Poor recruitment is changing the structure and species composition of an old-growth hemlock-hardwood forest

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ABSTRACT

Anthropogenic factors such as elevated deer populations, invasive earthworms or climate change may alter old-growth forests of the Upper Midwest region of the United States. We examined demographic trends of woody species across all size classes over 35 years in a late-successional forest dominated by hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) in Michigan's Upper Peninsula using two sets of permanent plots. For the duration of the study period, species that were less-preferred white-tailed deer (*Odocoileus virginianus*) forage, especially sugar maple, comprised a much higher fraction of all seedlings and saplings compared to overstory trees. The density of small sugar maple declined across the study period, but no other species became more abundant, creating a more open forest understory. By the most recent census, preferred species for deer browse had been nearly eliminated from the understory, and declines in unpreferred species such as sugar maple were also apparent. We found small changes in temperature (<0.5–1 °C rise in minimum and maximum temperatures depending on season) and precipitation (±28 mm depending on season) and little evidence of invasive earthworms impacts. Our results suggest that the sustained elevated deer density is shifting the structure and composition of this old-growth forest. A demographic model showed that if current recruitment, growth and mortality rates were to continue for 500 years the forest would eventually reach a new equilibrium with virtually no hemlock or yellow birch remaining.

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1. Introduction

Logging that accompanied European settlement reduced late-successional forests to a tiny fraction of the current land cover in the eastern United States (Davis, 1996). Today, old-growth remnants are sometimes seen as models for restoring eastern forests to more historical conditions (e.g., Mladenoff et al., 1993). However, remnant forests may be changing from anthropogenic impacts besides logging, making them imperfect templates for restoration. Identifying these impacts and measuring their effect on the forest community will lead to a clearer picture of the pre-European forest and inform restoration efforts.

In northern Michigan and Wisconsin, USA, eastern hemlock (*Tsuga canadensis*)-hardwood forest was one of the most abundant forest types prior to European settlement, and today covers only about 0.2% of its original extent (Frelich, 1995; Davis et al., 1996). Fires are rare in this forest type, and the primary form of disturbance is the treefall gap of one to a few trees (Frelich and Lorimer, 1991; Parshall, 1993; Frelich and Graumlich, 1994). The common species of the hemlock-hardwood forest are moderately to highly shade tolerant, with abundant advanced regeneration of shade-tolerant species such as hemlock and sugar maple (*Acer saccharum*) and regeneration within treefall gaps of moderately tolerant species such as yellow birch (*Betula alleghaniensis*) and American basswood (*Tilia americana*). Some species, such as hemlock and yellow birch, germinate well on the tip-up mounds and coarse woody debris that are abundant in old forests (Marx and Walters, 2008).

These forests also have pronounced separation into hemlock and hardwood dominated patches up to 40 ha in size due to the combined influence of neighborhood effects and environmental variation (Pastor and Broschart, 1990; Frelich et al., 1993; Frelich, 2002). Sedimentary pollen records indicate that the location of these patches has in many cases changed little since the

arrival of hemlock to the region 3000–4000 years ago (Davis et al., 1998).

Although many remnant old-growth hemlock-hardwood stands are now protected from logging, their composition and dynamics may be changing due to anthropogenic factors such as exotic earthworm invasion and elevated deer populations, with future changes likely due to invasive tree pests, diseases and climate change. There are no earthworms native to the Upper Midwest of the United States, but several species have been widely introduced. Earthworm species vary in their effect on the plant community, with the greatest impact coming from species that consume the duff layer, reducing soil nutrients and making the forest floor less hospitable for seed germination (Hale et al., 2005; Frelich et al., 2006; Holdsworth et al., 2007).

Modern white-tailed deer (*Odocoileus virginianus*) populations are significantly higher than historical levels in much of the eastern United States, including in the Upper Peninsula of Michigan, where Doepker et al. (1995) estimate modern populations to be around twice those of before European settlement. Studies have shown that deer herbivory changes the forest floor community, in particular decreasing the density and diversity of the forbs and tree seedlings that deer preferentially browse (Beals et al., 1960; Mudrak et al., 2009). Several studies have shown a close link between deer browsing and poor regeneration of hemlock (Anderson and Loucks, 1979; Frelich and Lorimer, 1985; Anderson and Katz, 1993; Rooney and Waller, 1998; Rooney et al., 2000). Moreover, a study in the boreal forest of Anticosti Island in Quebec, Canada found that after sustained elevated deer browsing had largely eliminated preferred species from the forest, deer consumed balsam fir (*Abies balsamea*) to such an extent that its composition in the canopy was declining while that of even less-preferred spruce (*Picea* spp.) increased (Tremblay et al., 2005). If similar processes are present in hemlock-hardwood forest, deer could disrupt the patch dynamics between sugar maple and hemlock that have been in place for the last few millennia by affecting both species negatively, but hemlock more negatively than sugar maple (Witt and Webster, 2010).

In this paper we use two multi-decadal data sets and a simple forest dynamics model to (1) examine trends in the density and species composition of woody stems from seedlings to canopy trees in an old-growth hemlock-hardwood forest and (2) explore possible evidence for mechanisms behind these trends. Given anthropogenic factors, we expect that density and composition will change across our census period and that deer browse will be a major cause of this change. We do not expect to find invasive earthworms because our sites are undisturbed and relatively remote from roads, characteristics correlated with uninvaded forests (Holdsworth et al., 2007). Furthermore, we hypothesize that tree species less preferred by deer will have different size class distributions and higher recruitment than more preferred species. Finally, we predict that changes in forest floor composition could feed up to subcanopy and canopy trees, changing the size structure and species composition of the forest.

