



The effect of logging on vegetation composition in Western Massachusetts

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ABSTRACT

Forest harvesting is one of the most significant disturbances affecting forest plant composition and structure in eastern North American forests, yet few studies have quantified the landscape-scale effects of widespread, low-intensity harvests by non-industrial private forest owners. Using spatially explicit data on all harvests over the last 20 years, we sampled the vegetation at 126 sites throughout central and western Massachusetts, one-third of which had not been harvested, and two-thirds of which had been harvested once since 1984. Seedling and sapling densities increased with increasing harvest intensity, but decreased to levels similar to unharvested sites by year 20 for all but the most intensive harvests. The composition of understory trees appears to be only slightly changed by harvesting, and was strongly correlated with adult tree composition. Regeneration was dominated by *Betula lenta* followed by *Pinus strobus*; *Quercus* spp. exhibited little sapling recruitment, even in *Quercus*-dominated stands. Total vascular plant species richness increased substantially with harvesting on low C:N sites (i.e., rich soils), but was only slightly increased on high C:N sites. While harvesting was associated with a statistically significant change in vascular plant composition, non-metric multidimensional scaling revealed that climate (temperature, precipitation) and C:N ratios were the major correlates of composition. Overall, the compositional impacts of harvesting were minor, perhaps because of the low-intensity of harvesting. However, our results support observations from elsewhere in the northeastern U.S. of limited oak regeneration on both harvested and unharvested sites. In addition, our results suggest that increased harvest intensity may be expected to alter forest composition, particularly on rich sites where invasive species may increase as a result of harvesting.

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1. Introduction

Southern New England, like much of the eastern United States, is characterized by extensive non-industrial private forests (NIPF). Individual forest landowners in the region generally own small properties, whose size has decreased over time as the landscape has become more parcelized (average <5 ha; Kittredge, 1996; Kittredge et al., 2003). Small parcel size, combined with landowner preferences that often do not prioritize income-generating activities from the land (Finley and Kittredge, 2006), has led to a pattern of relatively frequent, dispersed, low-intensity harvests. For instance, in western and central Massachusetts, the study area of this paper, about 1% of forest area was harvested each year over the past two decades. However, the average harvest volume was 43 m³/ha, which is about one-fifth of typical total stand volume (McDonald et al., 2006). We conducted field studies to determine

the effects of this low-intensity harvesting regime, attempting to answer two important questions.

First, there is regional concern about regeneration of moderately shade-tolerant tree species. In particular, although oaks (*Quercus* spp.) dominate extensive areas today, they appear to regenerate infrequently, mirroring a trend towards declining oak throughout the eastern U.S. (Abrams, 2003). Increased forest harvesting has been proposed as one solution to increase oak regeneration (e.g., Bellocq et al., 2005). However, it is unclear whether the low-intensity harvests typical of NIPF owners will have this effect. Low-intensity harvests may not dramatically alter the environment at the forest floor, and may merely release from suppression existing stems in the understory, especially of more shade-tolerant species, like red maple (*Acer rubrum*; cf., Abrams, 1998). In contrast, high-intensity harvests may allow intolerant and moderately shade tolerant species, including oaks, to regenerate in response to changes in light, temperature, and moisture and increased soil scarification (cf., Chen et al., 1993; Saunders et al., 1999; Davies-Colley et al., 2000; Newmark, 2001; Gray et al., 2002). We assess the effect of low-intensity harvests on the regeneration of two dominant taxa (*Pinus strobus* and *Quercus*

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rubra), evaluating time since harvest in order to determine whether increased seedling establishment immediately after a cut results in increased abundance of saplings over time.

Second, we evaluate whether harvesting significantly alters the composition and richness of the vascular vegetation in a landscape characterized by frequent, low-intensity cuts. Although this topic has been much discussed in the literature, results of stand-level studies have differed substantially (Gilliam, 2002), and it is not clear *a priori* whether harvesting will increase or decrease species richness across a varied landscape. Immediately after a harvesting event, a set of disturbance-tolerant species often thrives; these species may subsequently decline with increasing time since disturbance. In addition, a set of forest interior species may decrease locally because of direct harvesting impacts, altered resource conditions, increased competition in the post-harvest environment, or slow rates of re-establishment and growth (Meier et al., 1995; Roberts and Gilliam, 1995). In this analysis, we track how net vascular species richness changes with time since harvest, and evaluate whether harvesting effects vary across a gradient of soil fertility.

