors, and significance values are in Table A.3.

Predictor Variable	Species									
	BEAL	FRAM	ACRU	ACSA	TSCA	PRSE	PIST	PIRU	ABBA	FAGR
Main effects										
DAI	(+)	+	−	+	(−)	−	−	−	−	+
Forage area		+	(−)	+	−	+	−			
Canopy abundance	+	+	+	+	+	+	+	+	+	+
BA	−	−	−			−			(−)	(+)
Age	(+)	−	−	(−)		−	−	+	(−)	+
Forest type										
oak	+		+	(+)	(−)	(−)		(−)	(−)	−
spruce/fir	(+)		(+)	−	+	−		+	+	−
FAGR understory	+	−		(−)		−		−	−	
Annual precip		−		−	(+)			+		−
Annual temp	−		−	−			+	−	−	−
Latitude		+					+		(+)	
Longitude		−			+	−		−	+	
Nonlinear effects										
DAI	−	−		−				(−)		−
Canopy abundance	−	−	−	−	−	−	−	−	−	−
Interaction effects										
DAI × fortype										
oak	+		−	(−)	(+)			+		+
spruce/fir	−		(−)	(−)	+			+		(−)
DAI × FAGR understory	+	−		−				−	−	
DAI × forage area			−	(−)		−	−			
BA × age	−	−	−			−			+	−
Canopy abundance × age						+				−

2.3. Model framework and selection

Prior to model fitting, all variables were centered and standardized to reduce potential correlations, increase model fit stability, and allow comparisons of the effect sizes among variables (Dormann et al., 2013). To further guard against multicollinearity, we calculated (*i*) Pearson pair-wise correlation coefficients between all variables and did not allow pairs of highly correlated variables ($r > 0.7$, $P < 0.05$) to be included in the same model (Table A.1), and (*ii*) Variance Inflation Factors (VIF's) for each step in model fitting and excluded variables with $VIF > 5$.

Before model fitting, we randomly withheld 10% of the FIA plots (201 plots) to evaluate the predictive power of final models.

For each of the ten study species, we first fit a base model that controlled for site, stand, and climate effects on seedling regeneration (Table 2, Table A.2). DAI and forage area were the two variables not included in this model (Table 2). This approach allowed us to determine the effect of non-deer related drivers of seedling abundance before entering deer related variables into the model framework. All models were built in R 3.4.1 (R Core Team, 2017) using the glmmTMB package for non-linear mixed models (Brooks et al., 2017). All variables were treated as fixed effects in our models.

Seedling abundance data for all ten species contained a large number of zeros and low seedling counts. Consequently, we compared negative binomial, Poisson, and zero-inflated fits of the base model for each species to ensure that we used the most appropriate response distribution for each species model. AIC scores clearly indicated the negative binomial as best for all species ($\Delta AIC > 100$ in all cases).

Next, we fit a full, negative binomial model for each species that included the base covariates as linear terms as well as a squared term for canopy abundance and 2-way interaction terms related to stand structure (ba × age and canabun × age). We used backwards AIC selection ($\Delta AIC \geq 2$) to determine the best stand/environmental condition model(s) for each species (Table A.2). Backwards AIC selection was run using the MASS package in R (Venables and Ripley, 2002). We then added DAI and forage area variables as linear, non-linear, and interaction terms to those models, and once again used backwards AIC selection to determine the best overall model (Table A.2). The predictive capacity of final models was evaluated by comparing the root mean squared error (RMSE) and R^2 between predicted and observed seedling abundance at the 201 withheld plots.

2.4. Simulating effects of deer reductions

To gain a better understanding of the sensitivity of forest regeneration to potential manipulations of deer abundance, we compared predictions for seedling abundance under ambient conditions from our top models to three simulated levels of deer reductions by virtually decreasing DAI values in each WMU. Reduction levels were selected to simulate minor (25%), moderate (50%), and intense (75%) reductions in deer abundance, although we recognize that intense (and in some cases moderate) reductions may not be feasible management options. To accomplish this, we first predicted seedling abundance under ambient (current) conditions at all 2014 FIA plots using the top-ranked model for each species. Next, holding all other variables at ambient levels, we predicted seedling abundance given each simulated level of deer reduction. To summarize the overall forest regeneration response under each scenario, we summed the predicted seedling density across all species for each reduced level of DAI, and then calculated the percentage change relative to predictions under ambient conditions. To examine spatial patterns, we used Geospatial Analyst in ArcMap 10.5 (ESRI, 2018) to create a continuous prediction surface for the percentage change in seedling abundance across New York State under each deer reduction scenario. We used an ordinary kriging with the default parameters, as changing the underlying model, transforming coordinates, or adjusting bins did not improve model fit. Resulting spatial predictions were classified into positive or negative changes over ambient conditions with relative large (> 30%), moderate (15–30%), slight (5–15%) or marginal (< 5%) positive or negative changes in seedling abundance relative to ambient conditions.

Tree species showing non-linear, concave (humped) relationships between seedling regeneration and increasing deer abundance (i.e.,
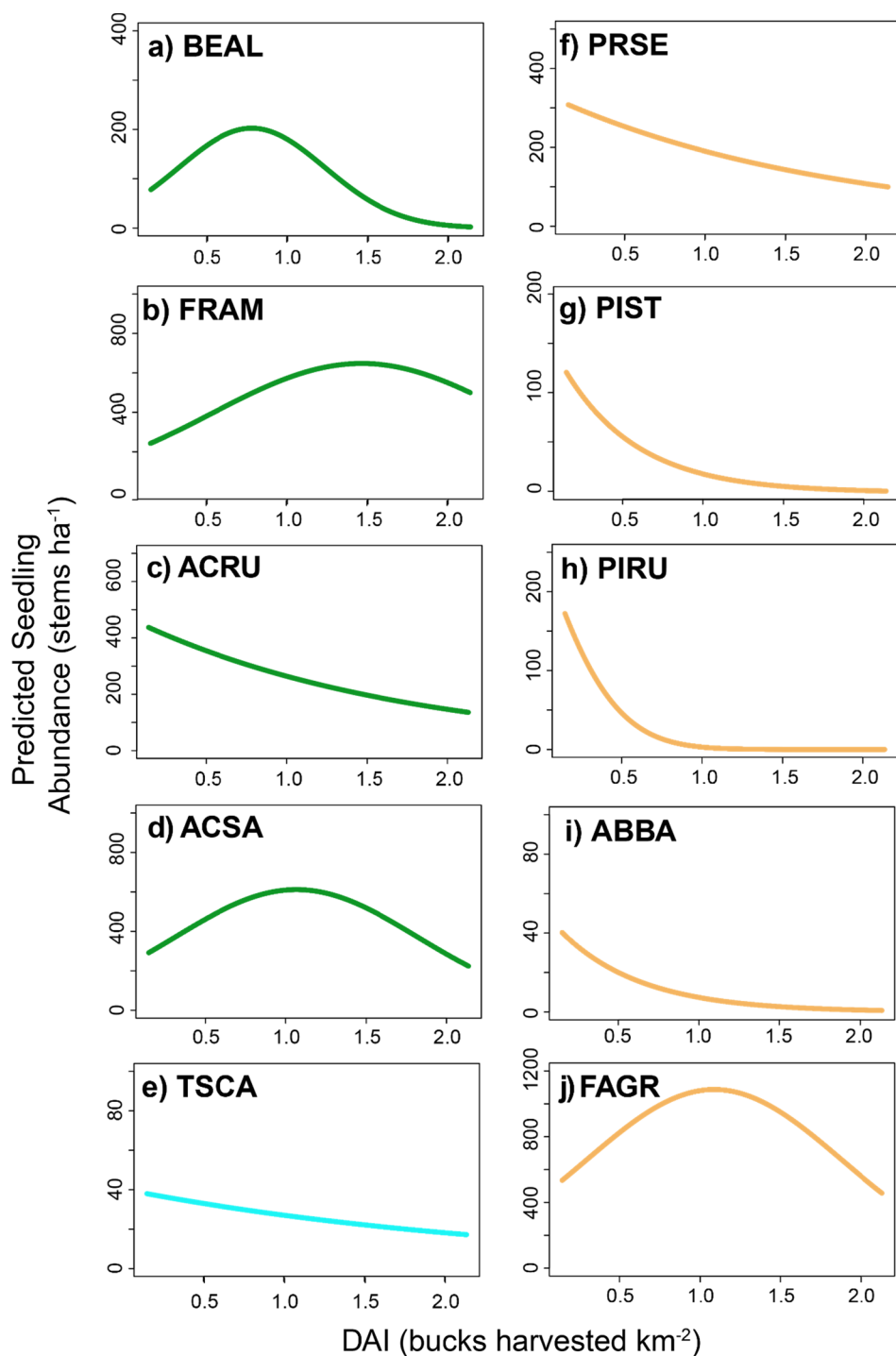
Fig. 2. Predicted seedling abundance with varying deer abundance index (DAI). DAI was varied in 0.002 increments between the minimum (0.15) and the maximum (2.14) values found across New York State, while all other model parameters were held constant at their mean values. Species are ordered (and colored) based on presumed deer preference; green = high, blue = intermediate, and orange = low (species codes are given in Table 1). Note changes in y-axis scale across panels. Note that the apparent decrease in seedling abundance with increasing DAI was not statistically significant for TSCA (f) (see Table 3). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

