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Interactions between white-tailed deer density and the composition of forest understories in the northern United States

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ABSTRACT

Forest understories across the northern United States (US) are a complex of tree seedlings, endemic forbs, herbs, shrubs, and introduced plant species within a forest structure defined by tree and forest floor attributes. The substantial increase in white-tailed deer (Odocoileus virginianus Zimmerman) populations over the past decades has resulted in heavy browse pressure in many of these forests. To gain an objective assessment of the role of deer in forested ecosystems, a region-wide forest inventory across the northern US was examined in concert with white-tailed deer density information compiled at broad scales. Results indicate that deer density may be an additional driver of tree seedling abundance when analyzed along with stand attributes such as aboveground biomass, relative density, and stand age. Tree seedling abundance generally decreased as deer density increased above 5.8 deer km^2 for all forest type groups with the exception of oak-dominated forests. Findings indicate that introduced plant species, of which 393 were recorded in this study, increased in areas with higher deer density. The abundance of white-tailed deer is just as important as forest stand and site attributes in the development of forest understories. Given the complexity of forest and land use dynamics across the northern US, this study provides directions for future research as more data linking forest-dependent wildlife and forest dynamics at regional and national scales become available.

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1. Introduction

Preferential browsing of vegetation by ungulates can influence forest vegetation dynamics (Rooney and Waller, 2003). Relative to their population size, white-tailed deer (Odocoileus virginianus Zimmerman) have a disproportionately large effect on their surrounding environment (Waller and Alverson, 1997) and can have an immediate impact on forest health and diversity by reducing the presence and abundance of commercially and ecologically important tree species through preferential browsing or can influence forests indirectly by altering habitat availability for other wildlife and forest-dependent organisms (Rooney and Waller, 2003). A number of plant community studies have employed methods including fenced exclosures (e.g., White, 2012; Frerker et al., 2014), enclosures (Horsley et al., 2003; Nuttle et al., 2014), and island studies (e.g., Mudrak et al., 2009; Cardinal et al.,

2012); however, studies linking deer density with forest structure across large geographic regions are limited. White-tailed deer have strong negative impacts on forest understory plant communities in North America, but future research should seek to evaluate the potential for plant species shifts in areas with differing deer densities (Habeck and Schultz, 2015). As deer may account for up to half of the variability in long-term forest vegetation dynamics (Frerker et al., 2014), understanding how deer density may affect future trends in vegetation growth and survival is essential to maintaining the ecosystem services that forests provide.

The role of deer browsing pressure should not be considered mutually exclusive of additional drivers of vegetation dynamics. Forests can regulate resources to tree seedlings and may be influenced by natural disturbance or management activities. Abiotic factors that influence the establishment and success of forest regeneration include climate, forest floor (e.g., duff and litter), and soil attributes. Nurse logs, i.e., decaying woody debris upon which tree seedlings grow, provide an important seedbed for trees in many temperate forest types. Tree seedlings growing on nurse

logs may be subject to less competition compared to seedlings growing on the forest floor (Harmon and Franklin, 1989). Meanwhile, the presence of woody debris increases soil water and nitrogen availability to promote tree seedling growth (Harrington et al., 2013), suggesting that the success of forest regeneration is tied to attributes such as dead wood. The spatial arrangements between tree seedlings and woody debris may influence survival depending on a seedling's location to woody debris (van Ginkel et al., 2013) and microsite conditions such as light availability (Rooney et al., 2000).

Browsing pressure from deer has undoubtedly led to altered understory vegetation communities, particularly in increasing the presence and abundance of less palatable or browse-resistant vegetation. Tree seedling recruitment for palatable species can be less successful in areas with high browse pressure (Tanentzap et al., 2009; Larouche et al., 2010; Palik et al., 2015), presenting a challenge to managing healthy and diverse forests. The overabundance of deer can facilitate the presence and abundance of invasive plant species through preferential browsing of native herbs (Knight et al., 2009) and act as an important seed dispersal agent for exotic plant species (Williams and Ward, 2006). High deer densities along with the presence of non-native earthworms can similarly influence the establishment of invasive plants (Fisichelli et al., 2012). As a consequence, forest management strategies may require species-specific actions to promote the growth and development of commercially and ecologically important tree seedlings (Palik et al., 2015).

Understanding the relationships between deer density and forest attributes can aid in designing forest management strategies to encourage successful regeneration. The degree to which specific forest attributes (e.g., forest floor characteristics and stand conditions) can lend insight into forest health and diversity remains unexamined across regional scales. Without a refined understanding of the ecological relationships that drive the development of forest understories and the presence and abundance of introduced plant species at regional scales, future management techniques to improve forest health across the northern US may be hampered.

