Impacts of white-tailed deer on regional patterns of forest tree recruitment

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ABSTRACT

Local, short- to medium-term studies make clear that white-tailed deer can greatly suppress tree growth and survival in palatable tree species. To assess how deer have broadly affected patterns of tree recruitment across northern Wisconsin, we analyzed recruitment success in 11 common trees species that vary in palatability across 13,105 USFS - FIA plots sampled between 1983 and 2013. We also examined how recruitment in these species covaried with estimated deer densities here. Saplings of five palatable species were scarce relative to less palatable species and showed highly skewed distributions. Scarcity and skew provide reliable signals of deer impacts even when deer have severely reduced recruitment and/or no reliable deer density data are available. Deer densities ranged from 2.3 to 23 deer per km^2 over a 30 year period. Sapling numbers in two maples (*Acer*) and aspen (*Populus*) with intermediate palatability declined sharply in apparent response to higher deer density. Path analysis also reveals that deer act to cumulatively depress sapling recruitment in these species over successive decades. Together, these approaches show that deer have strongly depressed sapling recruitment in all taxa except *Abies* and *Picea*. As these impacts are now propagating into larger sized trees, deer are also altering canopy composition and dynamics. The tools developed here provide efficient and reliable indicators for monitoring deer impacts on forest tree recruitment using consistent data collected by public agencies.

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1. Introduction

In the United States, forest products generate over $200 billion a year in sales nationwide (USDA Forest Service, 2014). To maintain recreational and commercial use of these forests, managers must sustain forest growth by ensuring the responsible harvest of forest products and successful tree regeneration. Foresters often adjust management practices to enhance natural regeneration of desired species. Nevertheless, several ecological factors may act to inhibit seedling establishment, growth, and sapling recruitment. These factors include the often intense competition of seedlings and saplings for water, soil nutrients, and light (Aarssen and Epp, 1990; Dalling et al., 2011). Thus, species traits like drought and shade tolerance strongly affect a tree's ability to persist and compete for these resources. Seeds, seedlings, and saplings are also vulnerable to seed predation and a broad spectrum of herbivores including insects, birds, and mammals (Kolb et al., 2007). For some species like *Betula alleghaniensis*, a valuable timber species, the proportion of seeds that survive and persist into the sapling size classes is so low that these filters now serve to limit sapling recruitment and population persistence (Lorenzetti et al., 2008).

White-tailed deer (*Odocoileus virginianus*) now act as a key herbivore across much of northeastern North America limiting regeneration in many tree species (Rooney and Waller, 2003; Côté et al., 2004). Deer consume seeds, seedlings, and the buds, flowers, leaves, and sometimes bark and branches of saplings in palatable woody species exerting strong impacts in winter and early spring. They prefer to graze on graminoids and palatable understory forbs in spring through summer (Healy, 1971; Stormer and Bauer, 1980; Berteaux et al., 1998). Even when deer do not consume whole plants, their consumption of nutrient rich flowers, terminal meristems, and photosynthetic tissues tends to curtail growth and reproduction. Collectively and cumulatively, deer consume considerable understory biomass, strongly affecting energy and nutrient pathways. Ungulates also tread on plants and paw at leaf litter, destroying some plants and exposing mineral soil (Hobbs, 1996; Persson et al., 2000; Russell et al., 2001). Deer can also act as seed predators and sometimes as vectors to disperse seeds (Ostfeld et al., 1996; Gill and Beardall, 2001).

Through the latter 20th century, populations of white-tailed deer increased across much of the Eastern and Midwestern United States. In Wisconsin, populations have increased several fold since

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the 1950s. Deer populations here now chronically exceed population goals in most Deer Management Units (WI DNR, 2015). Ecologists in the Upper Midwest (USA) first drew attention to the threats high deer populations pose to tree regeneration and forest plant communities in the 1940s and 1950s (Leopold et al., 1947; Dahlberg and Guettinger, 1956). Later ecological studies confirmed the reality of these threats by demonstrating shifts in the abundance, height, and demographic profiles of species sensitive to deer herbivory (Anderson and Loucks, 1979; Bratton, 1979; Marquis, 1981). In the Upper Midwest, the density and growth of several slow-growing, palatable woody species like *Tsuga canadensis*, *B. alleghaniensis*, and *Thuja occidentalis* have declined sharply in regions with abundant deer (Rooney and Waller, 2003; Rooney, 2001; Waller and Alverson, 1997). Understory forbs like *Trillium grandiflorum*, *Clintonia borealis*, and *Maianthemum canadense* also show strong declines where deer are abundant (Balgooyen and Waller, 1995; Frerker et al., 2014).

Because trees take many years to mature, declines in long-lived trees often occur long after deer herbivory occurs. This means we may not witness its full impact for decades (McGarvey et al., 2013). Forests subjected to prolonged, elevated deer densities continue to reflect these impacts for 20–70 years after release from deer browse pressure (Nuttle et al., 2014; Anderson and Katz, 1993; Balgooyen and Waller, 1995). In addition, these shifts in plant community structure and composition also strongly affect the abundance of birds, small mammals, and other components of diversity (Allombert et al., 2005; Cardinal et al., 2012; deCalesta, 1994; Fuller, 2001; Martin et al., 2012; McShea and Rappole, 2000; Ostfeld et al., 1996). These long-lasting impacts of deer herbivory could limit our ability to maintain and restore tree, understory plant, and animal diversity within North American forests. Such diversity supports significant ecological and economic values including populations of other wildlife species, an array of ecosystem services, recreational utility, and the timber value of commercially valuable hardwood species.