where seedling abundance peaked at intermediate deer abundance) required additional exploration relative to (*i*) the deer abundance associated with the maximum predicted seedling abundance, and (*ii*) the necessary percentage change (reduction or increase) in DAI required for each FIA plot to reach maximum seedling abundance (holding all other variables at ambient levels). Ultimately, we created a continuous prediction surface over New York State of the change in DAI required to maximize seedling abundance using Geospatial Analyst in ArcMap 10.5 (ESRI, 2018). Although increased seedling abundance may not always be necessary for successful forest regeneration, we defined optimal DAI as that which maximized seedling abundance. We then identified areas of the state where maximizing seedling abundance via reductions in deer abundance may be feasible by mapping the change in DAI

necessary to reach optimal DAI (associated with maximum seedling abundance). We used three categories to map areas where DAI reductions of (*i*) > 50%, (*ii*) 25–50%, and (*iii*) 0–25% may lead to improved forest regeneration relative to those areas where reducing DAI is not likely to increase forest regeneration (ambient DAI < optimal DAI).

3. Results

3.1. Ecological drivers of seedling abundance

The best supported model for each species contained deer related effects, but also included a total of 8 to 13 parameters (Table A.2). Species overstory abundance (canabun) had strong concave effects on
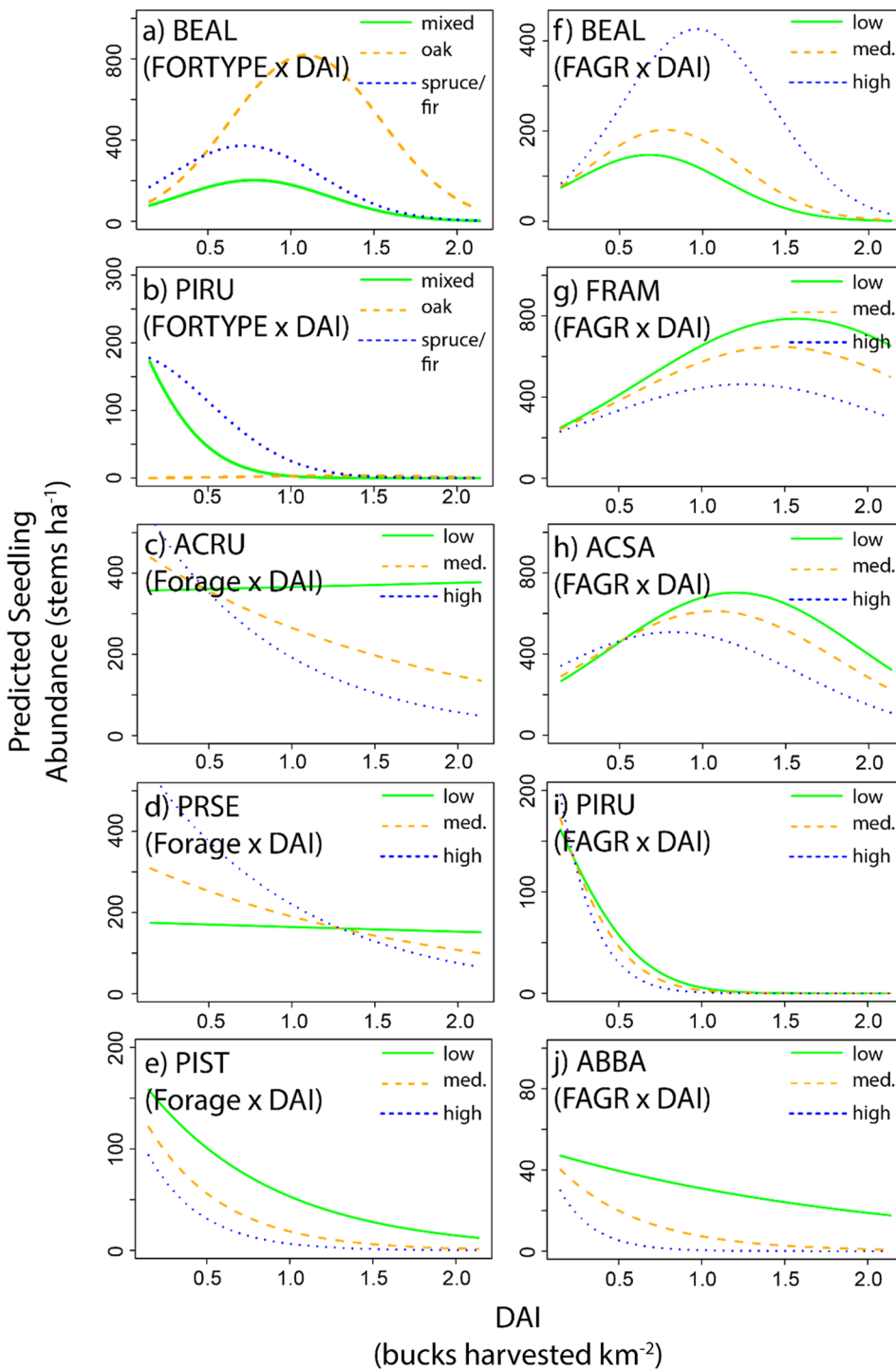
Fig. 3. Predicted seedling abundance as a function of deer abundance index (DAI) and its interactions with other covariates: (a-b) forest type (FORTYPE). Only species that had significant interactions at all forest type levels are shown. (c-d) forage area (Forage), and (f–j) understory beech abundance (FAGR). DAI was varied in 0.002 increments between the minimum (0.15) and the maximum (2.14) values found across New York State. The interacting covariate was varied at three levels (low = −1.5, medium = 0, and high = 1.5 of the centered and standardized values), except for the forest type modelled for each of its three categories (1 = mixed hardwood, 2 = oak dominated hardwood, 3 = spruce/fir). All other model parameters were held constant at their mean values. Species codes are in Table 1. The scale of y-axis varies among panels.

seedling abundance for all species (Table 3). For most species, final models also included climate (temperature, precipitation), geographic position (latitude, longitude), and forest characteristics (type, basal area, age) with varied effects and interactions across the ten species based on their ecological requirements (Table 3). As expected, stand basal area had negative effects on seedling regeneration for shade intolerant species (BEAL, FRAM, PRSE,) and no, or insignificant, effects on very shade tolerant species (FAGR, ABBA, ACSA, TSCA) (Table 3). Yet, for all species, the best models including deer influences were substantially better (ΔAIC > 6) than the best base model that accounted for stand/environmental conditions alone.