The objective of this study is to investigate the ecological impacts of white-tailed deer across northern US forests using regional datasets, including a systematic forest resource inventory and estimates of deer abundance. Specific objectives are to (1) quantify the impacts of deer density on the structure and composition of forest understories and (2) evaluate trends in tree seedling abundance and the presence/abundance of introduced plant species across varying deer densities and forest types in the northern US.

2. Materials and methods

2.1. Study area

Forests across the northern US are distinguished by strong climatic seasons and vary from conifer and mixed conifer and hardwood types in the north to hardwood-dominated forests characterized by tall tree species toward the southern boundary (Smith et al., 2009). The study area ranged eastward from the state of Minnesota to Maine in the north and from Missouri to Maryland in the south, spanning approximately 13° latitude and 30° longitude (Fig. 1a). Across the study area, mean annual temperatures ranged from 0.7 to 14.3 °C and precipitation from 46 to 170 cm (Rehfeldt, 2006; USDA Forest Service, 2014b).

2.2. Forest Inventory and Analysis data

The US Department of Agriculture Forest Service's Forest Inventory and Analysis (FIA) program has monitored forests by estab-
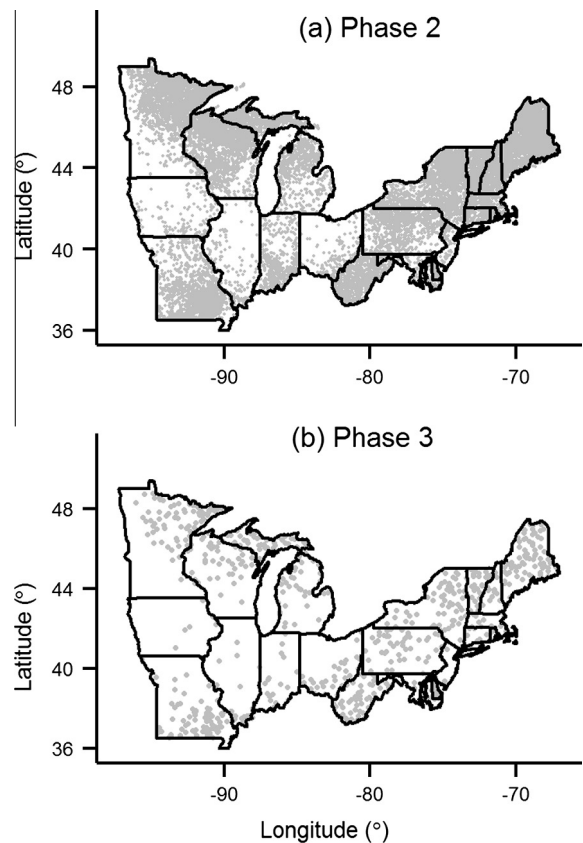

Fig. 1. Approximate locations of phase 2 (*n* = 14,343) and phase 3 Forest Inventory and Analysis plots (*n* = 769) across the northern US, 2008–2012.

lishing permanent sample plots across the US using a three phase inventory (Bechtold and Patterson, 2005). During the inventory's first phase (P1), sample plot locations were established at an intensity of approximately 1 plot per 2400 ha. If the plot lied partially or wholly within a forested area, field personnel visited the site and established a phase two (P2) inventory plot. Standard P2 inventory plots consisted of four 7.32-m fixed radius subplots for a total plot area of approximately 0.07 ha where standing tree and site attributes were measured. All live and standing dead trees with a diameter at breast height (DBH) of at least 12.7 cm were measured on these subplots. Within each subplot, a 2.07-m microplot was established where live trees with a DBH between 2.5 and 12.7 cm (i.e., saplings) were measured. Within each microplot all live tree seedlings were tallied, where conifer and hardwood seedlings were at least 15.2 and 30.5 cm in height, respectively, with both having a DBH $\leqslant$ 2.5 cm. The per-unit number of all seedlings (i.e., tree seedlings ha^{-1}) was subsequently computed for each FIA plot.

A total of 14,343 inventory plots were analyzed for a variety of characteristics related to forest structure and tree seedling abundance (Table 1; Fig. 1a). Plot and tree records were acquired from the FIA database (USDA Forest Service, 2014a) where measurements occurred between 2008 and 2012.

Aboveground tree biomass was estimated via the component ratio method (Woodall et al., 2011) which facilitated the calculation of tree component biomass as a ratio of bole biomass based on component proportions from Jenkins et al. (2003). Relative density (Woodall et al., 2005) was computed to characterize live-tree stocking. Stand age and site index, determined as the average height that dominant and co-dominant trees were expected to attain for even-aged stands that are well-stocked at 50 years, were obtained from the FIA database.