As is often the case when working at a landscape-scale, other confounding factors must be considered in such an analysis. Throughout the study area, there is a moderate gradient in temperature and precipitation, with higher elevations being cooler

and wetter. Similarly, soil texture and nutrient composition vary spatially and can substantially affect species composition. Of particular importance in the region are small areas of calcareous or mafic bedrock characterized by rich soils with high base saturation, which often have distinctive floras (Bellemare et al., 2005).

The legacy of past agricultural disturbance is also an important control of modern vegetation composition across the region (Foster and Aber, 2004). Southern New England was heavily forested prior to the arrival of European settlers, although Native Americans may have had significant effects on local forest composition and structure (cf., Cronon, 1983). By the mid-19th century, more than 60% of the region's forests were cleared for agriculture, leaving a patchwork of plowed fields, pastures, and active woodlots (Hall et al., 2002). Widespread agricultural abandonment by the early decades of the 20th century allowed most of these forests to re-grow, albeit with altered vegetation composition (e.g., Foster et al., 1998, 2003; Motzkin et al., 1999). In this paper, we assess potential effects of past land-use on soil characteristics and plant composition, while focusing our analysis on the effects of recent harvesting.

Specific questions addressed in this study include: (1) What affect does recent forest harvesting have on the composition of tree regeneration and has forest harvesting resulted in increased regeneration of commercially valuable species (especially *Q. rubra*

