



Long-term effects of deer browsing: Composition, structure and productivity in a northeastern Minnesota old-growth forest

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ABSTRACT

Although the immediate impacts of elevated deer (*Odocoileus* spp.) browsing on forest regeneration have been well documented, few studies have examined the longer term consequences. A deer enclosure experiment was initiated in 1991 in an old-growth northern mixed mesic forest in northeastern Minnesota, and resampled in 2008 to examine changes in composition, structure and productivity. Decades of overbrowsing by white-tailed deer have led to almost complete recruitment failure in size classes >2.5 cm dbh for preferred deer browse species *Thuja occidentalis* and *Pinus strobus* in unprotected plots. Other palatable browse species have been severely limited in understory development (*Populus tremuloides*, *Betula papyrifera*, *Fraxinus nigra*). Within enclosures, *P. strobus* gained in all size classes <20 cm dbh, while *F. nigra*, *B. papyrifera*, *T. occidentalis* all showed significant gains. Non-preferred *Picea glauca* increased outside enclosures, but has also gained within enclosures. The increase in *P. glauca* across treatments indicates a long-term legacy effect of preferential browsing. Browsing induced suppression of subcanopy density of preferred species and failure of canopy tree replacement may lead to a more open woodland structure dominated by *P. glauca*. Browsing pressure may negatively impact productivity, as whole tree biomass in enclosures increased at a rate twice that of unprotected plots. The low biomass levels recorded in 2008 (unprotected: 98.0 mg/ha⁻¹, enclosure: 104 mg/ha⁻¹) are approximately 1/2 of values typically recorded in later successional forests in this region indicating lower productivity may be another longer-term legacy of elevated deer population. Continued high browsing pressure is one of many factors contributing to the restructuring of northern Great Lakes forests away from historical variability conditions towards a novel and more homogeneous forested landscape. These simplified forests may be less resilient to the suite of emerging stressors such as climate change and less able to provide ecosystem services such as carbon storage, biological diversity and forest products. Sustained restoration efforts, along with reductions in deer density will be needed to restore species and structural diversity.

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1. Introduction

Ungulate browsers influence composition, structure and ecosystem processes in north-temperate forests by selectively foraging on preferred plant species (Pastor et al., 1993). Moose (*Alces alces*) at high densities alter vegetation biomass, productivity, composition, nutrient cycling and litterfall (McInnes et al., 1992), and also influence the spatial patterns of vegetation patches (Pastor et al., 1998). Rising deer populations (*Odocoileus* spp.) in many regions of North America now exert a pervasive influence on forest ecosystem dynamics. These include understory plant species diversity (Alverson et al., 1988; Stockton et al., 2005), understory and overstory woody vegetation composition and structure (Whitney, 1984; Horseley et al., 2003), forest songbirds (McShea and Rappole,

2000; Allombert et al., 2005a) and forest invertebrates (Allombert et al., 2005b).

Decades of high white-tailed deer (*Odocoileus virginianus*) populations in the northern Great Lakes region may contribute to a large-scale restructuring of forested communities in this region (Rooney and Waller, 2003). Extensive logging and large, slash-fueled fires of the European settlement period created a more homogeneous forested landscape across the northern Great Lakes region where dominance shifted from later successional or mid-seral conifer and hardwood species to early successional hardwood species (Friedman and Reich, 2005; Schulte et al., 2007). The subsequent shift to even-aged timber harvest as the primary disturbance factor perpetuated this compositional shift and also imposed a new spatial pattern dominated by small forest patches (White and Host, 2008). The predominance of small patches created high edge density and low interior forest space (Wolter and White, 2002), that along with early-successional forest favors

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species such as white-tailed deer, but negatively impacts edge-sensitive forest birds (Temple and Flaspohler, 1998) and tree regeneration due to herbivory (Alverson et al., 1988). Thus, white-tailed deer are one of a suite of related factors including land-use history, economics (timber markets and the forest products industry), development, exotic-invasive species and climate change that will have long-lasting impacts on the composition, structure and function of northern Great Lakes forests. Elevated populations of white-tailed deer in the northern Lake States region have led to limited regeneration success for many preferred browse species such as eastern hemlock (*Tsuga Canadensis* [L.] Carr), northern white cedar (*Thuja occidentalis* L.), eastern white pine (*Pinus strobus* L.) and northern red oak (*Quercus rubra* L.) (Anderson and Loucks, 1979; Cornett et al., 2000; Anderson et al., 2002; Rooney and Waller, 2003). Many herbaceous species are also prone to browsing damage as they never grow out of the zone of susceptibility (Rooney and Waller, 2003).