Table 1
Summary of stand condition and forest attribute data acquired from Forest Inventory and Analysis plots across northern US forests, 2008–2012.

Variable type	Variable	Mean	SD	Min	Max
Phase 2 plots (n = 14,343)					
Stand conditions	Seedlings (count ha^{-1})	7303.8	7852.3	185.2	194,875.6
	Aboveground biomass in live trees (Mg ha^{-1})	109.7	63.7	0.1	459.2
	Relative density[a]	0.51	0.20	0.00	1.00
	Site index (m at 50 years)	18.1	5.2	4.3	44.8
	Stand age (years)	66.6	26.7	0.0	210.0
Phase 3 plots (n = 769)					
Woody debris	Fine woody debris biomass (downed dead wood < 7.62 cm at transect intersection; Mg ha^{-1})	5.4	4.2	0.0	43.1
	Downed woody debris biomass (downed dead wood $\geqslant$ 7.62 cm at transect intersection; Mg ha^{-1})	9.6	10.9	0.1	112.9
Forest floor	Duff biomass (Mg ha^{-1})	56.5	247.8	0.0	3622.1
	Litter biomass (Mg ha^{-1})	20.5	13.5	0.0	123.7
	Woody cover of pieces $\geqslant$ 7.6 cm (proportion)	0.04	0.03	0.01	0.24
Vegetation cover	Vegetation cover 0–0.61 m in height (proportion)	0.54	0.25	0.02	1.00
	Vegetation cover 0.61–1.83 m in height (proportion)	0.31	0.22	0.00	0.95
Species richness by growth habit[b]	Forbs and herbs	21.5	13.0	0.0	36.0
	Graminoids	4.5	4.0	0.0	22.0
	Shrubs and subshrubs	8.1	3.8	0.0	22.0
	Trees	13.9	5.3	3.0	34.0
	Vines	2.5	2.5	0.0	10.0
	All species	55.8	24.1	6.0	136.0

[a] Relative density calculated from Woodall et al. (2005).
[b] Growth habits as defined in the USDA Plants Database (USDA NRCS, 2010).

A subset of P2 plots (sample intensity of one plot per 38,849 ha; 769 total plots) were sampled for additional variables related to forest ecosystem health during FIA's third phase inventory (P3; Table 1; Fig. 1b). Measurements of these variables included forest understory vegetation diversity and structure, downed woody materials, and forest floor attributes.

Understory vegetation (UVEG) measurements collected at the P3 sample intensity were used throughout this analysis. General assessments were made for UVEG on each FIA subplot (i.e., total percent cover within specified height layers) and more specifically by measurements of each individual species found within a subplot. Together, these two sets of measurements comprise the FIA's Vegetation Diversity and Structure Indicator (Schulz et al., 2009). Field observations of UVEG attributes were collected from June to mid-September. On each subplot, ocular canopy cover estimates for UVEG were recorded by field crews using a standard cover protocol (Daubenmire, 1959) with measurement error tolerances to mimic Braun-Blanquet (1932) cover classes. Vegetation cover was measured ocularly for all plants present on a subplot, in one-percent increments located in four height layers. For the purposes of understanding browse impacts by deer that may influence vegetation diversity and structure, UVEG cover was assessed individually for the 0–0.61 m and 0.61–1.83 m height layers (additional layers assess UVEG occurring at heights of 1.83–4.88 m and >4.88 m). Mean UVEG cover was averaged across FIA subplots on each plot and expressed as a proportion. Canopy cover assessments were also made individually for all vascular plant species with live stems within or with foliage hanging over forested portions of the subplots. Hence, species richness of the understory community (UVEG $\leqslant$ 1.83 m) was calculated for all species and for species occurring within an individual growth habit type.

Species, growth habits, and whether or not a species was designated as introduced were identified and are described in this analysis according to their listing in the PLANTS database (USDA NRCS, 2010). Introduced species were identified if their listing was "introduced", "probably introduced" or "cultivated" (Schulz and Gray, 2013). Throughout this analysis, UVEG data from forested subplots which were 100% accessible by field crews and contained measurements on all four subplots were utilized, for a total of 769 inventory plots. Additional information on the FIA's UVEG data

collection protocols can be found in Schulz et al. (2009) and Woodall et al. (2010).