The final, best supported models for all species contained DAI, but

responses to DAI varied by species (Table 3, Fig. 2). For some species (ACRU, TSCA, PRSE, PIST, PIRU, and ABBA), seedling abundance generally showed a sharp decline with increasing DAI. The remaining species (BEAL, ACSA, FRAM, and FAGR) showed nonlinear (concave) associations with DAI, with seedling abundance initially increasing up to a threshold value above which further increases in DAI corresponded to declining seedling abundance (Table 3, Fig. 2). For species demonstrating concave responses, peaks in predicted seedling abundance varied among species from starting to decline under relatively low (DAI = 0.78; BEAL), moderate (DAI = 1.07–1.09; ACSA and FAGR), or high deer pressure (DAI ~ 1.46; FRAM) (Fig. 2).

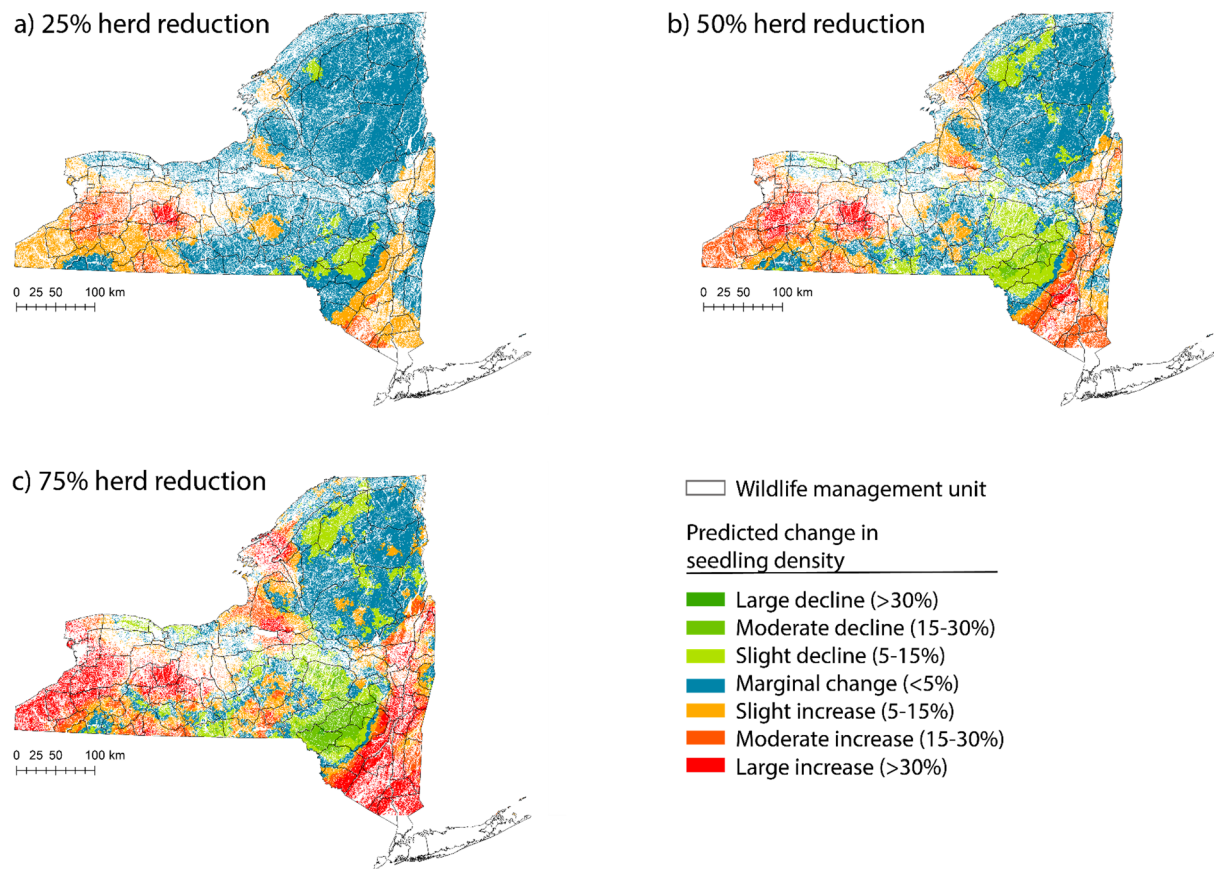Further, the effects of DAI on seedling abundance varied with forest

Fig. 4. Predicted response of total seedling abundance (all species pooled) across forest areas of New York State to simulated reductions in deer abundance (DAI). Three scenarios are shown: (a) 25%, (b) 50%, and (c) 75% reductions of deer abundance from ambient conditions. Colors indicate % change (increase or decrease) in total seedling abundance relative to ambient conditions (seedlings ha^{-1}).

type (BEAL and PIRU), the amount of forage area (ACRU, PRSE, and PIST), and the abundance of beech in the understory (BEAL, FRAM, ACSA, PIRU, and ABBA) (Table 3; Fig. 3). For yellow birch seedling abundance was higher in oak dominated forest types, while red spruce seedlings were most abundant in spruce/fir dominated forests compared to other forest types (Fig. 3a–b). Red maple, black cherry, and eastern white pine all showed lowest levels of seedling abundance at high DAI associated with high forage area (Fig. 3c–e). Abundance of understory beech apparently exacerbated the negative impacts of deer pressure on white ash, sugar maple, red spruce and balsam fir (Fig. 3g–j). In contrast, yellow birch showed a positive response to increasing understory beech (Fig. 3f).

Although our models identified statistically significant drivers of tree seedling abundance (as indicated by AIC model selection), the proportion of variance explained in seedling abundance was both low and highly variable, ranging from < 0.01 to 0.50 across species (Table A.4). The large portion of unexplained variance was expected, and highlights the potentially dominant influence of site-specific factors for which information is not readily available such as stand disturbance history, slope, aspect, and soil nutrient and moisture levels. Consequently, we consider our models useful for exploring the effects of selected factors (including deer pressure) on relative changes in seedling abundances over space, time, or given alternative DAI levels (cf. simulation results below) rather than for predicting the absolute magnitude of seedling abundances at any given location.

3.2. Effects of simulated reductions of deer abundance

Reducing DAI statewide by 25% resulted in slight to moderate increases (5–30%) in predicted seedling abundance (all species pooled)

on 43% of New York State's forested area, with the majority of the remaining forest area (56%) showing only marginal changes in seedling abundance (< 5%; Fig. 4a). Reducing DAI by 50 and 75% resulted in large increases (> 30%) in predicted seedling abundance on 10.3% and 20.4% of New York State forest area, respectively (Fig. 4b-c), but also increased the area where seedling abundances were predicted to decline (10.8% of forests under 75% DAI reduction; Fig. 4b-c) given the nonlinear associations observed between DAI and seedling regeneration.

Reducing DAI had a positive effect on seedling abundance of the species that showed monotonic declines in seedling abundance with increasing DAI (ACRU, PIRU, PIST, PRSE, and ABBA; Fig. 2). However, reducing DAI either increased or decreased seedling abundance for the species demonstrating humped responses to DAI (BEAL, ACSA, FRAM, and FAGR; Fig. 2) depending on how the ambient DAI and DAI reduction level compared to the DAI associated with peak seedling abundance. Reducing DAI to maximize seedling abundance was required on 11, 37, 37, and 62% of forest area in New York State for white ash, American beech, sugar maple, and yellow birch, respectively (Fig. 5). DAI reductions were required to maximize seedling abundance of these four species in the west and south of the state, while seedling abundance in northern and eastern areas did not increase with reduced DAI (Fig. 5).