2. Materials and methods

2.1. Study area

Sylvania Wilderness Area is a unit of Ottawa National Forest in Michigan's Upper Peninsula (46°13′N, 89°18′W). It is home to ~6000 ha of contiguous unlogged late-successional hemlock-hardwood forest. Although hemlock, sugar maple and yellow birch compose the majority of the trees in the canopy, American basswood, ash (*Fraxinus* spp.), red maple (*Acer rubrum*), white pine (*Pinus strobus*), ironwood (*Ostrya virginiana*), northern white cedar (*Thuja occidentalis*) and a few minor species are also present. The pitted outwash terrain that dominates Sylvania is part of the Wine-

gar Moraine (Bockheim and Jordan, 2004). The primary soil is the coarse-loamy Gogebic Series, with patches of sandier soil interspersed.

The climate in Sylvania is cold continental. We used data from the PRISM Climate Group (2010) to describe climatic values for the period 1895–2008. Mean annual precipitation was 812 mm, with 290 mm coming during the summer (June–August). The average annual daily high temperature was 10 °C, and low temperature was −2 °C. For June–August these values were 24 °C and 10 °C, respectively. Linear regressions of these climate values showed an approximately 1 °C rise in both summertime and annual minimum temperatures and a less than 0.5 °C change in summertime and annual maximum temperatures. Average annual precipitation increased by 27 mm, while average summertime precipitation decreased by 28 mm.

2.2. Davis plots

Between 1987 and 1990, members of the lab of Margaret Davis, University of Minnesota—Twin Cities, established four permanent plots (A–D) in Sylvania (Davis plots). The plots range from 5 to 10 ha in size, with a total area of 27.45 ha. These plots mainly consist of upland hemlock-hardwood forest, although there is also a small area of bogs, ash wetlands and small ponds. Plot locations were originally selected to include different spatial patterns in the hemlock-hardwood forest where there were small hollows suitable for paleoecological research (Frelich et al., 1993; Davis et al., 1994).

In each plot, all woody stems at least 5 cm in diameter at 1.4 m above the ground (dbh), were mapped and tagged, their species recorded and dbh measured. Each plot was recensused between 1993 and 1995 and again in 2006. At each recensus, all new trees were tagged and mapped using previously mapped trees as reference points. During the second and third censuses all woody stems >2 m tall, but <5 cm dbh (hereafter "saplings") in the plots were mapped and placed into one of two dbh classes: <3 cm or 3–5 cm.

The density of woody stems <2 m tall (hereafter "seedlings") were measured in permanent 2 m × 2 m subplots at randomly selected locations >20 m from plot boundaries. Subplot corners were marked with rebar poles. Subplots could, and often did, contain standing trees and coarse woody debris. Fifty subplots were installed in plot A in 1990 and the total number of stems <2 m tall for each woody species was counted, except for sugar maple, which was counted in three height classes: <50 cm, 50–100 cm and 100–200 cm. In 1991, 50 subplots in plot B and 25 subplots each in plots C and D were installed and the number of stems of each species was counted in three height classes (0–50 cm, 50–100 cm and 100–200 cm). Percent cover below two meters in height was estimated for each species.

In 2006, we recensused all of the subplots using the same methods as the 1991 census. We were unable to find the rebar corners for four subplots, in which case their location was estimated from their mapped location.

We sampled for earthworms between 29 September and 5 October 2006 adjacent to 68 randomly selected subplots scattered across the four mapped plots. We removed the leaf litter from 0.1 m² of ground and examined it for earthworms, after which 4 l of water mixed with approximately 80 cm³ of mustard powder were poured onto the bare soil, following the techniques of Holdsworth et al. (2007). All of the earthworms that emerged from the soil within 15 min or had been found in the leaf litter were preserved in 10% formalin for later identification.

2.3. Deer browse preference and size class distribution

We used the browse preference rankings of Dahlberg and Guettinger (1956) to categorize each species with at least 10 stems

Table 1

The browse preference rankings of Dahlberg and Guettinger (1956) for species with more than 10 stems >5 cm dbh in 2006 in the Davis plots in Sylvania Wilderness, Michigan. Species range from most preferred (I) to least preferred (IV) browse. We categorized species ranked I, II or II–III as "preferred browse" and species ranked III, III–IV or IV as "unpreferred browse".

Species	Browse preference rating (Dahlberg and Guettinger, 1956)
White cedar (*Thuja occidentalis*)	I
Hemlock (*Tsuga canadensis*)	I
Red maple (*Acer rubrum*)	I
Basswood (*Tilia americana*)	II
White pine (*Pinus strobus*)	II
Yellow birch (*Betula alleghaniensis*)	II
Black ash (*Fraxinus nigra*)	II–III
American elm (*Ulmus americana*)	III
Balsam fir (*Abies balsamea*)	III
Sugar maple (*Acer saccharum*)	III
White ash (*Fraxinus americana*)	III
Hop hornbeam (*Ostrya virginiana*)	III–IV
Black spruce (*Picea mariana*)	IV
Tamarack (*Larix laricina*)	IV
White spruce (*Picea glauca*)	IV
Green ash (*Fraxinus pennsylvanica*)	Not ranked

≥5 cm dbh in our plots as preferred browse – a rank of I, II or II–III – or unpreferred browse – a rank of III, III–IV or IV (Table 1). There was no ranking given for green ash (*Fraxinus pennsylvanica*), and since there were inconsistencies between census years in the identification of green ash versus the closely related white ash (*Fraxinus americana*), the two species were combined in analyses and assumed to share the deer browse ranking of white ash (III). We compared the size-class distributions of the species in the two groups using data from the third census, because the effects of deer herbivory should become increasingly apparent the longer the period of elevated deer density.