Measurements of downed (DWD) and fine woody debris (FWD) were included in FIA's Downed Woody Materials Indicator (Woodall and Monleon, 2008). All DWD pieces were defined as woody debris in forested conditions with a diameter greater than 7.62 cm along a length of at least 0.91 m and a lean angle greater than 45° from vertical, and were sampled on each of three 7.32-m horizontal distance transects radiating from each FIA subplot center at azimuths of 30, 150, and 270°. All FWD with transect diameters less than 7.59 cm but greater than 2.55 cm were tallied on a 3.05-m portion of the 150° transect, while all FWD between 0.62 and 2.54 cm and less than 0.61 cm were tallied separately on a 1.83-m portion of the 150° transect. To compute plot-level attributes of the woody debris pools, volume was first calculated for each DWD piece and then converted to biomass through implementing bulk density and decay class reduction factors. Similarly, the volume of FWD was estimated per unit area, and then converted to an estimate of biomass using bulk density and decay class reduction factors based on forest type (Woodall and Monleon, 2008).

Forest floor attributes were sampled on three subplots within each FIA plot using a 30.48-cm diameter circular sampling frame. Duff and litter layer thickness were measured to the nearest 0.25 cm at points in each cardinal direction within the sampling frame to the point where mineral soil (A horizon) begins (Woodall et al., 2010). The entire forest floor layer (excluding live vegetation, woody debris >0.64 cm in diameter, rocks, cones, and bark) within the confines of the sampling frame was removed for lab analysis upon which total biomass and carbon are calculated. Mean proportion of wood cover within a subplot as assessed in the UVEG inventory, including stumps, live tree trunks, roots, and woody pieces $\geqslant$7.62 in diameter, was similarly used as an attribute of forest floor structure.

2.3. Deer density data

White-tailed deer density estimates were compiled using information contained in the 2009 Quality Deer Management Association (QDMA) Annual Report which was compiled using state wildlife agency data from 2001 to 2005 (QDMA, 2009). The QDMA

spatial map depicting deer density (deer per km² of total land area) was subsequently digitized across the northern US (Walters et al., 2016; Fig. 2a). Estimates of deer density were overlaid onto the FIA plots, where a unique estimate of deer density was specified at each FIA plot location. Categories of deer density provided by the QDMA (2009) data were: (1) rare, absent, or urban area with unknown population, (2) <5.8 deer km² (<15 deer mi⁻²), (3) 5.8–11.6 deer km² (15–30 deer mi⁻²), (4) 11.6–17.4 deer km² (30–40 deer mi⁻²), or (5) >17.4 deer km² (>45 deer mi⁻²). These categories were non-continuous and represented coarse deer density levels (collected at scales ranging from wildlife management units to counties and regions within states) as identified in the QDMA (2009) report. The categories of <5.8 and <11.6 deer km² correspond to approximate values presented in Alverson et al. (1988) for regenerating browse-sensitive and standard species, respectively, at various levels of deer density.

2.4. Impacts of deer density and forest type group on tree seedlings and understory structure and composition

Generalized linear models were used to compare responses among deer density classes, the six most common forest type groups (aspen/birch, maple/beech/birch, oak/hickory, oak/pine, spruce/fir, and white/red/jack pine), and their interactions. Dependent variables analyzed as a part of the P2 dataset included number of tree seedlings while for the P3 dataset, dependent variables included number of tree seedlings, UVEG species richness, UVEG cover in the lowest two height layers (0–0.61 m and 0.61–1.83 m), and the number of introduced plant species. The number of tree seedlings, UVEG species richness, and number of introduced plant species were analyzed with a Poisson distribution using a log-link function. Analyses were performed with R statistical software (R Core Team, 2014). Results were considered significant at $P \leqslant 0.05$.

2.5. Modeling the impacts of deer on tree seedlings

To determine the sensitivity of forest understory characteristics, we used nonparametric random forests (RF; Breimen, 2001) by employing the 'randomForest' package and functions in R (Liaw and Wiener, 2002). The RF method ranked the relative influence that each variable had on the specific forest structure attribute of interest. This method involved building a set of regression trees based on bootstrapped samples of the data. For the P2 dataset,

we were interested in quantifying how sensitive tree seedling abundance was to variables such as deer density, forest type group, aboveground biomass, site index, relative density and stand age. For the P3 dataset, litter and duff biomass, woody debris cover, and downed and fine woody debris were also used. In the RF method, classification trees are taken as independently-sampled bootstraps of the data (Breimen, 2001). Random forests models can offer high classification accuracy and provide a method for assessing the relative importance of predictor variables (Cutler et al., 2007). Although RF models can be robust against overfitting (Breimen, 2001), we used an approach outlined in Weiskittel et al. (2011) to balance model parsimony with the risk of overfitting. To determine the optimal number of variables to use from the deer density and forest structure data, we performed the RF model iteratively, each time dropping the least influential variable as reflected in the RF variable importance score until the top three ranked variables remained. We defined this as the optimal model. We ultimately sampled 500 regression trees for each iteration of the RF model after confirming model performance was similar after using a 25% subset of the regression trees, as described in Liaw and Wiener (2002). One predictor (i.e., mtry = 1) was sampled for splitting at each node for all models after applying the 'tuneRF' function to the datasets.