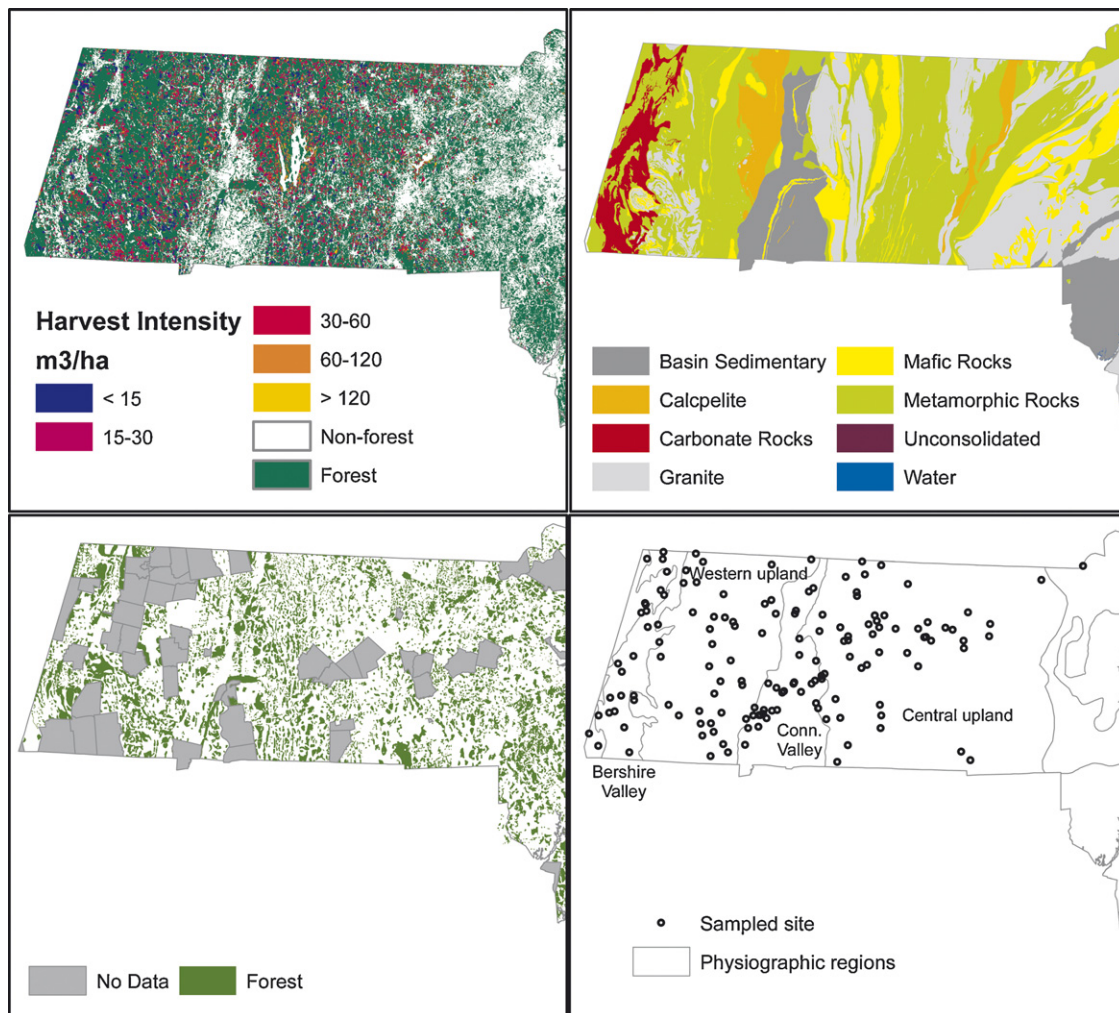


Fig. 1. Environmental variation and location of study sites in central and western Massachusetts. Upper left: Forested areas in 1999 that were unharvested over the period 1984–2003 (shown in green), versus forests harvested at various intensities. White areas were not forested in 1999. Upper right: Bedrock geology (from MassGIS). Lower left: Forest cover in the 1830s (Hall et al., 2002). Some towns do not have historical data available. Lower right: The distribution of sampled sites across the study area. Grey lines show the boundaries of the physiographic regions referred to in this paper (Motts and O'Brien, 1981).

and *P. strobus*)? (2) Does forest harvesting result in increased or decreased vascular plant species richness, and do such changes persist over time? (3) Does the influence of forest harvesting on species richness and composition vary depending on edaphic conditions?

2. Materials and methods

2.1. Site description

Our study area is the forested portions of Massachusetts west of the coastal lowlands (Fig. 1), as defined by Motts and O'Brien (1981). Bedrock is primarily granite, gneiss, and schist, with areas of calcareous and mafic bedrock in the western portion of the study area. The dominant soil parent material is glacial till, with alluvial deposits in the Connecticut and Berkshire Valleys. Soils for much of the region are Inceptisols, with valley floodplains dominated by Entisols, and the Western Upland (Fig. 1) having a mix of Inceptisols and Spodosols (Brady and Weil, 2002). The number of growing degree days varies from more than 3800 in the Connecticut River Valley ($^{\circ}\text{C}$, with 0°C baseline) to less than 2700 in high elevation sites in the Western Uplands. Precipitation varies along a similar gradient, being greatest in the Western Upland region (147 cm year^{-1}) and lowest in the Connecticut River Valley (97 cm year^{-1}), with snowfall being more prevalent at higher elevations (National Climatic Data Center, 2006).

2.2. Harvesting patterns

Massachusetts requires all commercial harvest operations above 87 m^3 volume to file a Forest Cutting Plan (FCP), which includes a map of the harvest area and information on species, harvest volumes, and silvicultural objectives. We digitized all FCP harvests from 1984 to 2003 (McDonald et al., 2006). Across the study area, harvesting is most frequent in the Western and Central Uplands (1.3% forest harvested annually) and least frequent in the Connecticut and Berkshire Valleys (0.8% forest harvested annually). Average reported harvesting volume is remarkably consistent over the study area (overall mean $43\text{ m}^3/\text{ha}$; McDonald et al., 2006). Previous research has found that, prior to harvest, logged sites are similar to unharvested sites with respect to site conditions, species composition, and structure (Kittredge et al., 2003).

2.3. Data collection

We selected 126 sites for sampling (Fig. 1). Two-thirds of the sites ($N = 89$), selected randomly from the larger FCP database, were harvested once between 1984 and 2003. Harvest volume varied from $3\text{ m}^3/\text{ha}$ to $231\text{ m}^3/\text{ha}$, with a mean of $43\text{ m}^3/\text{ha}$. The remaining one-third of the sites ($N = 37$) were control sites selected randomly from all forest areas that were unharvested since at least 1984. Sampled sites were predominately on non-industrial private forest land ($N = 105$), with some state ($N = 15$), municipal ($N = 5$), and industrial ($N = 1$) forest sites. Cutting patterns were similar across ownership types, although harvest intensity was slightly higher on state-owned land near the Quabbin Reservoir (see McDonald et al., 2006 for a detailed analysis).

The boundaries for our field surveys were those filed with the FCP for harvested sites, and were circular for control sites, proportional in size to the mean FCP in each physiographic region (Motts and O'Brien, 1981): Connecticut River Valley (10.7 ha), Central Upland (11.3 ha), Berkshire Valley and Taconic Mountains (12.6 ha), and the Western Upland (15.9 ha). For towns where information on 1830s land cover (i.e., open versus forested) was available (Hall et al., 2002), we insured that our field sites were of a

consistent land cover. Note that our sample sites were well-dispersed over the study area (Fig. 1), and encompassed the variety of past agricultural land-uses.