Overall, simulated DAI reductions had (*i*) consistent beneficial effects on seedling abundance in some areas of New York State (e.g., central New York State, and parts of the southeastern Hudson River Valley/Taconics corridor), and (*ii*) negligible or negative effects on seedling abundance in other areas (i.e., the Adirondacks in the north, areas of the southern tier in the southwest, much of the southeast).
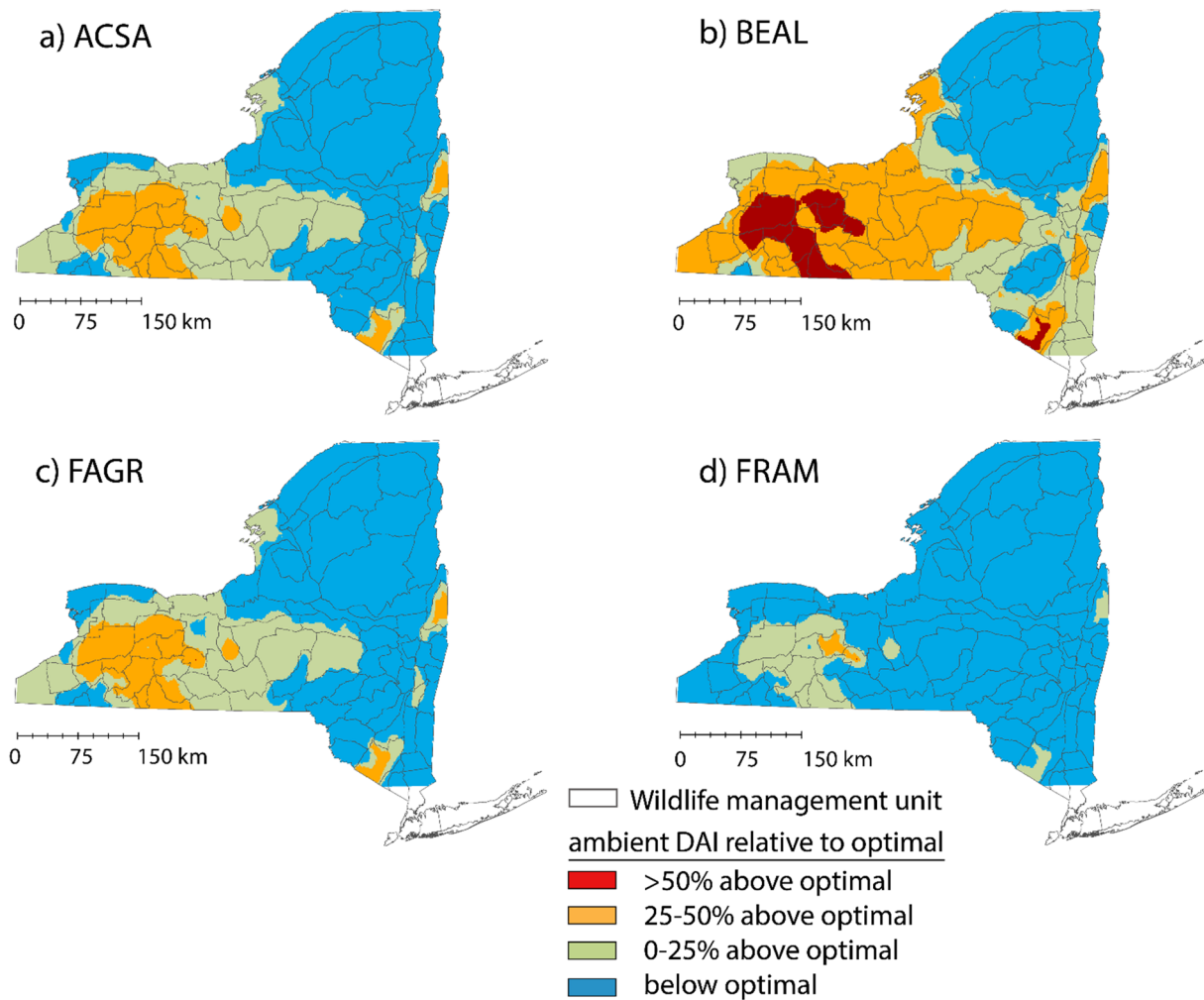
Fig. 5. Change in deer abundance (DAI, in %) relative to the ambient conditions that would optimize (maximize) modelled seedling abundance for the four species with concave responses of seedling abundance to DAI. DAI above optimal indicates that the deer herd should be reduced by the amount indicated (%), while DAI below optimal indicates that maximum seedling abundance is associated with higher deer abundance than ambient DAI (i.e., forest regeneration would not benefit from deer abundance reductions). Species codes are in Table 1.

4. Discussion

The mechanistic drivers of forest regeneration have been studied at fine-spatial scales (1–10 km^2), including local effects of deer browsing (Côté et al., 2004; Horsley et al., 2003; Sage et al., 2003). Likewise, variation in deer density has been implicated as a major driver of forest regeneration dynamics over large spatial extents, such as the entire eastern coast of the United States (Rooney and Waller, 2003; Russell et al., 2017). But hampering effective action to date has been, in part, the lack of insights and tools operating at the intermediate scales over which deer herds are managed. We helped fill that critical gap with predictive models for seedling regeneration based on readily available data targeting both fine- (site and stand) and broad-scale (landscape) drivers of forest regeneration, considering fundamental biotic aspects such as competition for light, and capturing contextual variation known to mediate or exacerbate local deer impacts. We did not assess whether existing seedling densities were adequate or inadequate for successful forest regeneration *per se*, but instead applied our models to identify the relative extent to which seedling abundance might change given reductions in deer abundance. As such, we set the stage for strategic management planning, recognizing that tactics will vary based on site-specific conditions.

Our models predict that reducing deer abundance from ambient conditions in NY State would have a largely positive effect on seedling abundance. Although Russell et al. (2017) came to a similar conclusion for the northeastern US (also using FIA data), we showed that the impact of reduced deer abundance on forest regeneration was likely to be highly spatially variable at scales relevant to deer and forest management (Fig. 4), which has nontrivial implications for resource managers attempting to implement meaningful strategies at local-scales. For example, a more liberal deer harvest target might be set for a given wildlife management unit but landscape heterogeneity within that unit will drive spatial variation in deer impacts on forest regeneration. The five-year cycle for resampling FIA plots provides a reasonable interval for assessing the degree to which changes in deer management might influence regeneration patterns, and recent additions to the FIA methodology that include directly recording deer browsing impacts at each site and quantifying understory vegetation (Phase 3), will further enhance the usefulness of FIA data for monitoring the management effectiveness.

Our hypothesis that deer would have greater negative impacts on preferred browse species was largely supported, but was not as straightforward as anticipated. Of the six species that had monotonic declines in seedling abundance with increasing deer abundance, three were considered as 'low browse preference' (PIST, PIRU, and ABBA), two considered as 'moderate' (PRSE, and TSCA), and only one (ACRU) considered as 'high'. However, less-desirable browse species may be targeted by deer when more preferred species are depleted by

overbrowsing (Rawinski, 2016). Moreover, overall declines in tree seedling abundance correspond often to understories dominated by interfering vegetation, such as ferns, that are unpalatable to deer (Horsley et al., 2003).

Importantly, our result that tree seedling abundance does not always decline monotonically with increasing deer density corroborates much research on intermediate herbivory theory (e.g., Holt and Polis, 1997; Tremblay et al., 2006). Two preferred browse species (ACSA, BEAL) showed concave responses to deer abundance in our study. Our results for yellow birch were similar to Horsley et al. (2003), but did not show the same pattern for sugar maple which declined linearly with increasing deer abundance in their study (however ACSA abundance was low in their study area and may not have been adequately represented). Consistent with the intermediate disturbance hypothesis, our results indicate that these two species respond positively to low browsing pressure but decline under high browsing pressure. Importantly, across large areas of New York State we identified that present levels of deer abundance are higher than that predicted to maximize seedling abundance for ACSA and BEAL in our models (Fig. 5). As a result, we predict that modest deer reductions (25%) would meaningfully improve regeneration of these two ecologically important tree species in this region (Fig. 4).