Using the RF results, we assessed the direction (positive or negative) and strength of the relationships between response variables and explanatory variables using Spearman correlation coefficients.

3. Results

Percentages of FIA plots in the deer density classes (deer km²) < 5.8, 5.8–11.6, 11.6–17.4, and >17.4 deer km² were 40.2, 40.3, 11.6, and 7.9%, respectively (Fig. 2a). Tree seedling abundance ranged from 185.2 to 194,875.6 seedlings ha⁻¹. While deer densities were generally >17.4 deer km² in central and southern Wisconsin, that area also saw abundant tree seedlings in some areas (Fig. 2b). For the P3 dataset, UVEG cover (expressed as a proportion) was higher in the 0–0.61 m layer (0.54 ± 0.25 [mean ± SD]) than the 0.61–1.83 m layer (0.31 ± 0.22). Of the 2555 understory species recorded, species richness by growth habit type was dominated by forbs and herbs, followed by trees, shrubs and subshrubs, graminoids, and vines (Table 1).

For the P2 dataset, deer density, forest type group, and their interaction were significant ($P < 0.001$) in determining the tree seedling abundance. Tree seedling abundance decreased as deer
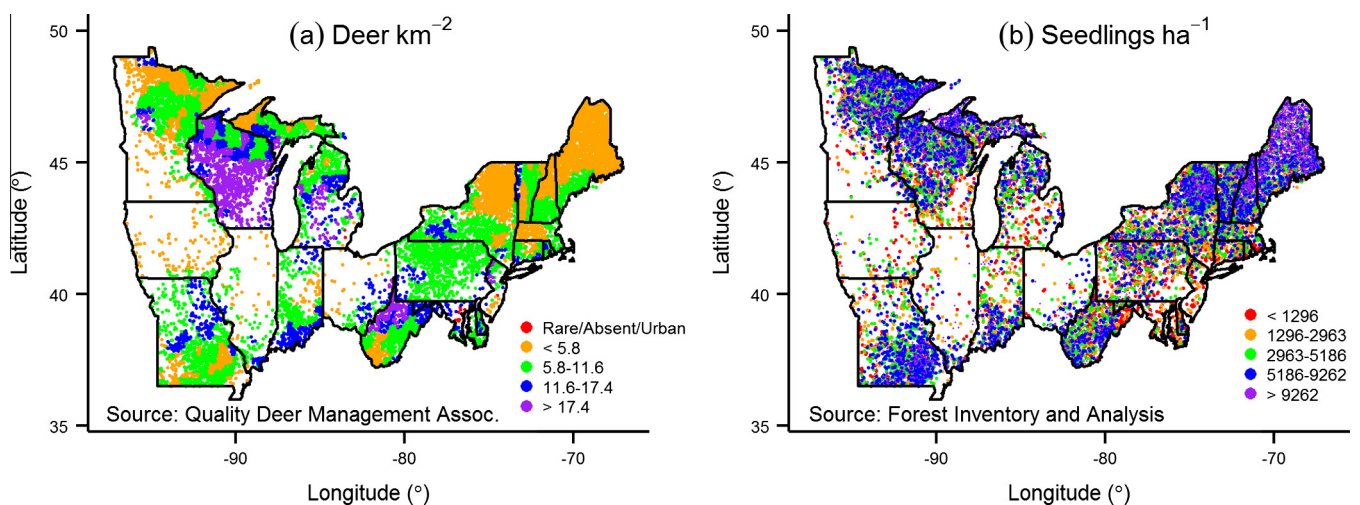

Fig. 2. Deer density km⁻² of total land area (2001–2005) and tree seedling abundance (2008–2012) across the northern US.

density increased from <5.8 deer km^2 to all greater deer densities for all forest type groups with the exception of the oak/pine and oak/hickory groups. Tree seedling abundance was not significantly different for all forest types groups for deer densities ranging from 5.8 to 11.6 deer km^2 to >17.4 deer km^2 (Fig. 3). The RF model indicated that deer density, forest type group, and stand age ranked first, second, and third respectively, in their importance scores for determining tree seedling abundance (Table 2), with an R^2 of 9.2%. Spearman rank correlation coefficients indicated a significant positive relationship (0.28; $P < 0.001$) between tree seedling abundance and stand age.