Field sampling was conducted during the summers of 2004 and 2005. While many vernal species were still present in some form, we may have missed a few ephemeral vernal species. Based on reconnaissance of the entire polygon, our field sampling first determined the distribution of harvesting within the polygon, identified the major stand type (i.e., hardwood, evergreen, or mixed), and recorded the presence and abundance of non-native invasive species (see McDonald et al., in press).

Within the major stand type (i.e., excluding small areas of the polygon of different types) we randomly placed 10 plots of 11.3 m radius (400 m^2), at least 50 m from one another. Tree basal area (m^2/ha) and density ($\#/ \text{ha}$) were measured for overstory ($>20\text{ cm}$ DBH) and midstory ($5\text{--}20\text{ cm}$ DBH) trees using the point-quarter method (Cottam and Curtis, 1956). As an estimate of local harvest intensity, the diameter of all stumps from harvested trees within each plot was also recorded. Seedlings (stems less than 1.37 m) and saplings (stems greater than 1.37 m and less than 5 cm DBH) were counted within 2 m and 5 m radius plots, respectively. Taxonomy follows Gleason and Cronquist (1991).

In addition, within the dominant stand, a $20\text{ m} \times 20\text{ m}$ intensive plot was randomly located in which we estimated the percent cover of each vascular plant species using an eight-class scale: (1 = $<1\%$, 2 = 1–3%, 3 = 3–5%, 4 = 5–15%, 5 = 15–25%, 6 = 25–50%, 7 = 50–75%, 8 = $>75\%$). Given the generally low species richness and herbaceous cover in these plots, we feel confident that all vascular plant species present were recorded. We also measured the basal diameter of all stumps within the plot and in a 5 m buffer around it. A soil pit was dug to 50 cm to examine the soil profile for evidence of a plow layer or other soil disturbance. Using this information, as well as other evidence of land-use such as the presence of stone walls, barbed wire, etc., we classified the site into one of three categories of historical land-use: woodlot, if the site showed no evidence of having been used for historical agriculture and was likely to have been continuously forested; pasture, if the site was used as rough, unimproved pasture; and plowed, if there was clear evidence of an Ap horizon (Motzkin et al., 1999). We then compared these field observations with land-use data from the 1830s (Hall et al., 2002) and from 1930s maps of the Works Progress Administration, where available, to assign each site to historical land-use categories. Based on our field reconnaissance and the historical data sources, we are confident that the land-use history determined for the $20\text{ m} \times 20\text{ m}$ plot is accurate for the majority of the area of each polygon. Two soil samples were taken of the organic soil and the 0–15 cm mineral soils, respectively, to characterize soil texture and nutrients (Brookside Laboratories). Slope, aspect, canopy closure, and percent surface rock were estimated for the plot. A 5 m resolution digital elevation model from MassGIS, re-sampled to 30 m resolution, was used to calculate topographic convergence index (TCI, Beven and Kirkby, 1979), a measure of topographically derived wetness, and to interpolate growing degree days and precipitation from meteorological stations, using published equations for the region (Ollinger et al., 1995).

2.4. Data analysis

Summary statistics of woody basal area and density were calculated for the overstory and midstory from the 10 plots within the major stands. Stump basal area, recorded at ground level, was calculated in aggregate for each polygon, as well as separately for each of the 10 plots. Vascular plant data from the intensive $20\text{ m} \times 20\text{ m}$ plot were converted to percent cover using the midpoint of the cover classes. For analyses comparing the percent

cover data to harvesting intensity, stump basal area in and around the 20 m × 20 m plot was used, rather than stand-wide averages. For descriptive purposes, overstory relative basal area was used to cluster our plots into a small set of discrete groups. All clustering was done using Ward's method for hierarchical grouping in PCORD 5.05, with dissimilarities calculated using a Euclidean distance metric, as is consistent with the intergroup distance calculation implicit in Ward's method (McCune and Grace, 2002). The average species composition in the overstory, midstory, sapling, and seedling strata was calculated for each of our compositional groups. Harvesting was categorized into two groups: moderate/heavy (greater than 10 m² of basal area of stumps per ha) or light/none (0–10 m² of basal area of stumps per ha).