Although there is strong documentation of the impacts of deer browsing on tree regeneration, there is little information about the longer term impacts on sapling, subcanopy and canopy layers in mature and old-growth northern Great Lakes forests. Ross et al. (1970) analyzed vegetation within and outside of one enclosure in a north-central Minnesota pine forest from 1946 to 1969. They determined that browsing suppressed growth of all preferred browse species, with only non-preferred species moving into the subcanopy. Zenner and Peck (2009) compared the same enclosure (Ross et al., 1970) to plots with no treatment, and recent repeated underburning. Only the enclosure contained sufficient mid-story density of white pine to maintain a pine canopy. The untreated plot will likely succeed to northern hardwoods. White pine regeneration was highest in the burned plot, but was restricted to the seedling layer due to deer browse and shrub competition. Salk et al. (2011) found that prolonged deer browse in an old-growth hemlock-hardwood forest in northern Michigan led to recruitment failure of preferred browse species (white cedar, eastern hemlock, yellow birch) leading to a long-term shift in dominance towards less preferred sugar maple.

Recent work shows that prolonged, intensive browse leads to top-down effects (extremely simplified understory vegetation) that have bottom up impacts on the food chain as understory invertebrate and shrub-dependent songbird communities also became more simplified (Martin et al., 2010). Evidence suggests that prolonged, intense browsing pressure may lead to profound change in forest composition and structure leading to altered food chains (Martin et al., 2010), declines in regional habitat and species diversity and changes in key processes such as nitrogen and carbon cycling (Rooney and Waller, 2003; Côté et al., 2004).

Exclosure studies have important limitations; varying and unknown deer densities, lack of replication (Horseley et al., 2003), and that fact that complete protection from browsing is an artificial condition, as they do not capture the background levels of herbivory that would occur under low ungulate density levels. However, they can still provide valuable insights into the role of herbivores in structuring plant communities and how ecosystems may recover when browsing is eliminated or reduced. Specifically, exclosure studies help us understand the potential for ecosystem recovery after being subjected to elevated deer browsing. This includes data on the length of time that browsing protection is necessary to ensure adequate regeneration. Exclosure studies may also indicate that other management actions in addition to browse protection may be needed; gap creation, thinning or brush control to release regeneration or actions such as prescribed fire or scarification to create favorable seed bed conditions.

At a site in northern Minnesota, the following questions were explored: (1) how did selective browsing on preferred tree species by white-tailed deer influence composition, structure and productivity

in unfenced compared to fenced plots over a 17 year period? (2) Did pre-fencing browsing create a legacy effect on composition and productivity?

The forest dynamics observed in this study are broadly applicable to mesic conifer-hardwood forests with elevated deer populations throughout the region. Although this study was conducted at a single site in northern Minnesota, the soils, glacial landforms, climate conditions and plant communities are representative of mesic forests within the North Shore Highlands subsection (MN Dept. Nat. Res., 1999) and more generally of mesic forests of the Lake Superior Basin. While impacts on tree regeneration and understory vegetation are well documented (Rooney and Waller, 2003), much less is known about how these impacts influence the complete stand age structure beyond the understory. This study presents one of the few longer-term data sets available for examining the impacts of herbivores on the full range of stand age structure.

1.1. Study area

The study area comprises 4200 ha located in the North Shore Highlands subsection of the Minnesota Ecological Classification System (MN Dept. Nat. Res., 1999) and includes a remnant 182 ha stand of old-growth eastern white pine and northern white cedar forest known as Cathedral Grove. Ten kilometers of the Lake Superior shoreline form the southern boundary of the study area. Proximity to Lake Superior influences local climate conditions, creating cool, moist conditions in spring and summer and warmer conditions in fall and winter relative to inland areas (Baker and Keuhnast, 1978; Baker et al., 1985). Part of the Nemadji–Duluth Lacustrine Plain, soils are typically deep, moderate to well-drained clays with shallow, rocky, well-drained soils on the ridges (Minnesota Soil Atlas, 1973). This area is part of a large white-tailed deer wintering yard paralleling Lake Superior from Duluth to Canada.

The study area consists of a complex mosaic of forest and wetland communities. The matrix upland forest is composed of northern mesic mixed forest, which includes varying mixtures of quaking aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.) and balsam fir (*Abies balsamea* [L.] Mill), white spruce (*Picea glauca* [Moench] Voss), white pine and white cedar (MN Dept. Nat. Res., 2003). Prior to European settlement (~1900) and the extensive logging of that period, high severity fires occurred at a rotation of approximately 220 years (MN Dept. Nat. Res., 2003). Catastrophic windthrow was uncommon in the North Shore Highlands, with a rotation period in the range of 3000 years (White and Host, 2008). Currently, the Cathedral Grove forests are in a late-successional growth stage where tree fall gaps created by tree mortality and small (1–3 tree) windthrow events are the primary canopy disturbances influencing tree growth and regeneration.