In contrast, two other species (FRAM, FAGR) indicated a prolonged positive relationship through high deer abundances before declining seedling density would be expected. As a result, these species are not likely to benefit from deer reductions because DAI across most of the state falls below their predicted optimum (Fig. 5). Interestingly, the positive response of FRAM to deer pressure was most clear in areas where competition with FAGR was low. Even so, FRAM was quite sensitive to deer pressure in areas with abundant FAGR (Fig. 3g), corroborating the susceptibility of FRAM to the legacy effects of overbrowsing and dense understories (de la Cretaz and Kelty, 2002; Aronson and Handel, 2011; Jenkins et al., 2015). The positive impacts of deer abundance may be mediated by decreased competition from other species (woody or non-woody; Webster et al., 2018), which seems to be needed in New York to effectively improve regeneration conditions for intermediately shade-tolerant FRAM. FAGR is highly shade-tolerant and of 'low browse preference' so it may only become browsed in the absence of more preferable species (i.e., under persistently high deer abundance). Importantly, FAGR abundance in forest understories in the region has been elevated due to beech bark disease as this species easily re-sprouts when damaged to form persistent beech thickets (Giencke et al., 2014) that negatively affect other tree species (Wagner et al., 2010). Eradication of beech thickets is an ongoing management problem in northeastern forests. That beech and deer browsing pressures interactively influence tree regeneration for many species underscores the difficulty of isolating and managing a single driver (e.g., deer) on forest regeneration.

Legacy effects of elevated deer abundance relative to historic conditions (cf. in the Hudson River Valley) may also negatively affect seedling abundance. Limited seed source or persistently altered habitat conditions (e.g., recalcitrant understories composed of species that deer avoid) may be the result of high levels of past browsing and the abundance of these species may drive regeneration failures over the long-term even under reduced deer abundances (George and Bazzaz, 1999; Royo and Carson, 2006; Webster et al., 2018). We found that negative effects of deer browsing may be compounded by the surrounding available forage area which was a significant negative predictor of seedling abundance for half of the studied tree species. Deer may preferentially use landscapes containing high forage area with embedded forest patches that optimize food availability and shelter. Forest fragmentation may thus play an important role in forest regeneration failure due to deer browsing (Augustine and DeCalesta, 2003; Augustine and Frelich, 1998). Further, our findings may underestimate the effect of forage area since we did not consider early successional forest stands as part of our forage land class. This may be particularly important in areas with high levels of forest harvesting (Royo et al., 2017).

4.1. Management implications

By including important site-specific variables and accounting for complex interactions, we showed that even modest reductions in the deer abundance (~25%) might meaningfully improve forest regeneration (up to 30% increase in seedling density) for wide swaths of New York State, particularly in areas with low regeneration (Shirer and Zimmerman, 2010). However, in many areas of the state our models predicted little to no change in seedling abundance even for a 75% reduction in deer abundance. In some areas, such as the Adirondack region of northern New York State, deer abundance may be sufficiently low that browsing is not currently a limiting factor for seedling regeneration (Didier and Porter 2003; but see Sage et al. (2003) for contradictory findings), and reducing deer numbers is not anticipated to positively improve regeneration. In other areas, invasive species, available sunlight, soil moisture, seedling recruitment, and other factors – potentially but not necessarily related to persistently high deer abundance – may be limiting local regeneration success such that reductions in deer density alone are unlikely to improve regeneration conditions (Rooney et al., 2000; Dovčiak et al., 2003; Harrington et al., 2013).

Our findings point to the need for coordinating forest management over larger landscapes with deer management in order to meet forest regeneration goals. Our predictions are likely conservative given that greater improvement of forest regeneration may be achieved via the combination of silvicultural practices and deer management. Our model predictions in combination with assessments of contemporary seedling densities can help identify those areas where not only seedling regeneration is of concern, but also where potential pathways towards improving those conditions through deer management alone or in combination with other local or landscape improvements is possible.

The magnitude of potential regeneration responses following any reduction in deer abundance will depend upon a suite of unknown factors, such as potential responses of other browsers (e.g., eastern cottontail) to changes in deer abundance, available seed supply, and soil conditions, as well as stand and site manipulations that might occur. Given these unknowns, we recommend an adaptive management framework in which our models guide site-specific actions, and the next complete cycle of FIA data can be used along with contemporary levels of deer abundance to ascertain the degree to which management actions achieved the desired response (Williams et al., 2009; Williams and Brown, 2014). Moreover, an adaptive management approach will better allow managers to deal with the relationship between deer management regulations and actual levels of deer harvest. The present model results can guide management that will lead to outcomes that can be used to refine the models, thus improving them over time (Williams and Brown, 2014).

As managers increasingly seek information applicable at forest management scales, tools that explore complex interactions and drivers at appropriate scales are critical for informing management decisions. In addition to assisting in deer management strategies, modelling tools, such as ours, can inform forest management decisions related to other pressures on forest health such as climate change (Millar et al., 2007), invasive pests and diseases (Pimentel et al., 2005; Trumbore et al., 2015), and forest fragmentation (Matlack, 1993).

Appendix A

Table A1

Correlations between model covariates. See Table 2 for variable abbreviations and details. Correlations between canopy abundance variables are not included as they were species specific and did not co-occur in models.

	DAI	Longitude	Latitude	Age	ba	Annual precip.	Annual temp.	Forest type	can_ABBA	can_ACRU
DAI	\	−0.67	−0.66	−0.33	−0.03	−0.38	0.66	0.01	−0.24	0.02
Longitude		\	0.40	0.24	0.03	0.27	−0.32	0.07	0.16	−0.05
Latitude				0.11	−0.08	−0.06	−0.59	−0.03	0.24	−0.02
Age				\	0.27	0.22	−0.29	0.02	0.02	−0.16
ba					\	0.10	0.00	0.00	0.13	0.18
Annual precip.						\	−0.45	0.00	0.20	0.04
Annual temp.							\	0.06	−0.30	0.03
Forest type								\	0.42	−0.09
Forage area									0.01	0.02

	can_ACSA	can_BEAL	can_FAGR	can_FRAM	can_PIRU	can_PIST	can_PRSE	can_QURU	can_TSCA	forage_area
DAI	0.01	−0.32	−0.33	0.27	−0.30	0.02	0.08	0.13	0.02	0.63
Longitude	−0.02	0.18	0.17	−0.19	0.16	0.10	−0.15	0.03	0.03	−0.49
Latitude	0.01	0.20	0.17	−0.15	0.24	−0.02	−0.02	−0.19	−0.06	−0.24
Age	0.10	0.19	0.28	−0.23	0.14	−0.08	−0.19	0.04	0.22	−0.38
ba	−0.01	0.07	0.00	0.03	0.12	0.17	0.06	0.05	0.31	−0.11
Annual precip.	0.05	0.34	0.26	−0.18	0.23	−0.15	0.01	−0.13	−0.04	−0.45
Annual temp.	−0.12	−0.37	−0.43	0.20	−0.38	0.17	0.05	0.23	0.12	0.52
Forest type	−0.19	−0.15	−0.19	−0.08	0.33	−0.01	−0.06	0.30	−0.07	−0.04
Forage area	0.00	−0.01	−0.03	0.01	−0.01	0.02	−0.02	0.00	−0.01	\

Table A2

The most parsimonious models of seedling abundance for ten ecologically or commercially important tree species in New York State. For each species, the base model AIC score is given followed by the difference in AIC from the base model (ΔAIC) for subsequent models. The number of predictor variables is indicated in parentheses. See Table 1 for species abbreviations.