A total of 393 introduced species were recorded across the study region within the FIA P3 plots (15% of all species observed). Deer density and forest type group were significant in determining UVEG species richness ($P = 0.002$ and $P < 0.001$), cover of all species in both height layers (0–0.61 m and 0.61–1.83 m; $P = 0.047$ and $P < 0.001$ for UVEG cover in height layer 1; $P < 0.001$ and $P < 0.001$ for UVEG cover in height layer 2), and the number of introduced species ($P < 0.001$ and $P = 0.041$). The mean number of introduced species increased as deer density increased across all forest type groups for which there were sufficient observations (i.e., ≥five observations within each forest type group-deer density category). The maple/beech/birch forest type group displayed

Table 2
Summary of top three ranked variables as shown by their importance scores (%IncMSE) used in random forests for predicting tree seedling abundance in phase 2 plots ($n = 14,343$) across the northern US.

Tree seedlings (count ha^{-1})	
Variable	%IncMSE
Deer density	90.0
Forest type group	51.2
Stand age	46.3
R^2	9.2
RMSE	7481.7

significantly more introduced species in FIA plots with high (i.e., >11.6 deer km^{-2}) compared low deer densities (i.e., <11.6 deer km^{-2}; Fig. 4). The RF analyses indicated duff biomass had the highest importance score for both understory species richness and the number of introduced species observed on an FIA plot (Table 3). Stand relative density and aboveground biomass in live trees displayed the highest importance scores related to UVEG cover in layer 1 (0–0.61 m) and 2 (0.61–1.83 m). Deer density
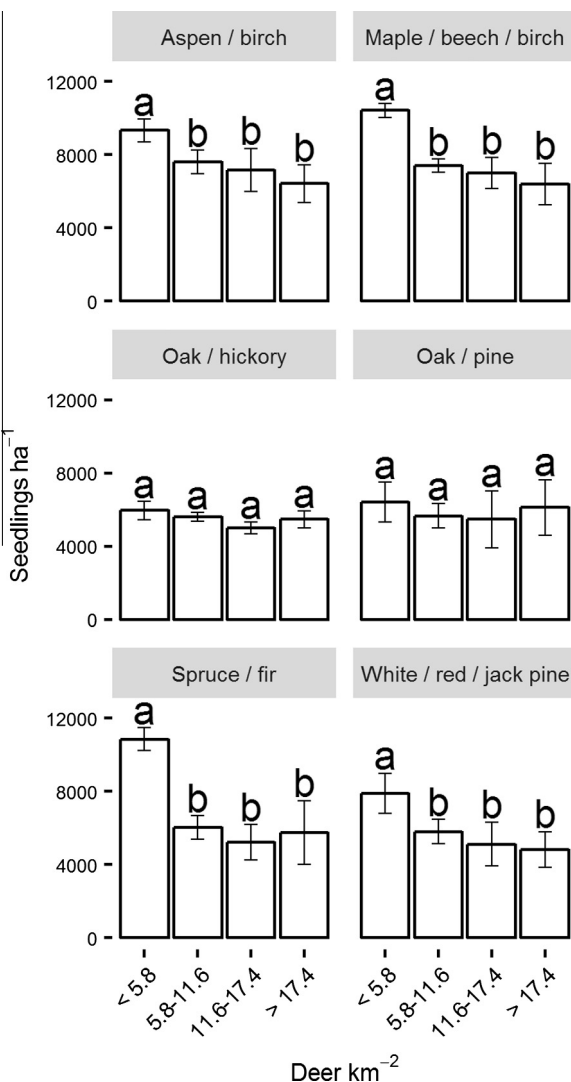

Fig. 3. Mean seedling abundance (±95% confidence limits) by white-tailed deer density class and forest type group across the northern US.
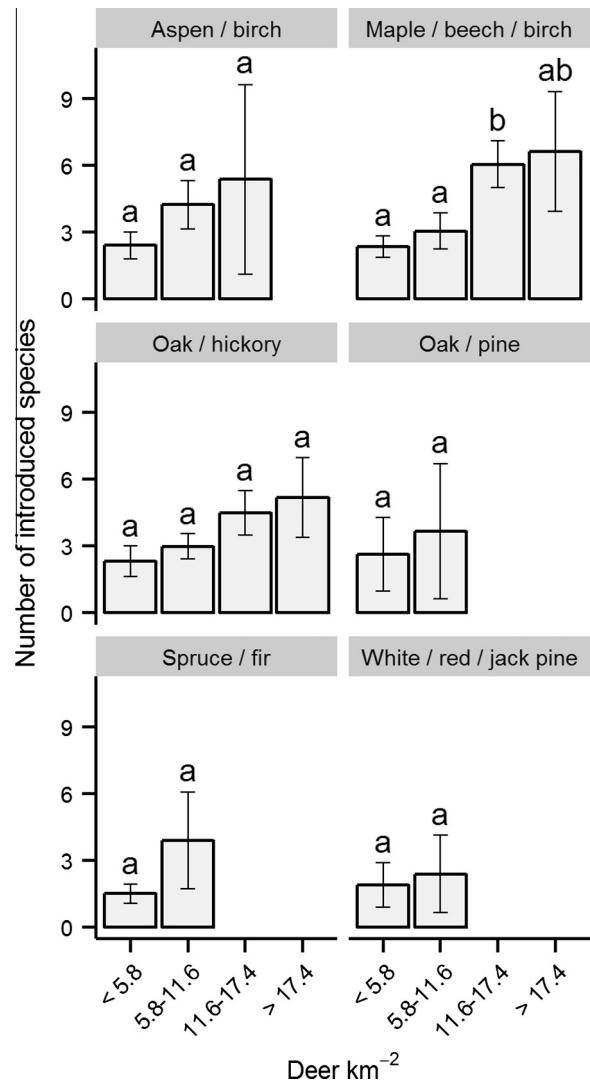