In the pre-European settlement period, upland forests in the North Shore Highlands subsection were dominated by mixtures of eastern white pine, eastern white cedar, white spruce, balsam fir, paper birch and quaking aspen. Northern hardwood patches composed of sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula allegheniensis* Britt.) and northern white cedar occurred on loamy uplands within the boreal conifer-hardwood matrix (White and Host, 2000). White pine (9–19% to 0.2–1.0%) and white cedar (6–11% to 3.2–4.2%) have both declined precipitously from the pre-European settlement period to present in the North Shore Highlands subsection (White, 2001).

Prior to European settlement, northeastern Minnesota's severe winters and mixed-conifer and hardwood forests were poor habitat for white-tailed deer, which occurred at very low densities or may have been absent from the area prior to the early 1900s (Nelson and Mech, 1981). The post-Euro-American settlement shift to

early-successional forests with abundant browse (Krefting, 1975) resulted in a significant expansion of white-tailed deer into north-eastern Minnesota; by 1938 deer populations ranged from 4 to 16/km² (Mech and Karns, 1977). Deer population density estimates ranged from 3 to 6.9/km² for this region from 1995 to 2009 (Peterson et al., 2009). However, at the northern edge of their range, deer migrate in late fall to yarding areas with lower snow depths and thermal cover that moderates cold temperatures (Lankester and Peterson, 1996). In northeastern Minnesota, the north shore of Lake Superior provides this habitat with lower snow depths and thermal cover in conifer forests (Lankester and Peterson, 1996). The Cathedral Grove site is within one of these yarding areas. Winter deer densities ranging from 39 to 50 deer/km² have been reported along Lake Superior's north shore (Mech and Karns, 1977; Lankester and Peterson, 1996). Deer densities as low as 4/km² can prevent regeneration of eastern hemlock (Alverson et al., 1988). Other herbivores inhabiting the study region that browse hardwood and conifer tree regeneration include moose and snowshoe hare (*Lepus americanus* Erxl.). The Cathedral Grove site is within the low moose population density zone, regionally, moose populations have declined over the last decade (Peterson et al., 2009). Snowshoe hare populations peak on a 10 year cycle (Jones and Birney, 1988) and can cause significant damage to tree regeneration during periods of high abundance (Krefting and Stoeckler, 1953). However, hare populations in northern Minnesota appear to have declined substantially over the last 30 years (Erb, 2004). White-tailed deer populations during the winter season in Minnesota's north shore have been consistently high for several decades, even during periods of regional population decrease (Mech and Karns, 1977). While snowshoe hare may periodically impact tree regeneration, browsing pressure by sustained high white-tailed deer populations is the primary factor limiting regeneration of preferred winter browse species such as white cedar and white pine in the North Shore Highlands (Cornett et al., 2000; Anderson et al., 2002).

2. Methods

In order to assess forest change related to deer browse, I compared forest composition and structure sampled in 1991 and 2008 for three 0.25 ha deer/snowshoe hare exclosures and three 0.25 ha control plots unprotected from herbivores. Exclosure and unprotected plots are hereafter referred to as fenced and unfenced, respectively.

2.1. Sampling

Three 0.25 ha, rectangular exclosures were established within the Cathedral Grove site from 1987 to 1990; A in 1987, B in 1988 and C in 1990. Fences were constructed from 10-cm × 10-cm steel wire mesh 2.5 m high and regularly monitored and maintained. Plastic mesh (1.5 m high, 2.8-cm × 7.5-cm) was attached to the base of each fence in 1991 to exclude snowshoe hare. Exclosure A is separated from B by 400 m and from C by 450 m. Exclosures B and C are separated by 150 m. In 1991 three reference or unprotected 0.25 ha plots were located in similar vegetation conditions directly adjacent to the fenced exclosures. In 1991 and 2008 field crews recorded all tree stems >2.5 cm dbh in each fenced and unfenced plot. Individuals were recorded by species, diameter at breast height and whether they were alive or dead. Only live stems were used in the following analysis.