2.4. Stearns and Sotala plots

In 1974–5 Forest Stearns and Dennis Sotala, University of Wisconsin-Milwaukee, established a series of permanent plots in Sylvania, including eight sites similar to the Davis plots—late-successional, uneven-aged stands dominated by sugar maple, hemlock, yellow birch, and/or basswood. Stearns and Sotala recensused these plots in 1990, and we did so in 2009. Each site consisted of two 30 m × 6.7 m (0.02 ha) plots where every tree >2.54 cm (1 in.) was measured and identified to species. Subplots for sampling stems >0.91 m tall but <2.54 cm dbh were situated at two corners of each plot at opposite ends of the 30 m axis. The subplot dimensions were 4 m × 1 m, with the long axis of the subplot parallel to the long axis of the larger plot.

2.5. Data analysis and demographic model

Because the four Davis plots had broadly similar patterns of relative composition, recruitment, growth and mortality, we combined data from all plots in our analyses. For example, sugar maple, hemlock and yellow birch each comprised at least 15% of all of the stems >35 cm dbh in the first census in each plot. Combined, the three species accounted for >70% of all stems >35 cm dbh in each plot in the first census. Data for each plot separately can be found in Appendix A. We did not perform formal analyses of statistical significance because we had a complete census of all stems within the Davis plots.

We created a simple model of future basal area of the three most common species – hemlock, sugar maple, and yellow birch – by projecting the measured species-specific recruitment, growth

and mortality rates from the Davis plots forward until equilibrium in the dbh-size class distribution occurred. Because there would likely be feedbacks between these rates and basal area, this model is intended as a tool to explore the power of current trends to alter the forest rather than a specific prediction of what the future forest will look like. Growth and mortality rates were calculated in 10 cm dbh classes starting at 5 cm dbh (i.e., 5–15 cm, 15–25 cm, etc.). Because the small numbers of stems in the largest size classes reduce confidence in our estimates of growth and mortality, we combined the largest classes into a single class consisting of all stems >75 cm dbh. Annual mortality rate, M, was calculated as

$$M = 1 - \left(\frac{N_t}{N_0}\right)^{1/t} \tag{1}$$

where N_0 is the number of stems alive at time = 0, N_t is the number of stems from the original cohort that are still alive, whether or not they changed size class, and t is the number of years between censuses. To simplify the model, growth was calculated as the annual probability of a stem transitioning into the next larger 10 cm dbh class. The transition rate, T, for a given size class was calculated in a manner similar to the mortality rate:

$$T = 1 - \left(\frac{G_t}{N_0}\right)^{1/t} \tag{2}$$

where N_0 is the number of stems alive at time = 0, G_t is the number of stems from the original cohort that did not grow into the next size class (i.e., either died or remained alive but stayed in the same size class), and t is the number of years between censuses. To calculate annual recruitment we started with the measured number of new stems ≥5 cm dbh divided by the number of years between censuses. We adjusted this rate upwards to account for stems that reached at least 5 cm dbh but then died before being censused, using the formula

$$R_A = R_m \left(\sum ((t - t_i)(M_m)^t i)\right) \tag{3}$$

where R_A is the adjusted recruitment rate, R_m is the measured recruitment rate, M_m is the measured mortality rate for stems 5–10 cm dbh, t is the number of years between censuses and t_i is the number of years until the next census.

Because the four Davis plots differed in the number of years between censuses, we calculated recruitment, transition and mortality rates by individual plots before combining those rates to create an overall rate by weighting based on the number of stems in each plot. To run the model, we started with our 2006 stem counts for each species, then created stem counts for the subsequent year by giving each individual stem a random chance to either die or transition into the next larger size group based on the transition and mortality rates calculated above, with new trees added to the smallest size class based on the adjusted recruitment rate. Because we were most interested in the implications of different recruitment rates on the forest, and because recruitment rates changed more during our study than transition or mortality rates, we ran the model twice for each species, once each for the adjusted recruitment rates for the intervals between the first and second censuses and between the second and third censuses. Using the measured rates as probabilities and starting with the size distributions from the 2006 census we ran 100 iterations, calculating annual changes in composition out to 1000 years, at which point all simulation runs had converged on equilibrium basal areas. To convert stem counts to basal area we calculated the average basal area for each size class based on the assumption that stem sizes were evenly distributed within the size class.
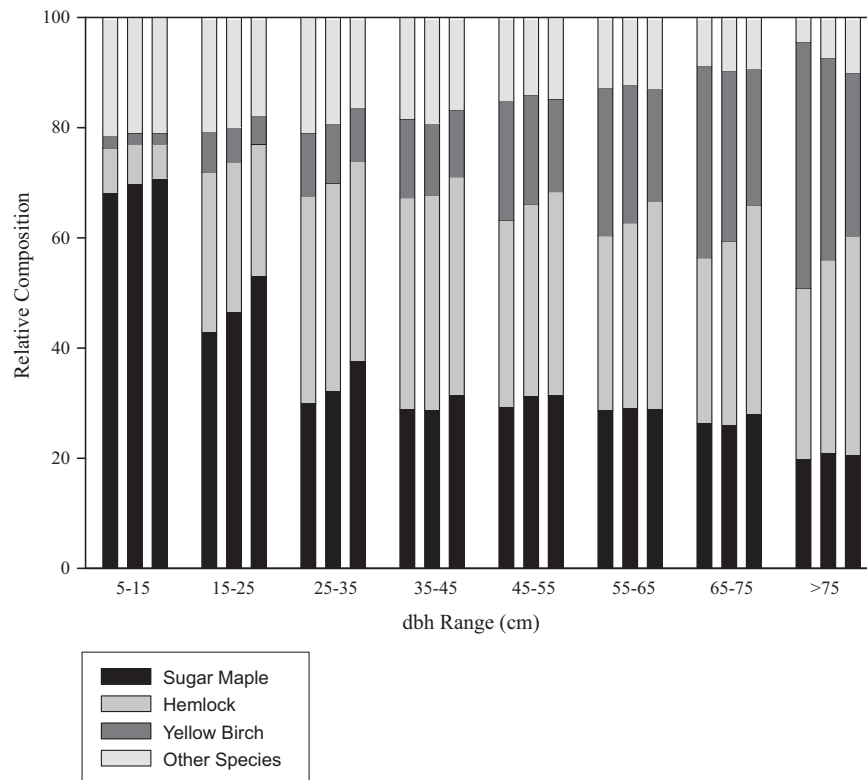
Fig. 1. The relative composition of the three most common tree species in the Davis plots in Sylvania Wilderness, Michigan. The three bars at each dbh size class represent, in order, the first (1987–90), second (1993–95) and third censuses (2006).