Data on species composition were ordinated with non-metric multidimensional scaling (McCune and Grace, 2002). All ordinations were conducted in PCORD, using the Bray-Curtis metric to quantify dissimilarity among sites (McCune and Grace, 2002). For vascular plant cover data, ordinations used presence/absence data for species that occurred in more than 5% of the sites sampled, to avoid bias from rare species. Ordination results using abundance data were similar, and are not presented here. Taxonomic lumping was conducted where necessary to insure consistency among field crews across the field season (see Table 5). For all ordinations, PCORD's "slow but thorough" autopilot algorithm was used, with 50 Monte Carlo samples. The potentially explanatory variables described above were correlated with the ordination axes to evaluate correlations with species composition.

To test the relationships between harvesting, soil fertility, and species composition, we used multi-response permutation tests (MRPP). With MRPP, the statistical question is: Are sites in the same group more similar in species composition than sites in different groups (McCune and Grace, 2002)? Harvesting was categorized into two groups as above: moderate/heavy or light/none. If the MRPP test was significant, an Indicator Species Analysis (Dufrene and Legendre, 1997) was used to determine what species have high abundance and frequency in each group. Finally, to compare species composition in the overstory and midstory (combined) with the sapling or seedling layer, we conducted a Mantel test (Mantel, 1967; Smouse et al., 1986) of correspondence between the two strata.

To examine the effect of forest harvesting on sapling and seedling densities, as well as species richness in the intensive plots, we used generalized linear models (GLMs). For sapling and seedling densities, a negative binomial error distribution and log link function was appropriate, and model fitting was done with function glm.nb in the MASS library of SPLUS. For species richness a Gaussian error distribution was used. The number of years since a harvest was added to our set of potential explanatory variables, but was allowed to enter the model only as an interaction with harvest intensity (m²/ha of stumps). For the sapling and seedling analyses, a fixed Polygon-level factor was added, to account for differences in means among sites. For all three analyses, forward stepwise selection was performed using function step.aic in the MASS library of SPLUS.

3. Results

Soil characteristics vary with bedrock-type and prior land-use (Table 1). Percent sand is correlated with prior land-use, with sandier soils in formerly pastured or plowed sites than in continuously wooded sites. Base saturation varies with bedrock type and prior land-use, with greater base saturation on calcareous than granitic bedrock, and greater base saturation in plowed sites than in continuously wooded sites. C:N ratios are lower on sites with calcareous versus granitic bedrock. P and S have no apparent relationship with bedrock-type or prior land-use.

Table 1

Soil characteristics for study sites, as a function of bedrock type and prior land-use (BS = base saturation)

	Bedrock type		
	Granitic	Mafic	Calcareous
Prior land-use			
Woodlot	47.1% ± 11.1% sand ^a 31.1% ± 6.4% BS ^a 34.1 ppm ± 60.0 ppm P ^a 18.8 ± 4.7 C:N ^a 43.5 ± 23.0 S ^a	46.6% ± 14.8% sand ^a 34.9 ± 1.1% BS ^{a,b} 26.3 ppm ± 12.8 ppm P ^a 17.9 ± 4.8 C:N ^{a,b} 34.3 ± 9.9 S ^a	42.9% ± 5.2% sand ^a 36.0% ± 9.0% BS ^b 16.0 ppm ± 7.7 ppm P ^a 15.7 ± 2.8 C:N ^b 49.0 ± 24.8 S ^a
Pasture	52.9% ± 13.6% sand ^{a,b} 31.7% ± 5.4% BS ^{a,c} 26.1 ppm ± 28.6 ppm P ^a 18.7 ± 3.8 C:N ^a 37.5 ± 14.3 S ^a	54.3% ± 13.9% sand ^{a,b} 38.7% ± 10.5% BS ^{a,b,c,d} 34.6 ppm ± 18.8 ppm P ^a 18.1 ± 2.1 C:N ^{a,b} 44.0 ± 14.2 S ^a	39.4% sand ^{a,b} 45.3% ± 14.1% BS ^{b,d} 10.0 ppm ± 1.4 ppm P ^a 13.7 ± 5.3 C:N ^b 25.0 ± 10.0 S ^a
Plowed	52.6% ± 12.0% sand ^b 37.3 ± 10.5% BS ^c 25.4 ppm ± 20.0 ppm P ^a 16.8 ± 4.7 C:N ^a 37.8 ± 10.0 S ^a	64.8% ± 16.5% sand ^b 35.5% ± 4.2% BS ^{c,d} 44.0 ppm ± 47.6 ppm P ^a 18.5 ± 0.5 C:N ^{a,b} 45.8 ± 9.2 S ^a	51.5% ± 11.3% sand ^b 48.0% ± 20.1% BS ^d 28.4 ppm ± 23.0 ppm P ^a 13.6 ± 3.3 C:N ^b 34.4 ± 16.7 S ^a

Superscript letters indicate which groups are statistically identical to one another, and which groups are significantly different. See text for details.