2.2. Statistical analysis

Multi-Response Permutation Procedure (MRPP), a non-parametric test based on a dissimilarity matrix of species composition

(McCune and Grace, 2002) was used to test for differences in overall tree species composition using tree density (live stems >2.5 cm dbh) between fenced and unfenced plots at each date. I then compared tree density within treatments over time (fenced 1991–2008, unfenced 1991–2008) using Mantel's test, another non-parametric test using a dissimilarity matrix that allows comparison the same samples over time (McCune and Grace, 2002).

One way analysis of variance (ANOVA) was used to compare the effects of treatments (fenced and unfenced) blocked by plot pair on stem density/ha⁻¹ (total, species, size class, species by size class) total basal area (m²/ha⁻¹) and biomass (mg/ha⁻¹) in live trees. All measures using total stem density, basal area and biomass included all live stems >2.5 cm dbh. Three size classes (<5 cm, 5–10 and 10–20 cm dbh) were used with the assumption that browsing control would have little effect on stem densities greater than 20 cm dbh over the 17 year period. I used the mean difference in stem density, basal area and biomass from 1991 to 2008 to calculate these statistics. For total density, basal area and biomass, I also used percent difference from 1991 to 2008. This design is similar to a before–after–control–impact model (BACI) (Stewart-Oaten et al., 1986; McInnes et al., 1992). In particular, the ANOVA analysis tests the effects of treatments (fenced vs. unfenced) on the density change of preferred browse species. Non-preferred white spruce would not be expected to show responses to fenced or unfenced treatments. Less preferred balsam fir would be expected to show less response than preferred species, but more than non-preferred white spruce. The square root transformation was applied to stem density data to make the variance and mean independent (Gotelli and Ellison, 2004). Because of the high variability in these forest systems, an alpha level of less than 0.10 was used to indicate likely significant differences.

I estimated whole tree biomass (mg/ha⁻¹) by species for all live stems >2.5 cm dbh. Species specific allometric equations developed in Minnesota and northern Wisconsin were used to calculate aboveground live tree biomass for tree species present on Cathedral Grove (Schmitt and Grigal, 1981; Pastor et al., 1984; Perala and Alban, 1994). Root biomass was calculated using the equation developed by Cairns et al. (1997) for temperate forests. Whole tree biomass is the sum of aboveground live tree and root biomass.

3. Results

3.1. Total basal area, density and biomass 1991–2008

Comparisons of treatment effects showed that mean tree density percent difference values were higher in fenced compared to unfenced plots ($F = 12.28$, $P = 0.073$) (Table 1). Basal area showed

Table 1
Mean difference and mean percent difference ±1 standard error from 1991 to 2008 for (A) stem density/ha⁻¹, (B) basal area/m²/ha⁻¹ and (C) whole tree biomass/mg/ha⁻¹ in live trees >2.5 cm dbh. $N = 3$ for unfenced and fenced treatments.

	Mean 1991	Mean 2008	Mean difference	Percent difference
<i>(A) Stem density</i>				
Unfenced	1617 (705)	3219 (1858)	1602 (1170)	81 (31)
Fenced	1375 (370)	4836 (897)	3461 (527)	274 (42) ^a
<i>(B) Basal area</i>				
Unfenced	15.3 (3.8)	22.9 (6.0)	7.6 (2.4)	50 (11)
Fenced	11.1 (0.8)	24.8 (2.1)	13.7 (1.7) ^b	125 (15) ^a
<i>(C) Biomass</i>				
Unfenced	72.4 (12.9)	97.9 (19.2)	25.5 (10.7)	36.7 (15.1)
Fenced	53.2 (3.0)	104.0 (8.1)	50.8 (4.7) ^a	95.5 (5.3) ^b

^a $P < 0.10$ for one-way ANOVA by treatment.

^b $P < 0.05$ for one-way ANOVA by treatment.

a 1.8-fold increase in fenced compared to unfenced ($F = 77.7$, $P = 0.013$), percent difference was also significant ($F = 16.7$, $P = 0.055$). Whole tree biomass showed a twofold increase in fenced relative to unfenced plots ($F = 17.6$, $P = 0.052$), percent difference was also significant ($F = 34.4$, $P = 0.028$). Overall, stem density, basal area and carbon all gained in fenced plots compared to unfenced.

3.2. Forest composition 1991–2008

In 1991, at the onset of this study, tree species composition did not differ between fenced and unfenced plots (MRPP, $T = 1.03$, $P = 0.224$) (Fig. 1). By 2008 tree composition had diverged between fenced and unfenced plots (MRPP, $T = -1.29$, $P = 0.0988$). Unfenced plots (1991–2008) did not differ over time (Mantel's test, $T = -0.811$, $P = 0.417$), while fenced plots showed a strong difference in tree composition over the same time period (Mantel's test, $T = 2.32$, $P = 0.020$) (Fig. 1). Composition was similar between treatments at the onset of the study, but diverged with 17 years of browse protection in the fenced plots.