3. Results

3.1. Davis plots

3.1.1. Relative composition by size-class

Together, sugar maple, hemlock and yellow birch comprised >78% of the total stems in every size class in every census, but the relative composition (RC) of each of the three species varied among size classes and censuses (Fig. 1). More than 65% of stems 5–15 cm dbh were sugar maple. Relative composition was more evenly distributed among sugar maple, hemlock and yellow birch in the larger size classes. Between the first and third censuses, the RC of sugar maple stems 5–35 cm dbh increased. In contrast, the RC of yellow birch at every size class decreased between censuses, with the greatest declines at the largest size classes. Hemlock was more variable. The RC of hemlock 5–25 cm dbh declined between the first and third censuses. The RC of intermediate-sized hemlocks remained stable, while the RC increased for size classes larger than 45 cm dbh.

The relative composition of seedlings and saplings shifted minimally. Sugar maple was the dominant species at all sizes in all censuses. It represented >90% of the stems in every seedling height class (0–50 cm, 50–100 cm and 100–200 cm) in the 1991 census of the subplots in plots B, C and D combined. In these three plots in 2006, sugar maple comprised 89% of seedlings 0–50 cm tall, 98% of stems 50–100 cm tall, and 100% of stems 100–200 cm tall. There were no hemlock seedlings >50 cm in height in either census. In 1991 there were no yellow birch seedlings >100 cm in height, and in 2006 there were none >50 cm in height. The subplots in plot A showed similar trends (data not shown). In total, sugar maple comprised >95% of all stems <2 m tall in 1990 and 2006. Sugar maple comprised >75% of all saplings (stems >2 m tall, but <5 cm dbh) in both the second and third censuses, whereas hemlock and yellow birch, respectively, represented <1% and <3% of all saplings in both censuses.

3.1.2. Mortality

There were no fires or major wind disturbances in our plots during the study period. Mortality was likely due to age, local disturbances and other stochastic events. The three most abundant species – hemlock, sugar maple and yellow birch – all exhibited "boat-shaped" mortality curves, with high mortality in the 5–15 cm dbh class, low mortality at intermediate size classes, and increasing mortality in the largest size classes (Fig. 2). In most size classes, yellow birch had the highest mortality rate, followed by sugar maple and hemlock.
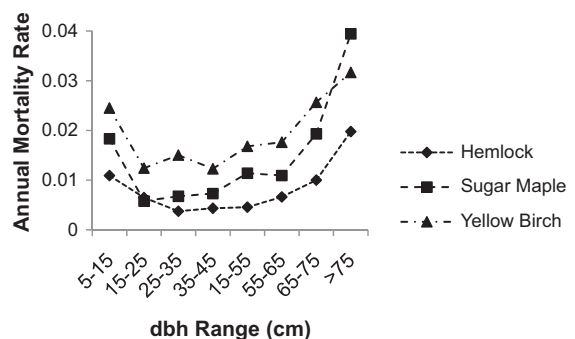