Cluster analysis of overstory trees identified four relatively distinct groups: Mixed hardwood, *Quercus*-dominated, *Tsuga canadensis*-dominated, and *P. strobus*-dominated forests. The Mixed hardwood group is characterized by *A. rubrum*, *A. saccharum*, and *Q. rubra* in the overstory (Table 2). Midstory composition is similar, with *Q. rubra* generally replaced by *Fagus grandifolia*. Harvested Mixed hardwood sites have lower *A. rubrum* and *Q. rubra* basal area, and more *A. saccharum*, than unharvested sites. On unharvested sites, the seedling layer is dominated by *A. rubrum* and *A. saccharum*, and the sapling layer has abundant *F. grandifolia*. On harvested sites, the seedling layer has substantially more *P. strobus* and *Betula lenta* than unharvested sites. The sapling layer has more *B. lenta* and less *F. grandifolia*, relative to unharvested sites.

The *Quercus* group is dominated by *Q. rubra* in the overstory. Midstory composition is a mix of *A. rubrum*, *Q. rubra*, and *B. lenta*. On unharvested sites, the seedling layer is dominated by *Q. rubra* and *A. rubrum*, while the sapling layer has abundant *B. lenta* and *A. rubrum*. On harvested sites, the seedling layer has more *B. lenta*, *P. strobus*, and less *F. grandifolia*, while the sapling layer has more *F. grandifolia*, relative to harvested sites.

The *T. canadensis* group is dominated by *T. canadensis* in the overstory and midstory. On unharvested sites, the seedling layer is dominated by *T. canadensis* and *A. rubrum*, and the sapling layer by *F. grandifolia* and *T. canadensis*. The seedling layer of harvested sites has more *P. strobus* and *Q. velutina*, while the sapling layer has more *B. lenta* and less *T. canadensis*, relative to unharvested sites.

The *P. strobus* group is dominated by *P. strobus* with some *Q. rubra*. *Q. rubra* is less abundant in harvested than unharvested sites. Midstory composition is a mix of *P. strobus*, *A. rubrum*, *B. lenta*, and *T. canadensis*. On unharvested sites, the seedling layer is dominated by *P. strobus* and *A. rubrum*, as is the sapling layer. The seedling layer of harvested sites is characterized by more *A. rubrum*, *Q. rubra* and *B. lenta*, and less *P. strobus*, while the sapling layer has more *B. lenta*, relative to unharvested sites.

Oak regeneration in the oak (and other) forests we sampled is less than that of other species, and harvesting appears to have minor effects on oak regeneration (Fig. 2). Within the *Quercus* group, there is a trend towards harvested sites (average stump BA: 24.9 m²/ha) having more *Quercus* seedlings than not/lightly harvested sites (average stump BA: 2.4 m²/ha), but this is not statistically significant ($t = -0.91$, $P = 0.48$). In addition, because

Table 2

Tree composition of the four forest types defined by cluster analysis, by strata and harvesting level

