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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.

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

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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 establishing 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.

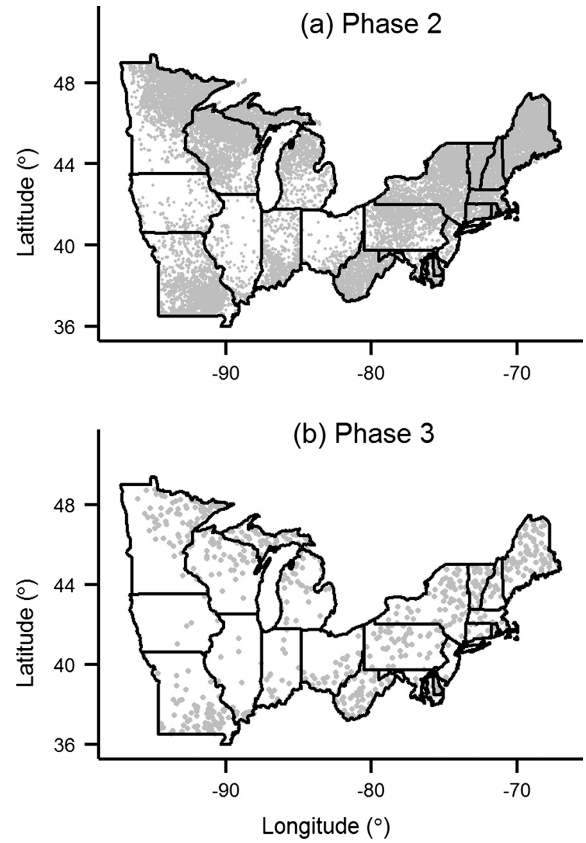

Fig. 1. Approximate locations of phase 2 (n = 14,343) and phase 3 Forest Inventory and Analysis plots (n = 769) across the northern US, 2008–2012.

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.