Fig. 4. Mean number of introduced species (±95% confidence limits; categories with ≥5 observations) by white-tailed deer density class and forest type group across the northern US.

Table 3
Summary of top three ranked variables as shown by their importance scores (%IncMSE) for predicting understory vegetation attributes in phase 3 plots (*n* = 769) across the northern US.

Tree seedlings (count ha^{-1})		Understory species richness; Layers 1 and 2		Number of introduced understory species (Layers 1 and 2)	
Variable	%IncMSE	Variable	%IncMSE	Variable	%IncMSE
Deer density	16.3	Duff biomass	56.2	Duff biomass	40.4
Aboveground biomass in live trees	14.0	Forest type group	31.3	Deer density	24.8
Relative density	12.4	Stand age	17.6	Forest type group	20.7
R^2	4.2	R^2	23.3	R^2	21.4
RMSE	6806.4	RMSE	20.0	RMSE	2.8

Understory vegetation cover (Layer 1; 0–0.61 m)		Understory vegetation cover (Layer 2; 0.61–1.83 m)	
Variable	%IncMSE	Variable	%IncMSE
Relative density	35.9	Relative density	29.4
Duff biomass	22.4	Aboveground biomass in live trees	18.4
Forest type group	18.7	Duff biomass	15.9
R^2	13.9	R^2	7.7
RMSE	22.6	RMSE	20.3

displayed the second highest importance score for determining the number of introduced species and ranked moderate to low in importance for other forest understory variables. Values of R^2 ranged from 4.2% to 23.3% depending on the variable of interest from the P3 dataset (Table 3). The RF model output for the full suite of variables for predicting P2 and P3 variables appear in Supplemental Material 1 and 2, respectively.

For the P3 plots, Spearman rank correlation coefficients for the top three ranked variables indicated a significant negative relationship between duff biomass and understory species richness (−0.41; *P* < 0.001), the number of introduced species (−0.38; *P* < 0.001), and UVEG cover in layer 1 (−0.11; *P* = 0.005). Spearman's coefficients indicated a significant negative relationship between tree seedlings and aboveground biomass in live trees (−0.11, *P* = 0.003) and a positive relationship with relative density (0.71; *P* < 0.001). Relative density also showed significant negative relationships with UVEG cover in layers 1 (−0.35; *P* < 0.001) and 2 (−0.29; *P* < 0.001). Significant negative relationship were observed between aboveground biomass in live trees and UVEG cover in layer 2 (−0.13, *P* = 0.001) and understory species richness and stand age (−0.10; *P* = 0.01).

4. Discussion

Density above four deer km^2 has been suggested as a population where deer densities could provide detrimental impacts to browse-sensitive tree seedlings (Alverson et al., 1988). Our data suggest that less than 40% of northern US forests may have deer densities below this level. As deer habitually feed in areas where forage is most available (White, 2012; Palik et al., 2015), the link between tree seedlings and understory attributes suggests a more thorough understanding of understory characteristics and their dynamics may be necessary in determining the establishment and success of tree seedlings in an ecological and management context at the regional scale.