Fig. 2. The annual mortality rate by original size class in the Davis plots in Sylvania Wilderness, Michigan, between the first (1987–1990) and third census (2006) for the three most abundant species.
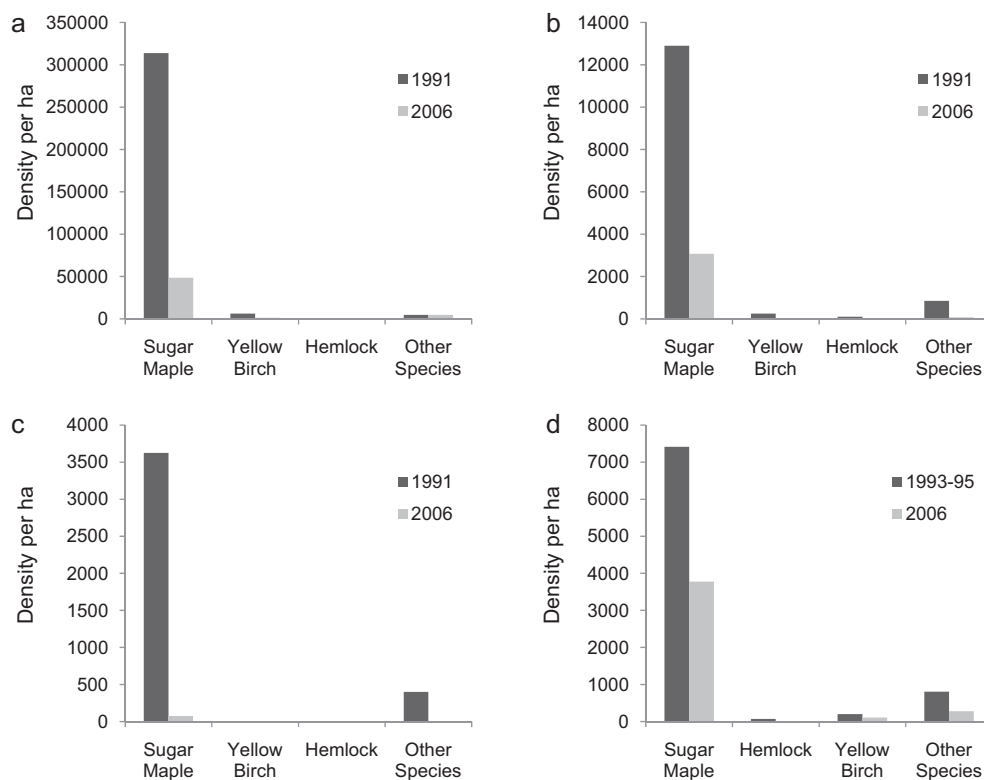
Fig. 3. The density of seedlings across three of the Davis plots in Sylvania Wilderness, Michigan, in 1991 (black) and 2006 (gray) in height classes of (a) 0–50 cm, (b) 50–100 cm, (c) 100–200 cm and (d) the density of saplings (stems >2 m tall but <5 cm dbh) across all four Davis plots in 1993–1995 (black) and 2006 (gray). Note that each panel has a different y-axis scale.

3.1.3. Recruitment

Adjusting for mortality between censuses created up to a 300% increase in annual rates of recruitment of stems into the $\geq$5 cm dbh class compared to observed recruitment rates, but there was little shift in the relative rates among hemlock, sugar maple and yellow birch. In both census intervals sugar maple averaged at least 20 times more new recruits/ha than either hemlock or yellow birch. Hemlock recruitment declined from 0.06 to 0.03 new recruits ha^{-1} $year^{-1}$ and sugar maple recruitment declined from 3.29 to 2.25 new recruits ha^{-1} $year^{-1}$. Yellow birch, on the other hand, increased from 0.06 to 0.11 new recruits ha^{-1} $year^{-1}$.

3.1.4. Shifts in stem density

For all species combined, the number of stems in the smallest size classes declined over the course of the study, while the number of stems at the largest size classes increased (data not shown). The numbers of stems 5–15 cm dbh declined by 21%. Trends were less clear for intermediate size classes, with no 10 cm dbh class shifting by more than 7%. Stems >55 cm dbh increased by 21%. In the second and third censuses there were 590 and 1102 new stems above >5 cm dbh, respectively, with sugar maple comprising >70% of these stems in both censuses.

Between the second and third census, the total density of all saplings combined decreased by 50% (Fig. 3). Total seedling stem density declined by more than 80% in the small height classes of 0–50 cm, 50–100 cm and 100–200 cm, respectively, between 1991 and 2006 (Fig. 3). The sum of the averages of percent cover for each woody species in the subplots declined from 41% in 1991 to 7% in 2006. Since estimates were obtained for each species individually, these numbers would be higher than a measure of percent cover of all species taken at once, where overlapping leaves of different species would not be counted twice.

3.1.5. Earthworms

We found earthworms at 44 of the 68 locations surveyed in the Davis plots, including locations in each of the four plots. All of the earthworms belonged to one species, *Dendrobaena octaedra*.

3.1.6. Deer browse preference and size-class distribution

Species differed in whether their size-class distribution followed a classic "reverse J" or rotated sigmoid shape typical of late-successional old-growth forests (Frelich, 2002). In the third census, each of the eight species classified as unpreferred browse by Dahlberg and Guettinger (1956) had more stems in the 5–15 cm dbh class than in any larger class (Fig. 4a). Of the seven preferred-browse species, only one, red maple (*A. rubrum*), had more stems in the smallest size class than in any larger size class (Fig. 4b). Except for red maple, the counts for preferred species had their highest density at intermediate size classes.

There were more new recruits (stems that had grown to $\geq$5 cm dbh) of unpreferred browse species than preferred browse species in both the second and third censuses. There were 6 new recruits of unpreferred browse species in the second census per 100 trees of unpreferred species in the first census, while the ratio for preferred species was 1:100. There were 11 new recruits of unpreferred species in the third census per 100 trees of unpreferred species in the second census, while the ratio for preferred species was 2:100. The ratio of new recruits to trees that died among preferred browse species was 19:100 for the second census and 18:100 for the third census, compared to ratios for unpreferred browse species of 84:100 and 59:100 for the second and third censuses, respectively.