Mixed hardwood forest (species)	Unharvested				Harvested			
	BA	relBA	Density	relDens	BA	relBA	Density	relDens
Overstory								
<i>A. rubrum</i>	5.4	18.2%	65	20.3%	2.2	10.1%	25	11.1%
<i>A. saccharum</i>	4.3	14.5%	45	14.1%	6.4	29.1%	61	27.6%
<i>Q. rubra</i>	4.3	14.5%	34	10.7%	2.2	10.0%	19	8.6%
<i>T. canadensis</i>	2.2	7.3%	22	7.0%	1.5	6.8%	15	6.6%
<i>P. strobus</i>	2.0	6.7%	13	4.1%	1.4	6.3%	14	6.2%
<i>Fraxinus americana</i>	2.0	6.7%	21	6.6%	1.4	6.5%	12	5.2%
<i>Fagus grandifolia</i>	1.5	4.9%	18	5.5%	1.4	6.6%	16	7.4%
Other	8.2	27.3%	101	31.7%	5.4	24.6%	60	27.3%
Midstory								
<i>A. rubrum</i>	1.2	21.5%	99	20.1%	0.5	10.5%	37	7.8%
<i>F. grandifolia</i>	0.8	15.2%	91	18.5%	0.5	11.0%	63	13.3%
<i>A. saccharum</i>	0.7	12.9%	67	13.7%	1.2	25.1%	129	27.1%
<i>T. canadensis</i>	0.5	8.8%	47	9.6%	0.7	14.8%	55	11.5%
<i>Betula lenta</i>	0.4	7.7%	38	7.7%	0.2	3.5%	19	4.0%
<i>Betula alleghaniensis</i>	0.3	4.8%	26	5.3%	0.3	6.3%	27	5.7%
Other	1.6	29.1%	124	25.0%	1.4	28.8%	146	30.6%
Sapling								
<i>B. lenta</i>			62	5.0%			353	16.3%
<i>A. saccharum</i>			111	8.9%			345	15.9%
<i>A. rubrum</i>			142	11.4%			310	14.3%
<i>A. pensylvanicum</i>			152	12.2%			241	11.1%
<i>F. grandifolia</i>			391	31.4%			207	9.5%
<i>P. strobus</i>			56	4.5%			169	7.8%
Other			331	26.6%			542	25.0%
Seed								
<i>P. strobus</i>			378	3.1%			2012	15.5%
<i>A. rubrum</i>			2479	20.0%			1945	15.0%
<i>A. saccharum</i>			2248	18.1%			1922	14.9%
<i>B. lenta</i>			136	1.1%			1233	9.5%
<i>Prunus serotina</i>			869	7.0%			1106	8.5%
<i>A. pensylvanicum</i>			1482	12.0%			995	7.7%
<i>Q. rubra</i>			955	7.7%			901	7.0%
Other			3844	31.0%			2828	21.9%
Oak forests (species)								
Oak forests (species)	Unharvested				Harvested			
	BA	relBA	Density	relDens	BA	relBA	Density	relDens
Overstory								
<i>Q. rubra</i>	18.1	69.7%	170	62.6%	14.0	63.4%	131	58.1%
<i>B. lenta</i>	1.5	5.7%	16	6.0%	1.0	4.5%	13	5.6%
<i>P. strobus</i>	1.4	5.3%	12	4.5%	1.3	6.0%	13	5.9%
<i>T. canadensis</i>	1.3	5.1%	14	5.1%	2.9	12.9%	27	12.0%
<i>A. rubrum</i>	1.1	4.3%	18	6.5%	0.4	1.7%	6	2.6%
Other	2.6	9.9%	42	15.3%	2.6	11.5%	36	15.8%
Midstory								
<i>A. rubrum</i>	1.2	28.6%	143	33.8%	1.1	30.7%	103	32.3%
<i>Q. rubra</i>	0.7	16.7%	45	10.7%	0.4	11.0%	23	7.3%
<i>B. lenta</i>	0.6	13.8%	58	13.9%	0.2	5.6%	25	8.0%
<i>P. strobus</i>	0.5	11.3%	51	12.1%	0.3	9.2%	18	5.8%
<i>T. canadensis</i>	0.4	10.3%	45	10.7%	0.6	17.4%	58	18.0%
Other	0.8	19.2%	79	18.7%	0.9	26.1%	91	28.7%
Sapling								
<i>B. lenta</i>			583	44.7%			621	31.3%
<i>A. rubrum</i>			382	29.4%			330	16.6%
<i>F. grandifolia</i>			27	2.1%			318	16.1%
<i>A. pensylvanicum</i>			33	2.5%			183	9.3%
Other			277	21.3%			529	26.7%
Seed								
<i>Q. rubra</i>			2033	24.0%			3657	29.7%
<i>B. lenta</i>			743	8.8%			2065	16.8%

Table 2 (Continued)