Model	Species									
	ABBA	ACRU	ACSA	BEAL	FAGR	FRAM	PIRU	PIST	PRSE	TSCA
Base Stand Condition	2616.1 (12)	4696.0 (12)	5318.0 (12)	3169.1 (12)	8171.8 (12)	6294.1 (12)	3003.1 (12)	1958.4 (12)	4005.1 (12)	1939.4 (12)
Reduced Stand Condition	−2.0 (10)	−2.8 (10)	−7.4 (7)	−3.6 (10)	−1.9 (10)	−4 (10)	−6.2 (8)	−6.1 (7)	−1.4 (10)	−10.6 (5)
Deer Related + Stand Condition	−3.6 (16)	−25.2 (16)	−31.4 (13)	−26.1 (16)	−20.2 (16)	−40.4 (16)	−76.9 (14)	−54.1 (13)	−4.5 (16)	−15 (11)
Reduced Deer related + Stand Condition	−8.7 (12)	−29.7 (13)	−33.4 (13)	−32.3 (12)	−22.6 (13)	−46.1 (12)	−81.3 (12)	−62.7 (8)	−9.0 (12)	−20.5 (8)

Table A3

AIC-selected, negative binomial models predicting seedling abundance (seedlings/ha) as a function of site covariates (see Table 1 for species descriptions and Table 2 for variable descriptions). For each species, the estimated coefficient (B) is given for the centered and standardized variable along with the coefficient standard error (SE). Coefficient estimates different from zero given $P < 0.10$ are indicated by '*'. Nonlinear responses were fit using quadratic terms (X and X^2), and two-way interactions are indicated by '×'. Deer-related effects are highlighted using light gray for the main effects of deer abundance (DAI) and dark gray for interactions involving DAI. Also reported for each model is the estimated overdispersion parameter (c) model degrees of freedom (df), and R^2.

Variable	ABBA B	SE	ACRU B	SE	ACSA B	SE	BEAL B	SE	FAGR B	SE
Intercept	−2.70	0.32*	0.51	0.11*	1.09	0.13*	0.08	0.15	1.66	0.05*
Forest type										
oak	−17.85	2419.57	1.08	0.31*	0.33	0.28	1.10	0.33*	−0.49	0.15*
spruce/fir	1.19	0.33*	0.36	1.31	−17.63	10.56*	0.61	1.83	−2.19	0.98*
Canopy abundance	2.41	0.16*	0.68	0.11*	1.37	0.11*	1.35	0.16*	1.74	0.06*
Canopy abundance²	−0.24	0.02*	−0.18	0.04*	−0.29	0.04*	−0.26	0.04*	−0.29	0.01*
BA	−0.03	0.10	−0.15	0.08*			−0.35	0.10*	0.01	0.06
Age	−0.05	0.09	−0.31	0.09*	−0.13	0.09	0.13	0.11	0.24	0.04*
FAGR understory	−2.01	0.67			−0.10	0.08	0.62	0.12*		
Annual precip.					−0.35	0.08*			−0.14	0.05*
Annual temp.	−0.98	0.14*	−0.41	0.12*	−0.68	0.12*	−0.72	0.15*	−0.44	0.06*
Latitude	0.19	0.13	0.23	0.11*					−0.17	0.06*
Longitude	0.69	0.22*	−0.53	0.11*						
BA × age	0.15	0.08*	−0.12	0.07*			−0.31	0.10*	−0.07	0.03*
Canopy abundance × age									−0.11	0.02*
DAI	−1.01	0.37*	−0.30	0.17*	0.29	0.13*	0.09	0.16	0.28	0.07*
DAI²					−0.23	0.12*	−0.62	0.14*	−0.20	0.04*
Forage area			−0.16	0.12	0.43	0.12*				
DAI × FAGR understory	−1.47	0.64*			−0.22	0.08*	0.46	0.13*		
DAI × forage area			−0.31	0.11*	−0.17	0.12				
DAI × forest type										
oak			−0.68	0.31*	−0.28	0.28	0.77	0.35*	0.29	0.12*
spruce/fir			−0.44	1.39	−14.35	9.42	−0.14	0.13*	−0.72	0.98
c	0.276		0.149		0.156		0.110		0.76	
df	1794		1792		1792		1793		1792	

Variable	FRAM B	SE	PIRU B	SE	PIST B	SE	PRSE B	SE	TSCA B	SE
Intercept	0.94	0.08*	−2.57	0.22*	−1.72	0.14*	0.17	0.09*	−1.78	0.11*
Forest type										
oak	−0.54	0.18*	−1.92	1.27			−0.12	0.24	−0.60	0.40
spruce/fir	−3.16	0.70*	1.48	0.72*			−1.25	0.48*	3.08	0.81*
Canopy abundance	0.89	0.09*	1.14	0.09*	1.87	0.19*	0.92	0.13*	1.93	0.14*
Canopy abundance²	−0.17	0.02*	−0.07	0.01*	−0.22	0.03*	−0.07	0.02*	−0.25	0.03*
BA	−0.24	0.06*					−0.15	0.07*		
Age	−0.39	0.07*	0.20	0.06*	−0.19	0.11*	−0.41	0.09*		
FAGR understory	0.19	0.07*	−0.79	0.38*			−0.16	0.07*		
Annual precip.	−0.54	0.07*	0.38	0.07*					0.15	0.10
Annual temp.			−0.54	0.14*	1.24	0.16*				
Latitude					0.41	0.14*				
Longitude			−0.42	0.17*			−0.47	0.09*	0.33	0.14*
BA × age	−0.13	0.06*					−0.22	0.07*		
Canopy abundance × age							0.26	0.11*		
DAI	0.42	0.08*	−2.74	0.44*	−1.12	0.21*	−0.29	0.11*	−0.20	0.16
DAI²	−0.15	0.05*	−0.52	0.34						
Forage area	0.32	0.07*			−0.81	0.17*	0.28	0.11*	−0.34	0.15*
DAI × FAGR understory	−0.12	0.06*	−0.79	0.36*						
DAI × forage area					−0.47	0.19*	−0.25	0.08*		
DAI × forest type										
oak			3.90	1.46*					0.51	0.37
spruce/fir			1.25	0.72*					1.65	0.86*
c	0.257		0.465		0.132		0.148		0.181	
df	1794		1793		1799		1794		1797	

Table A4

Comparison of predicted and observed seedling abundances by species for a subset (10%) of FIA plots withheld from model building. Root mean-squared error (RMSE; seedlings per plot) and R^2 values are based on seedling abundances predicted using the final model for each species and compared to the withheld observed (test) data set.

Species	RMSE	R^2
ABBA	185.75	0.360
ACRU	6.53	0.007
PIRU	3.25	0.132
PIST	2.55	0.500
PRSE	4.31	0.402
ACSA	6.05	0.025
TSCA	2.34	0.180
FAGR	7.53	0.321
BEAL	4.47	0.032
FRAM	12.28	0.045

References

Aronson, M.F.J., Handel, S.N., 2011. Deer and invasive plant species suppress forest herbaceous communities and canopy tree regeneration. Nat. Areas J. 31, 400–407. https://doi.org/10.3375/043.031.0410.

Augustine, D., DeCalesta, D.S., 2003. Defining deer overabundance and threats to forest communities: from individual plants to landscape structure. Ecoscience 10, 472–486.

Augustine, D.J., Frelich, L.E., 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. Conserv. Biol. 12, 995–1004.

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

Averill, K.M., Mortensen, D.A., Smithwick, E.A.H., Kalisz, S., McShea, W.J., Bourg, N.A., Parker, J.D., Royo, A.A., Abrams, M.D., Apsley, D.K., Blossey, B., Boucher, D.H., Caraher, K.L., DiTommaso, A., Johnson, S.E., Masson, R., Nuzzo, V.A., 2018. A regional assessment of white-tailed deer effects on plant invasion. AoB Plants 10. https://doi.org/10.1093/aobpla/plx047.

Bailey, R.G., 1980. Description of the ecoregions of the United States. U.S Department of Agriculture, Forest Service.

Barrett, K.J., Schmitz, O.J., 2013. Effects of deer settling stimulus and deer density on regeneration in a harvested southern New England forest. Int. J. For. Res. 2013, 1–11. https://doi.org/10.1155/2013/690213.

Brooks, M.E., Kristensen, K., van Benthem, Koen J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. R J. 9, 378–400.

Burkman, B., 2005. Forest inventory and analysis sampling and plot design, FIA fact sheet series. FIA fact sheet series. U.S. Dep. Agric. For Serv.