Ecologists use several methods to study deer impacts. These include tracking differences in growth rates, reproductive condition, the relative abundance of species, long-term shifts in community composition, natural experiments (Diamond, 1983, e.g., islands with and without deer), and manipulative experiments (e.g., fenced exclosures) (Côté et al., 2004; Waller, 2013). Although such studies provide valuable data, they are typically of short duration and apply primarily to the particular species that were studied and the local areas where the work was done. Exclosure studies that rigorously demonstrate strong deer effects on local plant communities are also sometimes criticized for making an extreme comparison between ambient deer effects and no deer at all. In addition, building and maintaining many exclosures over many years is expensive, often forcing us to rely on data from just a few exclosures at particular locations, reducing the generality of what we can infer. These concerns suggest that it would be useful to assess impacts of deer on tree regeneration across larger areas and a more natural range of variation in deer abundance. It would also be ideal if we could study deer impacts across multiple forest types, ages, and longer time periods, e.g., by linking local exclosure studies to longer-term regional trends (Frerker et al., 2014).

Here, we investigate regional variation in sapling abundance (recruitment) in 11 tree species in relation to variation in deer density that occurred over a 30 year interval and across all of northern Wisconsin. The broad scope of this study complements more intensive local short-term studies by providing a big picture of how deer are affecting tree recruitment in this region. To obtain this picture, we use systematic surveys of forest conditions pursued by the U.S. Forest Service in their Forest Inventory and Analysis (FIA DataMart, 2015) program (http://www.fia.fs.fed.us/). The FIA program surveys permanent plots arrayed on a regular grid at regular intervals

(about 5-years). The number and dispersion of these plots (covering all forest lands in the U.S. since 1999) provide data of high statistical power from an unbiased set of samples. This allows us here to systematically compare variation in sapling recruitment among the chosen taxa in our region. In particular, we assess recruitment in 11 common tree species chosen to include taxa that differ in their palatability. These range from species that deer avoid (*Picea*) to species known to be highly palatable and susceptible to deer browsing impacts (*T. occidentalis* and *T. canadensis*). We hypothesized that saplings of species that are more palatable and susceptible to deer would be: (a) generally scarcer across the landscape, (b) absent altogether from many sites, and (c) scarcer at sites and in decades where they encountered higher deer densities. The deer density estimates we use for (c) also derive from a public source, namely the Wisconsin Department of Natural Resources (Wis-DNR). Because the metrics and approaches we describe use only publicly available data systematically collected by professional agencies, they do not require forest or wildlife managers to acquire new data or conduct local research.

Many local factors also affect patterns of tree recruitment including local soil and light conditions, local canopy composition and seed inputs, local deer browse preferences, and tree harvest history. We lacked consistent data for these and also note that obtaining such data would be impractical for most managers. In addition, our goal here was to analyze variation in recruitment at the coarser spatial scale of whole DMUs in order to obtain reliable aggregated signals of deer impacts for making management decisions. Our coarser scale of analysis ensures such averaging by filtering out much of the "noise" generated by the many variable local factors also affecting tree recruitment and deer-tree interactions.

2. Methods

2.1. Study region and estimates of deer density

Our study region encompasses the northern third of Wisconsin dominated by mixed hardwood forestlands (Fig. 1) providing a relatively homogenous set of landscapes for testing how deer affect tree recruitment. By limiting our study to this state, we could also use a single consistent set of deer density estimates from the Wis-DNR. They estimate annual post-hunt deer density using a Sex-Age-Kill (SAK) model in each of the 48 Deer Management Units (DMU) located in northern Wisconsin. Implementation of this model by the Wis-DNR provides relatively robust and reliable estimates of overwintering deer density with defined and limited amounts of error and bias (Millspaugh et al., 2009; VanDeelen, pers. commun.). Comparing SAK estimates with more rigorous Statistical Age-at-Harvest estimates that explicitly incorporate changing age structure and harvest rates indicates that the SAK model, as implemented in Wisconsin during our study period, tracked SAH estimates very closely in the northern forested DMUs (Norton et al., 2013). In addition, we only use the deer data in a comparative context to assess how variation in estimated deer numbers over DMUs and decades affects patterns of sapling recruitment in the chosen tree species.

The FIA plots occur at a density of about 1 plot per 1500 ha. We spatially divided these FIA plots into groups according to DMUs. The boundaries of these DMUs remained stable during the period of this study except for two large DMUs that were each split into two smaller units and one small DMU that was merged into a neighboring unit. For these, we recalculated estimated deer densities to match the new DMU areas. Our approach to hypothesis (c) assumes that enough variation exits in deer density among the DMUs and study periods to alter the abundances of small saplings.