Analysis of density change for tree species from 1991 to 2008 showed that fenced plots had significantly higher mean density gains relative to unfenced for the following species: black ash (*F. nigra* Marsh.) ($F = 40.56$, $P = 0.024$), paper birch ($F = 11.83$, $P = 0.075$) and white pine ($F = 22.04$, $P = 0.042$) (Fig. 1). The non-preferred white spruce and less preferred balsam fir showed similar increases in both treatments.

3.3. Change 1991–2008: structure-stem density by size class

Although data suggest that stem density in fenced plots increased from 1991 to 2008 relative to unfenced in the <5 cm and 5–10 cm dbh size classes, differences were not statistically significant (Fig. 2). Density change in the 10–20 cm size class was similar for both treatments. The unfenced plot density increases in the <5 cm and 5–10 cm dbh size classes values were due to increases in less-preferred balsam fir and non-preferred white spruce in unfenced plots (Fig. 2).

3.4. Species density by size class

White pine in fenced plots increased in all three size classes relative to unfenced plots (<5 cm dbh, $F = 16.01$, $P = 0.057$; 5–10 cm dbh, $F = 28.8$, $P = 0.033$; 10–20 cm dbh, $F = 231.7$, $P = 0.004$).

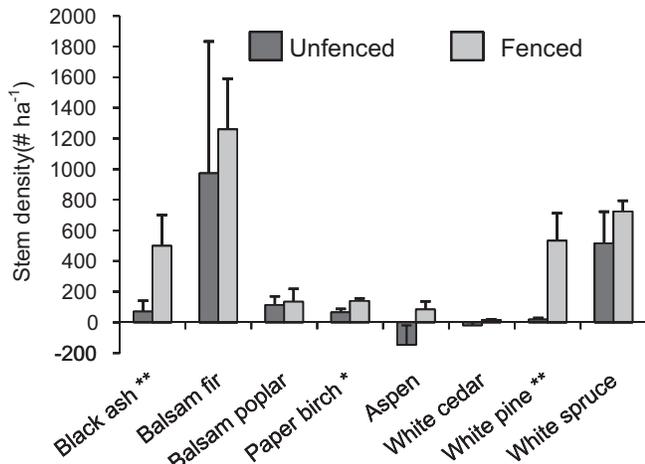


Fig. 1. Mean density change from 1991 to 2008 by species for fenced and unfenced plots ($N = 3$). Error bars equal 1 standard error of the mean. For one-way ANOVA comparing the effects of unfenced and fenced treatments: * $P < 0.10$, ** $P < 0.05$.

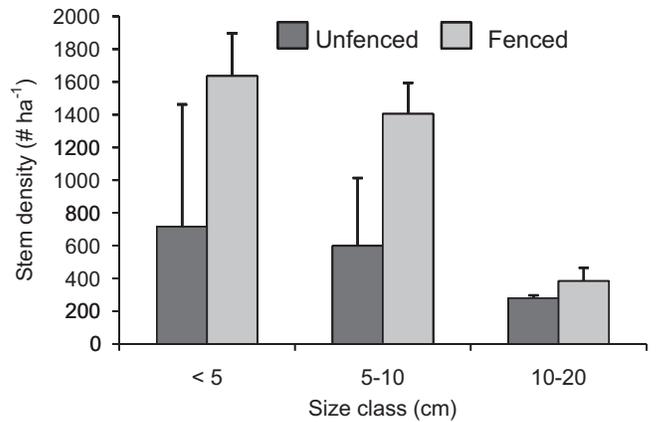


Fig. 2. Mean density change from 1991 to 2008 for three size classes for fenced and unfenced plots ($N = 3$). Error bars equal 1 standard error of the mean. For one-way ANOVA comparing the effects of unfenced and fenced treatments: * $P < 0.10$, ** $P < 0.05$.

Black ash also gained in fenced plots relative to unfenced in all three size classes; (<5 cm dbh, $F = 21.7$, $P = 0.004$; 5–10 cm dbh, $F = 63.7$, $P = 0.015$; 10–20 cm dbh, $F = 16.02$, $P = 0.057$). Aspen also showed a significant increase in the 5–10 cm dbh class ($F = 15.57$, $P = 0.058$) (Fig. 3). White cedar in fenced plots gained in the <5 cm class ($F = 26.5$, $P = 0.036$). The less-preferred balsam fir and non-preferred white spruce showed similar density gains in the fenced and unfenced plots.