Champagne, E., Dumont, A., Tremblay, J.-P., Côté, S.D., 2018. Forage diversity, type and abundance influence winter resource selection by white-tailed deer. J. Veg. Sci. 29. https://doi.org/10.1111/jvs.12643.

Clark, D.A., Clark, D.B., 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the janzen-connell model. Am. Nat. 124, 769–788. https://doi.org/10.1086/284316.

Collard, A., Lapointe, L., Ouellet, J.P., Crête, M., Lussier, A., Daigle, C., Côté, S.D., 2010. Slow responses of understory plants of maple-dominated forests to white-tailed deer experimental exclusion. For. Ecol. Manage. 260, 649–662. https://doi.org/10.1016/j.foreco.2010.05.021.

Connelly, N.A., Smallidge, P.J., Goff, G.R., Curtis, P.D., 2010. Foresters' Perceptions of Forest Regeneration and Possible Barriers to Regeneration in New York State HDRU Series No 10–2. Human Dimensions Research Unit, Department of Natural Resources, Cornell University, Ithaca, NY.

Côté, S.D., Rooney, T.P., Tremblay, J., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Syst. 35, 113–147. https://doi.org/10.2307/annurev.ecolsys.35.021103.30000006.

De Jager, N.R., Drohan, P.J., Miranda, B.M., Sturtevant, B.R., Stout, S.L., Royo, A.A., Gustafson, E.J., Romanski, M.C., 2017. Simulating ungulate herbivory across forest landscapes: a browsing extension for LANDIS-II. Ecol. Modell. 350, 11–29. https://doi.org/10.1016/j.ecolmodel.2017.01.014.

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

deCalesta, D., 2010. Achieving and maintaining sustainable white-tailed deer density with adaptive management. Hum.-Wildl. Interact. 11, 99–111.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography (Cop.) 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Dovčiak, M., Reich, P.B., Frelich, L.E., 2003. Seed rain, safe sites, competing vegetation, and soil resources. Can. J. For. Res. 33, 1892–1904.

ESRI, 2018. ArcGIS 10.5 for Desktop.

Felix, A.B., Walsh, D.P., Hughey, B.D., Campa, H., Winterstein, S.R., 2007. Applying landscape-scale habitat-potential models to understand deer spatial structure and movement patterns. J. Wildl. Manage. 71, 804–810. https://doi.org/10.2193/2006-366.

Frelich, L.E., Peterson, R.O., Dovčiak, M., Reich, P.B., Vucetich, J.A., Eisenhauer, N., 2012. Trophic cascades, invasive species and body-size hierarchies interactively modulate climate change responses of ecotonal temperate-boreal forest. Philos. Trans. R. Soc. B Biol. Sci. 367, 2955–2961. https://doi.org/10.1098/rstb.2012.0235.

Frerker, K., Sabo, A., Waller, D., 2014. Long-term regional shifts in plant community composition are largely explained by local deer impact experiments. PLoS One 9, e115843. https://doi.org/10.1371/journal.pone.0115843.

Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., Barnes, C., Herold, N., Wickham, J., 2011. Completion of the 2006 National Land Cover Database for the conterminous United States. PE&RS 77, 858–864.

George, L.O., Bazzaz, F.A., 1999. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. Ecology 80, 833–845.

Giencke, L.M., Dovčiak, M., Mountrakis, G., Cale, J.A., Mitchell, M.J., 2014. Beech bark disease: spatial patterns of thicket formation and disease spread in an aftermath forest in the northeastern United States. Can. J. For. Res. 44, 1042–1050. https://doi.org/10.1139/cjfr-2014-0038.

Gill, R., Beardall, V., 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry 74, 209–218.

Hamann, A., Wang, T., 2006. Potential effects of cliamte change on ecosystem and tree species distribution in British Columbia. Ecology 87, 2773–2786. https://doi.org/10.1890/0012-9658(2006) 87[2773:PEOCCO]2.0.CO;2.

Harrington, T.B., Slesak, R.A., Schoenholtz, S.H., 2013. Variation in logging debris cover influences competitor abundance, resource availability, and early growth of planted Douglas-fir. For. Ecol. Manage. 296, 41–52. https://doi.org/10.1016/J.FORECO.2013.01.033.

Hille Ris Lambers, J., Clark, J.S., Beckage, B., 2002. Density-dependent mortality and the latitudinal gradient in species diversity. Nature 417, 732–735. https://doi.org/10.1038/nature00809.

Holt, R.D., Polis, G.A., 1997. A theoretical framework for intraguild predation. Am. Nat. 149, 745–764.

Horsley, S.B., Stout, S.L., DeCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol. Appl. 13, 98–118.

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.

Jenkins, L.H., Murray, B.D., Jenkins, M.A., Webster, C.R., 2015. Woody regeneration response to over a decade of deer population reductions in Indiana state parks. J. Torrey Bot. Soc. 142, 205–219. https://doi.org/10.3159/TORREY-D-14-00047.1.

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

Kie, J.G., Bowyer, R.T., 1999. Sexual segregation in white-tailed deer: density-dependent changes in use ofspace, habitat selection, and dietary niche. J. Mammol. 80, 1004–1020.

Knapp, W.M., Wiegand, R., 2014. Orchid (Orchidaceae) decline in the Catoctin Mountains, Frederick County, Maryland as documented by a long-term dataset. Biodivers. Conserv. 23, 1965–1976. https://doi.org/10.1007/s10531-014-0698-2.

Latham, R.E., Beyea, J., Benner, M., Dunn, C.A., Fajvan, M.A., Freed, R.R., Grund, M., Horsley, S.B., Rhoads, A.F., Shissler, B.P., 2005. Managing White-tailed Deer in Forest Habitat from An Ecosystem Perspective. Pennsylvania Case Study Report of the Deer Management Forum.

Matlack, G.R., 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biol. Conserv. 66, 185–194. https://doi.org/10.1016/0006-3207(93)90004-K.

McEuen, A.B., Curran, L.M., 2004. Seed dispersal and recruitment limitation across spatial scales in temperate forest fragments. Ecology 85, 507–518.

Mcwilliams, W.H., Service, U.F., Forest, N., Station, E., Box, P.O., Stout, S.L., Bowersox, T.W., Mccormick, L.H., 1995. Adequacy of advance tree-seedling regeneration in Pennsylvania's forests. North. J. Appl. For. 12, 187–191.

Messier, C., Parent, S., Bergeron, Y., 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. J. Veg. Sci. 9, 511–520. https://doi.org/10.2307/3237266.

Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: maanging in the face of uncertainty. Ecol. Appl. 17, 2145–2151. https://doi.org/10.1890/06-1715.1.

Nesslage, G.M., Porter, W.F., 2001. A geostatistical analysis of deer harvest in the Adirondack Park. Wildl. Soc. Bull. 29, 787–794.

Nuttle, T., Royo, A., Adams, M.B., Carson, W.P., 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. Ecol. Monogr. 83, 3–17.

Nyland, R.D., 2016. Silviculture: Concepts and Applications, third ed. Waveland Press Inc., Long Grove, Illinois.

NYSDEC, 2012. Management Plan for White-tailed Deer in New York State 2012-2016. Albany, NY.

NYSDEC, 2005. Comprehensive Wildlife Conservation Strategy (CWCS) Plan.

PA DCNR, 2013. White-Tailed Deer Plan 2013-2018.

Pacala, S.W., Canham, C.D., Silander Jr., J.A., 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. Can. J. For. Res. 23, 1980–1988.

Pacala, S.W., Canham, C.D., Silander Jr, J.A., Kobe, R.K., 1994. Sapling growth as a function of resources in a north temperate forest. Can. J. For. Res. 24, 2172–2183.

Patterson, B.R., Power, V.A., 2002. Contributions of forage competition, harvest, and climate fluctuation to changes in population growth of northern white-tailed deer. Oecologia 130, 62–71. https://doi.org/10.1007/s004420100783.

Pimentel, D., Zuniga, R., Morrison, D., 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol. Econ. 52, 273–288. https://doi.org/10.1016/J.ECOLECON.2004.10.002.