3.2. Stearns and Sotala plots

In the 1974–75 census, sugar maple stems >2.54 cm dbh were recorded at 6 of the 8 sites, hemlock stems at 7 sites and yellow
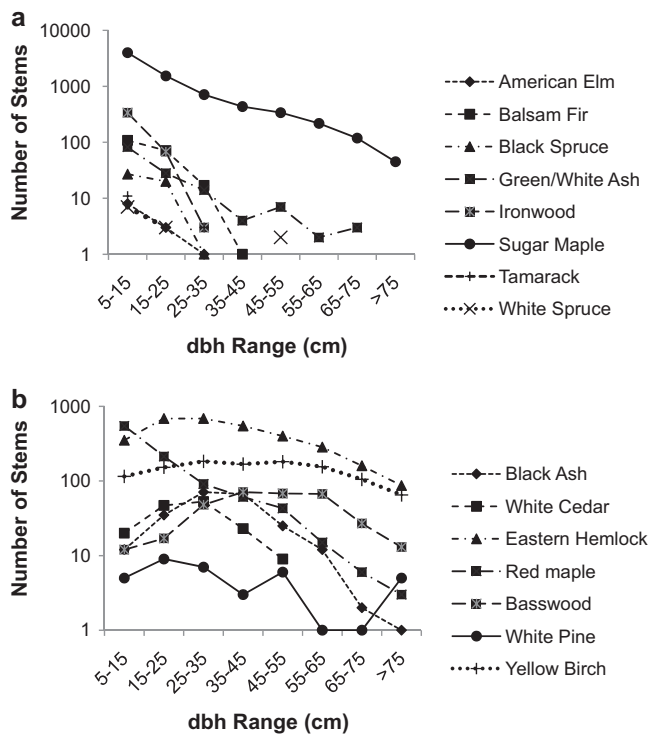
Fig. 4. The total number of stems in the Davis plots in Sylvania Wilderness, Michigan by species in 10 cm dbh size classes. Species in (a) are unpreferred browse and species in (b) are preferred browse. Data are from the third census (2006).

birch stems at 6 sites. Although most sites had only limited change in the canopy, by 2009 hemlock had disappeared from one of the sites where it had been present and yellow birch had disappeared from two sites.

Over a longer time period and at a wider variety of sites throughout the Sylvania Wilderness, regeneration trends in the Stearns and Sotala plots corroborate trends found in the Davis plots. The Stearns and Sotala plots all had either steeply declining or consistently low regeneration between census intervals, with sugar maple comprising a disproportionate fraction of the regeneration compared to its abundance in the canopy. Sugar maple comprised >90% of all stems >0.91 m tall but less than 2.54 cm dbh in the subplots in the first two censuses, and was the only species found in any subplot in 2009. Seven of the eight sites had at least one sugar maple sapling in a subplot in both 1974–75 and 1990. Across all plots, the total number of sugar maple saplings declined from 304 to 189 between the 1974–75 and 1990 censuses. In 2009 there were only a total of three sugar maple saplings, on two sites. All three stems were >2 m in height. No other species had more than six saplings in any census, and no hemlock saplings were found in any of the plots.

3.3. Demographics model

Our demographics model predicts that if observed rates of recruitment, growth and mortality in the Davis plots continue, at equilibrium there would be little to no hemlock and yellow birch remaining in the forest, while the basal area (BA) of sugar maple would remain similar to its current level (Fig. 5). In all runs, the population approached equilibrium within 500 years, at which time all of the stems present at year 0 had died. Results differed to a moderate degree depending on whether the model used the recruitment rates from the first to second census or the second to third census. Using the first recruitment rate for sugar maple yielded a BA of 15.2 m^2/ha, slightly higher than the observed BA of 12.2 m^2 ha^{-1} from the third census, while the second recruit-

ment rate yielded a lower BA of 10.4 m^2 ha^{-1}. Predicted hemlock BA was 0.8 m^2 ha^{-1} and 0.4 m^2 ha^{-1} for the first and second census intervals, respectively—in both cases a sharp decline from hemlock's third census observed BA of 12.9 m^2 ha^{-1}. Yellow birch BA was 0.1 m^2 ha^{-1} and 0.2 m^2 ha^{-1}, for the first and second census intervals, respectively—again much below the observed BA of 8.8 m^2 ha^{-1} in the third census. Thus the combined basal area of the three dominant tree species declined from a third census value of 33.9 to 16.1 or 11 m^2 ha^{-1} depending on model parameters.

We approximated the recruitment rates that would be required for each species to maintain the observed BA from the third census. We ran the model using different recruitment rates to estimate that rate to the nearest 0.1 new stems ha^{-1} $year^{-1}$ that after 1000 years most closely approximated the BA measured in the third census. These were 1.0, 2.9 and 4.8 new recruits ha^{-1} $year^{-1}$ for hemlock, sugar maple and yellow birch, respectively.

4. Discussion

Old-growth forests of the eastern United States hold social value as places to encounter "wilder" (i.e., less human-altered) nature, and environmental value as a rare habitat and a template for restoration of more disturbed sites. Although they have never been clear-cut, old-growth forests in the Great Lakes region may be changing due to multiple anthropogenic factors including elevated deer browsing, exotic earthworm invasion and climate change (Frelich and Reich, 2009). Two multi-decadal sets of permanent plots in the old-growth forests of Sylvania Wilderness in Northern Michigan show virtually no recruitment for preferred deer browse species including cedar, hemlock and yellow birch extending back at least to the 1970s. This recruitment limitation is slowly altering the structure and composition of the forest canopy (Fig. 4).