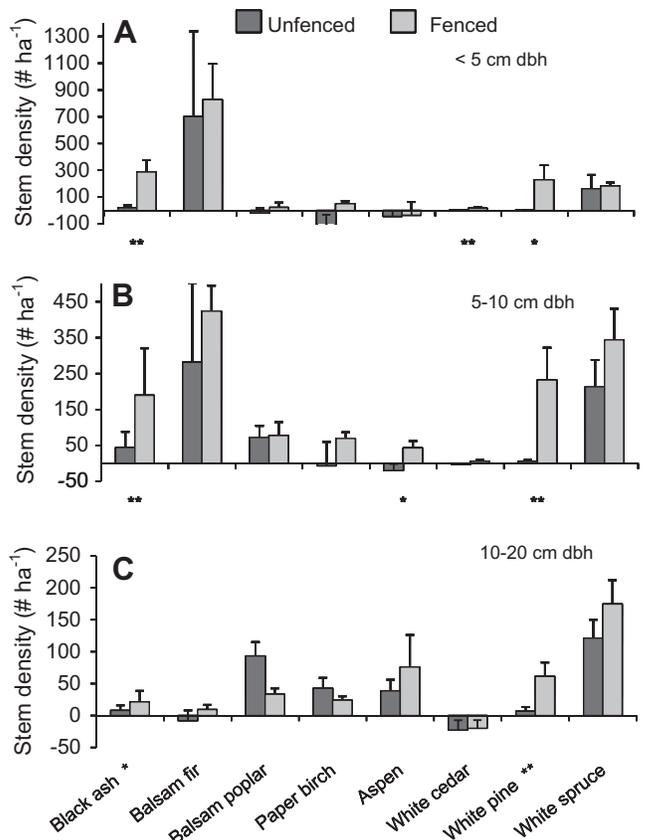


Fig. 3. Mean density change from 1991 to 2008 by species for fenced and unfenced plots ($N = 3$) for three size classes: (A) <5, (B) 5–10 and (C) 10–20 cm dbh. Error bars equal 1 standard error of the mean. For one-way ANOVA comparing the effects of unfenced and fenced treatments: * $P < 0.10$, ** $P < 0.05$.

4. Discussion

The overall results show a strong contrast between fenced and unfenced plots in composition, structure and productivity and demonstrate the long-term legacy of elevated deer browsing in northern forests. Important species such as white cedar and white pine are failing to regenerate in unfenced areas and may not replace their counterparts in the canopy as non-preferred browse species slowly become more dominant. Structure may be shifting to more open woodland conditions with lower basal area and whole tree biomass.

4.1. Composition and structure

The suppression of preferred browse species has led to a shift in dominance towards white spruce, which is rarely browsed by white-tailed deer (Figs. 1 and 3). McInnes et al. (1992) and Pastor et al. (1993) showed that long-term preferential browsing from a high moose population led to a shift towards white spruce canopy dominance on Isle Royale National Park. Similarly, in the boreal forest of Anacosti Island, Quebec, Canada, several decades of high deer populations ($\sim 20 \text{ km}^2$) shifted forest dominance from balsam fir to white spruce (Potvin et al., 2003). Forests at Cathedral grove and in the North Shore Highlands have been subject to high deer populations for several decades prior to the onset of this study in 1991 (Mech and Karns, 1977). While the unfenced plots show a strong shift towards white spruce dominance, white spruce density also increased within the fenced plots (Figs. 1 and 3). This trend indicates a legacy effect of high browsing pressure which allowed white spruce to accumulate over time and eventually access more canopy space, even in fenced plots. Although fenced plots may allow white pine and other species (balsam fir, paper birch, quaking aspen, white cedar) to recover over time, browsing has produced a legacy effect of increased spruce abundance that likely will persist for many decades. Reduction of deer density below threshold levels (e.g. $< 4 \text{ km}^2$) (Alverson et al., 1988) should allow for recovery of composition and structure, however, this may be a protracted process due to the longer-term legacy of elevated deer browsing (Tanentzap et al., 2011) which has led to nearly complete regeneration failure of preferred (white cedar, white pine) and somewhat preferred (black ash, balsam poplar, paper birch, quaking aspen) browse species. Tanentzap et al. (2011) showed only small increases in small tree recruitment in deciduous forests of southwestern Ontario, Canada after substantial reductions in deer density, indicating a longer term legacy of high browsing pressure. In northeastern Minnesota, white cedar may require 30 years or more of browsing protection to increase into the larger size classes (Cornett et al., 2000). Without dramatic reductions in deer populations, or sustained restoration efforts, the abundance of preferred species will continue to decline in this region, particularly those species that rely on seedling establishment rather than vegetative reproduction (white cedar, white pine, yellow birch). This decline in abundance driven by high deer populations follows regional decreases in tree species diversity that began with the extensive logging and slash fires of the settlement era (Schulte et al., 2007).