Price, D.T., Zimmermann, N.E., van der Meer, P.J., Lexer, M.J., Leadley, P., Jorritsma, I.T.M., Schaber, J., Clark, D.F., Lasch, P., McNulty, S., Wu, J., Smith, B., 2001. Regeneration in gap models: priority issues for studying forest responses to climate change. Clim. Change 51, 475–508. https://doi.org/10.1023/A:1012579107129.

PRISM, 2004. PRISM climate group. Oregon State University [WWW Document].

Rawinski, T.J., 2016. White-tailed deer in northeastern forests: understanding and assessing impacts. USDA For. Serv. NA-IN-02-14.

Rhodes, A.C., Larsen, R.T., St. Clair, S.B., 2018. Differential effects of cattle, mule deer, and elk herbivory on aspen forest regeneration and recruitment. For. Ecol. Manage. 422, 273–280. https://doi.org/10.1016/J.FORECO.2018.04.013.

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.

Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. For. Ecol. Manage. 181, 165–176. https://doi.org/10.1016/S0378-1127(03)00130-0.

Rosenberry, C.S., Fleegle, J.T., Wallingford, B.D., 2009. Management and Biology of White-tailed Deer in Pennsylvania 2009–2018. Pennsylvania Game Commission, Harrisburg, Pennsylvania.

Royo, A.A., Carson, W.P., 2006. On the formation of dense understory layers in forests worldwide. Can. J. For. Res. 36, 1345–1362.

Royo, A.A., Kramer, D.W., Miller, K.V., Nibbelink, N.P., Stout, S.L., 2017. Spatio-temporal variation in foodscapes modifies deer browsing impact on vegetation. Landsc. Ecol. 32, 2281–2295. https://doi.org/10.1007/s10980-017-0568-x.

Runkle, J.R., 1981. Gap regeneration in some old-growth forests of the eastern United States. Source Ecol. 62, 1041–1051.

Russell, F.L., Zippin, D.B., Fowler, N.L., 2001. Effects of white-tailed deer (Odocoileus virginianus) on plants, plant populations and communities: a review. Am. Midl. Naturlist 146, 1–26.

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. For. Ecol. Manage. 384, 26–33. https://doi.org/10.1016/j.foreco.2016.10.038.

Sage, R.W., Tierson, W.C., Mattfeld, G.F., Behrend, D.F., 1983. White-tailed deer visibility and behavior along forest roads. J. Wildl. Manage. 47, 940–953.

Sage, R.W.J., Porter, W.F., Underwood, H.B., 2003. Windows of opportunity : white-tailed deer and the dynamics of northern hardwood forests of the northeastern US. J. Nat.

Conserv. 220, 213–220.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E., Swift, D.M., 1987. Large herbivore foraging and ecological hierarchies. Bioscience 37, 789–795.

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

Shirer, R., Zimmerman, C., 2010. Forest regeneration in New York State. Nat. Conserv.

Stout, S.L., Royo, A.A., Decalesta, D.S., Mcaleese, K., Finley, J.C., 2013. the Kinzua Quality Deer cooperative: can adaptive management and local stakeholder engagement sustain reduced impact of ungulate browsers in forest systems? Boreal Environ. Res. 18, 50–64.

Team, R.C., 2014. R: A language and environment for statistical computing.

Thuiller, W., Lavorel, S., Araújo, M.B., 2005. Niche properties and geographical extent as predictors of species sensitivity to climate change. Glob. Ecol. Biogeogr. 14, 347–357. https://doi.org/10.1111/j.1466-822X.2005.00162.x.

Torssonen, P., Strandman, H., Kellomä Ki, S., Kilpelä Inen, A., Jylhä, K., Asikainen, A., Peltola, H., 2015. Do we need to adapt the choice of main boreal tree species in forest regeneration under the projected climate change? Forestry 88, 564–572. https://doi.org/10.1093/forestry/cpv023.

Tremblay, J.-P., Huot, J., Potvin, F., 2007. Density-related effects of deer browsing on the regeneration dynamics of boreal forests. J. Appl. Ecol. 44, 552–562. https://doi.org/10.1111/j.1365-2664.2007.01290.x.

Tremblay, J.-P., Huot, J., Potvin, F., 2006. Divergent nonlinear responses of the boreal forest field layer along an experimental gradient of deer densities. Oecologia 150, 78–88. https://doi.org/10.1007/s00442-006-0504-2.

Trumbore, S., Brando, P., Hartmann, H., 2015. Forest health and global change. Science (80-) 349, 814–818. https://doi.org/10.1126/science:aac6759.

Ueno, M., Solberg, E.J., Iijima, H., Rolandsen, C.M., Gangsei, L.E., 2014. Performance of hunting statistics as spatiotemporal density indices of moose (Alces alces) in Norway. Ecosphere 5, 1–20.

Urgenson, L.S., Halpern, C.B., Anderson, P.D., 2013. Level and pattern of overstory retention influence rates and forms of tree mortality in mature, coniferous forests of the Pacific Northwest, USA. For. Ecol. Manage. 308, 116–127. https://doi.org/10.1016/j.foreco.2013.07.021.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, fourth ed. Springer, New York.

Wagner, S., Nakashizuka, T., Nyland, R.D., 2010. Beech regeneration research: from ecological to silvicultural aspects. For. Ecol. Manage. 259, 2172–2182. https://doi.org/10.1016/J.FORECO.2010.02.029.

Walck, J.L., Hidayati, S.N., Dixon, K.W., Thompson, K., Poschlod, P., 2011. Climate change and plant regeneration from seed. Glob. Chang. Biol. 17, 2145–2161. https://doi.org/10.1111/j.1365-2486.2010.02368.X.

Ward, J.S., Williams, S.C., Worthley, T.E., 2013. Comparing effectiveness and impacts of Japanese barberry (Berberis thunbergii) control treatments and herbivory on plant communities. Invasive Plant Sci. Manag. 6, 459–469. https://doi.org/10.1614/IPSM-D-13-00004.1.

Wason, J.W., Dovciak, M., 2017. Tree demography suggests multiple directions and drivers for species range shifts in mountains of Northeastern United States. Glob. Chang. Biol. 23, 3335–3347. https://doi.org/10.1111/gcb.13584.

Webster, C.R., Dickinson, Y.L., Burton, J.I., Frelich, L.E., Jenkins, M.A., Kern, C.C., Raymond, P., Saunders, M.R., Walters, M.B., Willis, J.L., 2018. Promoting and maintaining diversity in contemporary hardwood forests: confronting contemporary drivers of change and the loss of ecological memory. For. Ecol. Manage. 421, 98–108. https://doi.org/10.1016/j.foreco.2018.01.010.

Widmann, R.H., Crawford, S., Kurtz, C.M., Nelson, M.D., Miles, P.D., Morin, R.S., Riemann, R., 2015. New York Forests 2012. U.S. Dep. Agric. For. Serv. Resour. Bull. NRS-98. https://doi.org/10.2737/NRS-RB-98.

Williams, B.K., Brown, E.D., 2014. Adaptive management: from more talk to real action. Environ. Manage. 53, 465–479. https://doi.org/10.1007/s00267-013-0205-7.

Williams, B.K., Szaro, R.C., Shapiro, C.D., United States. Department of the Interior. Adaptive Management Working Group., 2009. Adaptive management : the U.S. Department of the Interior technical guide. U.S. Dept. of the Interior, Adaptive Management Working Group.

Williams, D.M., Dechen Quinn, A.C., Porter, W.F., 2011. Landscape effects on scales of movement by white-tailed deer in an agricultural–forest matrix. Landsc. Ecol. 27, 45–57. https://doi.org/10.1007/s10980-011-9664-5.

Woudenburg, S.W., Conkling, B.L., O'Connell, B.M., PaPoint, E.B., Turner, J.A., L., W.K., Boyer, D., Christenson, G., Ridley, T., 2011. The Forest Inventory and Analysis Database : Database Description and Users Manual Version 5. 1 for Phase 2.