In this study, all tree species classified as unpreferred browse had size distributions characteristic of late-successional forests (i.e., highest densities in the smallest size classes). In contrast, all but one of the preferred browse species had their highest density at intermediate size classes, suggesting that recruitment of these species has declined in recent decades (Fig. 4). Both preferred browse species and unpreferred browse species ranged from medium to highly shade-tolerant and varied considerably in drought tolerance, (Niinemets and Valladares, 2006), suggesting that recent disturbance or climate patterns were not the dominant force in determining which species regenerated well or poorly.

The one species that did not follow general trends of size distribution was red maple, which had its highest stem density in the smallest size class, despite being ranked as highly preferred browse. This is probably due to red maple's bimodal habitat distribution; it is found on well drained upland soils where it can grow to a canopy tree >50 cm dbh, but it is also very dense within low wetlands in our plots, where it rarely exceeds 15 cm dbh. In the one Davis plot without any wetland areas the size-class distribution of red maple was similar to that of other preferred browse species: it was three times more abundant in the 35–45 cm dbh size class than in the 5–15 cm dbh size class. Thus, red maple does follow the predicted pattern of effects by deer browsing when upland forests are considered separately.

Our results provide support for previously published studies that demonstrate that high deer populations and recruitment failure of hemlock in the region around Sylvania Wilderness extends back to the 1940s (Leopold, 1943; Graham, 1954; Frelich and Lorimer, 1985). Stand histories reconstructed using tree rings show regular hemlock recruitment and episodic yellow birch recruitment in Sylvania and other unlogged forest remnants in the surrounding region from the oldest reconstructed period in the mid-1700s until the mid-1900s, while regular sugar maple recruitment continued
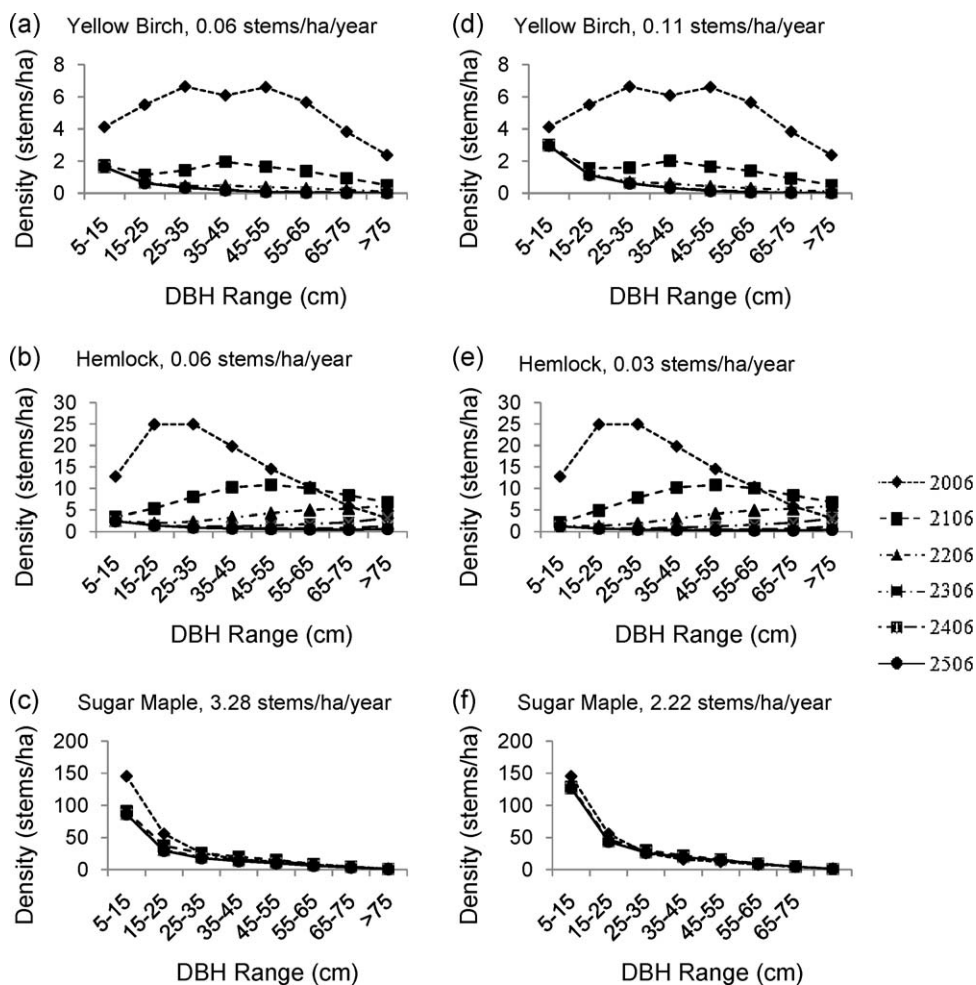
Fig. 5. Measured and future predicted size distribution curves for hemlock, sugar maple and yellow birch in the Davis plots in Sylvania Wilderness, Michigan.

at least to the end of the 1980s (Frelich and Lorimer, 1991; Parshall, 1993; Frelich and Graumlich, 1994).

Long-term lack of recruitment stemming from high deer populations, eventually leading to change in the composition of the forest overstory, has also been shown in numerous temperate forests around the world. For example, deer give the advantage to black cherry (*Prunus serotina*) over sugar maple in Pennsylvania, USA (Horsley et al., 2003), and are strongly implicated as the cause of compositional shifts in woodlands of New Zealand (Husheer et al., 2003), Great Britain (Fuller and Gill, 2002), and Poland (Kuijper et al., 2010).