While there were no significant differences for density by size class, data still suggest that stem density increased at a greater rate within fenced plots relative to unfenced in subcanopy tree layers ($< 10 \text{ cm dbh}$) (Fig. 2). The changes in subcanopy density in unfenced plots were due to increases in the non-preferred white spruce and less-preferred balsam fir (Fig. 3). White-tailed deer typically only consume balsam fir under starvation conditions when other food sources are unavailable (Tremblay et al., 2005). Balsam fir is now being consumed on this site (White, personal observation). Continued browsing on balsam fir will lead to lower understory density. Basal area in fenced plots increased 1.8 times that

of unfenced plots (Table 1). Current basal area values of $23\text{--}25 \text{ m}^2/\text{ha}^{-1}$ are $25\text{--}35\%$ lower than values found in late-successional stands of this type in areas with lower deer density (Grigal and Ohmann, 1975; Reich et al., 2001). These data indicate that browsing limits recruitment into subcanopy and canopy layers and may be maintaining structure in a more open state. Regionally, in similar plant communities, deer browsing pressure has favored grasses and sedges over forbs (Rooney and Waller, 2003; Mudrak et al., 2009). Graminoids may be more resistant to browsing damage due to basal meristems and the silica content of foliage (Rooney and Waller, 2003). Deer browsing limits regeneration of preferred species directly through consumption, and indirectly by favoring graminoid cover and further limiting tree regeneration (Stromayer and Warren, 1997; Rooney and Waller, 2003). The more open canopy in unfenced plots may have led to increased graminoid cover relative to fenced plots (White, unpublished data). The increased density of non-preferred white spruce along with increased graminoid cover may limit the establishment of other plant species (Rooney and Waller, 2003; Royo and Carson, 2006) even under lower deer densities.

The unbrowsed plots may represent the beginning of an alternative stable state as canopy tree mortality of browsed species continues without replacement (Stromayer and Warren, 1997). Alternatively, over time less-preferred species may accumulate and restore structural conditions, but without the characteristic species composition. Complete browsing protection over 17 years in the fenced plots showed that density of preferred species recovered (Fig. 1). There is also recruitment into all three size classes (Fig. 3) indicating a high probability of canopy tree replacement on fenced sites. The fenced sites appear to be moving towards more typical late-successional forest conditions with canopy dominance by white pine and white spruce, balsam fir in the subcanopy, with less shade tolerant species (paper birch, quaking aspen) regenerating in larger canopy gaps ($> 20 \text{ m}$ diameter) (Frelich, 2002). White cedar may take significantly longer to recover (Cornett et al., 2000). The unfenced sites are moving towards more novel conditions with white spruce canopy dominance with white spruce and balsam fir in the sapling and subcanopy layers. Graminoid cover may increase, further limiting regeneration opportunities (Stromayer and Warren, 1997; Royo and Carson, 2006).

4.2. Productivity; biomass and carbon storage

Whole tree biomass showed a twofold increase in fenced plots compared to unfenced indicating a strong negative influence of browsing pressure on productivity. However, 2008 biomass values at $98 \text{ mg}/\text{ha}^{-1}$ in unfenced and $104 \text{ mg}/\text{ha}^{-1}$ in fenced plots are significantly lower than other late successional mesic hardwood conifer forests in the region not subjected to high browsing pressure. On these sites, whole tree biomass values range from 200 to $300 \text{ mg}/\text{ha}^{-1}$ (Bradford and Kastendick, 2010; Powers et al., 2011, White, unpublished data). The low biomass values on the Cathedral Grove site may also be a longer-term legacy of elevated deer populations as deer severely limit recruitment of faster growing tree species such as quaking aspen and white pine into the subcanopy and canopy layers. Deer may decrease productivity directly by limiting recruitment into the tree stratum; however, the long-term shift to higher abundance of white spruce may also lower productivity and potential long-term carbon storage through the processes of litterfall, decomposition and mineralization. On Isle Royale National Park, heavy moose browsing on preferred species also shifted composition towards white spruce (Pastor et al., 1993). This shift lowered litterfall quantity, as white spruce has high leaf retention rates, and quality, because of high levels of leaf lignin, structural cellulose and secondary metabolites. This in turn led to low levels of nitrogen mineralization, which favors species

tolerant of lower resource levels, and ultimately may depress productivity (Pastor et al., 1993). However, in subboreal forests of Quebec, nitrogen mineralization was unrelated to deer density in intact forests (Dufresne et al., 2009). Lowered productivity may impact a variety of forest ecosystem services including forest products, carbon storage for climate change mitigation and biological diversity.