We observed that deer density was strongly correlated with total tree seedling and invasive plant abundance. The total abundance of tree seedlings for all species across the northern US is more influenced by deer abundance than by live tree attributes such as aboveground biomass, stand age, and relative density. Deer density, aboveground biomass in live trees, and relative density were the most highly influential variables in predicting tree seedling abundance using the P3 dataset. Areas with both high deer densities and abundant tree seedlings (e.g., central and southern Wisconsin) could reflect differing forest management strategies and the presence of non-palatable and/or introduced plant species occupying those forests. Although most correlations among attributes are moderate to weak, significant predictors may serve as indicators for understanding the complex relationships among understory vegetation structure and deer density. Such coarse estimates of deer density across large geographic regions can be used as browse indices to inform tree regeneration stocking to better understand the composition of future forest understories (e.g., Brose et al., 2008). Managers will seek the appropriate scale to address tree regeneration issues related to deer density, ranging from the stand, township, county, state, or regional scales. In particular, understanding the spatial patterns of successful tree regeneration (and the appropriate resolution of deer density data) will provide better insights into the role that deer densities have on vegetation impacts ranging from stand to landscape scales (e.g., Didier and Porter, 2003).

The number of introduced plant species increased in areas with higher deer density, highlighting additional ecological concerns that large deer populations bring. White-tailed deer can disperse native and alien invasive seeds through ingestion and defecation (Myers et al., 2004) and reduce seed bank abundance resulting in a greater number of short-lived plant species (DiTommaso et al., 2014). As observed in the maple/beech/birch forest type group, tree seedlings were less abundant in high compared to low deer density areas, a finding that was similarly observed by Matonis et al. (2011) in Michigan's Upper Peninsula. The number of introduced species in maple/beech/birch forests was significantly larger for deer densities >11.6 deer km^2 than for those <11.6 deer km^2. This could be due to the observed effects of deer on grazing native forbs in these forests such as *Trillium* spp. (Augustine and Felich, 1998) and the habitat suitability for both non-native and native species such as *Carex pensylvanica* Lam. to establish (Powers and Nagel, 2009). The lack of a trend between deer density and tree seedling abundance in oak forest types may be explained by the tremendous difficulties in regenerating oak species related to their shade and drought tolerance and long time period required for successful reproduction (Larsen and Johnson, 1998).

Potentially serving as a surrogate for disturbance impacts, our results similarly indicate that as duff biomass decreases, the number of introduced species and species richness increases, a finding that is potentially related to the presence of earthworms in forests of the northern Great Lake States (Fisichelli et al., 2012). This was similarly highlighted by Laughlin et al. (2004), who showed that plant species richness declined as duff depth increased following

wildfire. Linking these forest floor attributes to understand the presence and abundance of introduced species may facilitate future analyses of forest health issues related to white-tailed deer as a disturbance agent.

Deer populations, harvest goals, and monitoring techniques differ by state across the US, contributing to variability when aggregating data across regions. Hence, as the same or similar forest types occur across state boundaries, deer density estimates such as those archived in Walters et al. (2016) that are designed using state wildlife agency information, may show major changes across multiple states. As an example, Minnesota uses harvest data and a population model to monitor deer populations (Minnesota Department of Natural Resources, 2015), while New York uses a combination of harvest data and deer sighting rates by bowhunters to monitor population changes (New York State Department of Environmental Conservation, 2011). While coarse deer density estimates such as those contained in the QDMA (2009) report may provide useful indicators of trends in deer herbivory as noted here, careful attention should be paid to the years in which deer density estimates are used to compare with forest understory measurements. Within the FIA program, a subset of invasive plant species are monitored across P2 plots which could be linked to biological resistance with a suite of forest attributes across regional scales (e.g., Oswalt et al., 2015; Iannone et al., 2016). Currently, FIA field crews are directly recording deer browse severity as a part of a new regeneration indicator (McWilliams et al., 2015). As this information becomes available on an increasing number of FIA plots, analyses can incorporate these more rigorous and regionally consistent browse assessments into various aspects of forest health and management planning.

5. Conclusions

Using a coarse deer density assessment in combination with a regionally consistent forest inventory of numerous forest attributes (e.g., overstory density, understory diversity, tree seedling density, and invasive plant abundance), an exploration of the ecological effects of white tailed deer in northern U.S. forests was possible. The future forests of the northern US may be shaped heavily by white-tailed deer populations as deer abundance was strongly correlated with tree seedling and invasive plant abundance. Unfortunately for natural resource managers, forest regeneration management strategies in high deer density forests, e.g., establishing exclosures, protecting young trees through caging or other methods, are expensive if the goal is to restore ecological services and economic value. Additionally, forest management strategies may require species-specific actions to promote the growth and development of tree seedlings. In terms of monitoring the effects of deer, the coarse deer density data used in this study should be succeeded by much more consistent and rigorous data in order to refine our understanding of deer impacts in forest ecosystems and associated human communities. As this study provides evidence of a complex relationship between deer and forest stand dynamics, future studies may need to include the entire suite of forest overstory, understory, and forest floor characteristics to provide robust insights into the effects of white-tailed deer in northern US forests.

Acknowledgements

Appendix A. Supplementary material

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