White-tailed deer have been shown to shift to less preferred species after more preferred species are mostly cleared from the landscape in the Apostle Islands in Wisconsin (Beals et al., 1960) and Anticosti Island in Quebec (Tremblay et al., 2005). We hypothesize that a similar process has occurred in Sylvania. By the time of the establishment of the Stearns plots in 1974–5, selective browsing of hemlock and yellow birch had already virtually eliminated those species from the understory, forcing deer to turn to sugar maple for winter forage. Photos and field observations from 1987 to 1991 in the Davis and Stearns plots show that most hardwood stands had a dense seedling layer dominated by heavily browsed but annually resprouting sugar maple stems (Fig. 6a). In 2006 and 2009 the vast majority of remaining sugar maple seedlings greater than 0.5 m tall had been browsed by deer, often multiple times (personal observation). A rising deer to seedling ratio may have led to an accelerated loss of seedlings as the remaining stems became subject to more intense browsing (Augustine and Frelich, 1998),

leading to a large reduction in density of the sugar maple seedling layer by 2006 (Fig. 6b).

The demographics model shows that if current rates of growth, recruitment and mortality were to continue into the future, larger size classes would become increasingly like the seedling and sapling layer: sparse and maple-dominated. The model indicates that, to maintain their basal area from 2006 in the future, hemlock and yellow birch would require a recruitment rate 17 and 39 times higher, respectively, than the higher of the recruitment rates observed between censuses. Unlike hemlock and yellow birch, the demographics model shows that sugar maple could maintain its basal area with current observed recruitment rates, although the recent decline in abundance of seedlings could be a harbinger of future reduced recruitment.

Several factors in addition to deer browsing could prevent sugar maple and other species from replacing hemlock and yellow birch. First, although the climate has only changed slightly over the last century, this is not likely to be the case in the future. Much warmer, effectively drier summers are projected for the area over the next century (Wuebbles and Hayhoe, 2004), which could increase mortality and perhaps place Sylvania outside the current climate range of a number of species found there today – including hemlock, white spruce, black spruce, tamarack, white cedar and balsam fir – that are near their southern or western range limit in Sylvania (Prasad et al., 2007; Walker et al., 2002). Sugar maple could also be affected by increased dryness associated with warmer, drier summers, since its optimum site characteristics include silty soils with high water holding capacity and cation exchange capacity, and its

Fig. 6. Photos from one of the Davis plots in Sylvania Wilderness, Michigan from 1990 (top) and 2006 (bottom), showing the decline in forest floor vegetation. Photos are of different, but representative, locations within the same 5-ha plot. In the 25 subplots in this plot in 1991 there were 44 sugar maple/m^2 <50 cm tall and 0.7 sugar maple/m^2 50–200 cm tall; in 2006 there were 0.7 sugar maple/m^2 <50 cm tall and no sugar maple 50–200 cm tall in any of the subplots. There were no hemlock or yellow birch 50–200 cm tall in either census. In 1991 there were 0.46 yellow birch/m^2 and 0.04 hemlock/m^2 <50 cm tall; in 2006 those numbers were 0.12 and 0.0, respectively.

sufficient recruitment to maintain its historic abundance and diameter distribution, but it could be affected by continued heavy deer browse, climate change and the spread of *Lumbricus* earthworms (Holdsworth et al., 2007; Frelich and Reich, 2010).

Of the three major agents of change impacting the future of Sylvania forests – deer browsing, earthworm invasion, and climate change – deer browsing appears to be the factor that has had the biggest impact in the late 20th century, is expected to exacerbate the impacts of earthworm invasion and climate change in the future (Holdsworth et al., 2007; Frelich and Reich, 2010), and is the only factor of the three that can be effectively managed at the current time. Therefore, active management to counter the impacts of high deer populations (which are in part a response to human changes on the landscape) is necessary to maintain historically "natural" dynamics that have maintained this forest for millennia (Davis et al., 1998). In Sylvania, management policies that reduce the deer herd, such as protecting populations of wolves and cougars, lengthening the antlerless deer hunting season, hiring sharpshooters and encouraging the community to stop feeding deer and to hunt antlerless deer would likely allow hemlock, yellow birch and other species to recover. Continued research on these permanent plots will be key for identifying the impacts of future environmental changes as well as potential management strategies in old-growth forest.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.02.026.

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presence on the sandy, relatively nutrient poor soils in places like Sylvania benefits from a cool climate with frequent recharge of the soil water (Godman et al., 1990; Henne et al., 2007).

A second factor with likely negative consequences for sugar maple is European earthworm invasion. The invasion of sugar maple forests in this region by *Lumbricus terrestris* and *Lumbricus rubellus* has been linked to recruitment failure by altering seedbed conditions, changing the mycorrhizal community, and reducing N and P availability, particularly when combined with the effects of deer browsing (Frelich et al., 2006). *D. octaedra*, the only earthworm species we found on the Davis plots, has only minor impacts on seed germination and seedling survival (Holdsworth et al., 2007). However, *Lumbricus* earthworms are common around Sylvania's lakeshores, and are now present within 0.5 km of two of the Davis plots (personal observation).

Our data suggest that changing recruitment patterns caused by high seedling mortality are altering the structure and species composition of the Sylvania forest, and deer browsing is likely the major cause. Two of the dominant species, hemlock and yellow birch, are highly preferred by deer and their diameter distributions (Fig. 4) are not the descending monotonic shape typical of old-growth forests. A third dominant species – sugar maple – has maintained

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