With the certainty of climate change, using forests as carbon sinks is considered one of the key strategies that can be implemented on a global scale to reduce atmospheric greenhouse gas concentrations (Canadell and Raupach, 2008). These results showing a near doubling of biomass stored in fenced vs. unfenced plots indicate that high deer population levels could have significant negative impacts on regional whole tree forest carbon storage. However, other carbon pools (mineral soil, dead wood, forest floor) may compensate for lower whole tree values. Estimates of carbon storage in forest ecosystems should include the potential effects of high herbivore populations as well as other threats such as native and non-native pests and pathogens.

4.3. Management implications

Restoration and adaptive management will be necessary to maintain resilient forests as climate change and other factors influence forest ecosystems in the northern Great Lakes region (Galatowitsch et al., 2009). While land management agencies in northern Minnesota have plans (MFRC, 2003) in place to restore and maintain composition and structural diversity based on natural-disturbance-based-management (NDBM) approaches (Drever et al., 2006), high white-tailed deer populations severely limit these efforts across a large part of this region (Frelich and Reich, 2009). In areas of high deer population density, restoration work typically requires planting, fencing or other browse protection for individual trees or groups of trees, site preparation and mechanical release. Costs range from \$500 to \$1200/ha (C. Dunham, personal communication), depending on management intensity, making large scale restoration efforts effecting 10^{-4} – 10^{-5} ha⁻¹ cost prohibitive for many agencies and organizations. Without significant reductions in deer density, restoration work is likely the only reliable way to maintain diversity in forest composition and structure. However, Reimoser and Gassow (1996) suggest a shift from clearcut to selection silvicultural systems that are 'close to nature' will yield less game damage to susceptible tree species in montane and subalpine of Austria. This may be viable on sites with relatively low deer density; however, on sites such as Cathedral Grove, intensive restoration work is still necessary. NDBM approaches (Drever et al., 2006) should be investigated for their potential for mitigating browsing damage and restoring composition and structural diversity in matrix forests of the northern Great Lakes region. NDBM, with a shift to longer rotations, less clearcutting and more partial harvesting that mimics intermediate disturbances (Raymond et al., 2009) could create more variable forest conditions along with less available browse, which could help maintain sustainable white-tailed deer populations. However, given the probable slow pace of recovery even with lower deer densities, sustained restoration efforts may be the most important strategy for maintaining regional forest diversity. In addition to restoration, NDBM, and policies the lead to lower deer population densities will be key strategies that can increase diversity and resilience in northern Lake States forests.

5. Conclusion

Results from this study strongly support other evidence that elevated white-tailed deer populations are a key factor in the large-scale restructuring of northern Great Lakes forests away from

natural variability towards more homogeneous, novel forest conditions. In this case there is a clear deer-driven shift towards white spruce dominance coinciding with a lack of regeneration and replacement of trees in larger size classes for preferred and somewhat preferred browse species.

With complete browse protection, forests may recover composition and structural attributes relatively quickly, as in this study there were significant shifts towards characteristic late-successional forest conditions on fenced plots over a 17 year period. However a strong legacy of browsing remains as white spruce continues to increase in both fenced and unfenced plots. Reduced deer density may allow for recovery of composition and structural characteristics, but this may be a protracted process because of the legacy of elevated deer populations. This includes the shift towards spruce dominance, the almost complete suppression of regeneration of species other than non-preferred white spruce and less preferred balsam fir, and a possible shift towards more open woodland conditions that favor graminoids and may limit natural regeneration opportunities for tree species.

Unfenced forests at Cathedral also show significantly lower productivity compared to fenced as measured by whole tree biomass. The low biomass values on the Cathedral Grove site may also be a longer-term legacy of elevated deer populations. These results, along with the shift towards more simplified forests suggest that forest landscapes subjected to high browsing pressure may be limited in their capacity to supply key ecosystem services such as carbon storage, forest products and habitat for biological diversity.

In areas with chronically high deer populations, intensive and costly restoration work is the only reliable way to restore species and structural diversity. While this approach can be effective at small scales, the cost is limiting for larger matrix forests. At the regional, matrix forest level, efforts to reduce deer density could be combined with focused restoration and NDBM to shift forest ecosystems towards greater diversity in forest composition and structure.

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