Oak forests (species)	Unharvested				Harvested			
	BA	relBA	Density	relDens	BA	relBA	Density	relDens
<i>P. strobus</i>			881	10.4%			1863	15.1%
<i>A. rubrum</i>			2288	27.0%			1720	14.0%
<i>F. grandifolia</i>			32	0.4%			796	6.5%
Other			2484	29.4%			2202	17.9%
Hemlock forests (species)	Unharvested				Harvested			
	BA	relBA	Density	relDens	BA	relBA	Density	relDens
Overstory								
<i>T. canadensis</i>	16.2	43.8%	159	43.3%	14.2	44.7%	154	42.5%
<i>A. rubrum</i>	4.1	11.1%	41	11.2%	3.6	11.2%	58	16.0%
<i>Q. rubra</i>	3.7	10.0%	31	8.4%	2.9	9.3%	31	8.5%
<i>P. strobes</i>	2.7	7.2%	21	5.8%	3.7	11.5%	30	8.2%
<i>B. lenta</i>	2.2	6.1%	25	6.7%	1.8	5.5%	21	5.9%
Other	8.0	21.8%	90	24.6%	5.6	17.7%	69	18.9%
Midstory								
<i>T. canadensis</i>	2.2	45.9%	190	43.3%	2.3	47.8%	174	46.9%
<i>A. rubrum</i>	0.7	13.4%	56	12.7%	1.1	22.1%	69	18.5%
<i>F. grandifolia</i>	0.3	6.3%	33	7.5%	0.1	3.0%	12	3.3%
<i>B. lenta</i>	0.3	6.0%	29	6.7%	0.3	6.5%	33	8.8%
<i>P. strobes</i>	0.3	5.3%	20	4.5%	0.3	5.2%	17	4.5%
Other	1.1	23.1%	110	25.2%	0.8	15.5%	66	17.8%
Sapling								
<i>B. lenta</i>			70	11.6%			653	35.1%
<i>F. grandifolia</i>			139	23.0%			443	23.8%
<i>A. pensylvanicum</i>			44	7.2%			350	18.8%
<i>T. canadensis</i>			230	38.1%			210	11.3%
<i>P. strobus</i>			34	5.6%			94	5.1%
Other			87	14.4%			109	5.9%
Seed								
<i>A. rubrum</i>			3844	37.4%			4749	33.3%
<i>T. canadensis</i>			1290	12.5%			2862	20.1%
<i>P. strobes</i>			252	2.4%			1742	12.2%
<i>Q. velutina</i>			77	0.7%			965	6.8%
<i>A. pensylvanicum</i>			643	6.3%			960	6.7%
<i>Q. rubra</i>			610	5.9%			826	5.8%
Other			3569	34.7%			2161	15.1%
White pine forests (species)	Unharvested				Harvested			
	BA	relBA	Density	relDens	BA	relBA	Density	relDens
Overstory								
<i>P. strobes</i>	18.1	62.5%	145	50.8%	12.5	53.0%	98	43.2%
<i>Q. rubra</i>	2.9	10.2%	33	11.7%	0.9	4.0%	9	3.8%
<i>T. canadensis</i>	1.7	6.0%	20	6.9%	2.2	9.4%	24	10.8%
<i>A. rubrum</i>	1.6	5.7%	25	8.7%	2.0	8.5%	30	13.4%
Other	4.5	15.6%	62	21.9%	5.9	25.1%	65	28.9%
Midstory								
<i>P. strobes</i>	1.3	29.6%	127	31.7%	0.9	25.3%	90	23.3%
<i>A. rubrum</i>	0.8	19.0%	81	20.1%	0.7	20.9%	75	19.4%
<i>B. lenta</i>	0.5	11.8%	52	12.9%	0.4	10.1%	51	13.2%
<i>T. canadensis</i>	0.4	10.5%	32	8.0%	0.4	12.3%	41	10.7%
<i>A. saccharum</i>	0.4	8.8%	39	9.8%	0.4	12.2%	45	11.7%
<i>Q. velutina</i>	0.2	5.4%	20	4.9%	0.2	4.3%	10	2.7%
Other	0.6	14.8%	51	12.6%	0.5	14.9%	74	19.0%
Sapling								
<i>B. lenta</i>			149	8.2%			962	31.6%
<i>P. strobus</i>			711	39.3%			891	29.3%
<i>A. rubrum</i>			250	13.8%			305	10.0%
<i>A. saccharum</i>			83	4.6%			161	5.3%
Other			615	34.0%			725	23.8%
Seed								
<i>A. rubrum</i>			2444	14.9%			5387	30.6%

Table 2 (Continued)

White pine forests (species)	Unharvested				Harvested			
	BA	relBA	Density	relDens	BA	relBA	Density	relDens
<i>P. strobus</i>			7078	43.0%			3245	18.4%
<i>B. lenta</i>			199	1.2%			2574	14.6%
<i>Q. rubra</i>			1162	7.1%			1972	11.2%
<i>Q. velutina</i>			581	3.5%			1780	10.1%
Other			4992	30.3%			2644	15.0%

In a stratum in a particular forest type, only the most dominant species are listed. Basal area (BA) values are in m²/ha.

the total number of seedlings is greater on harvested sites, the relative abundance of *Quercus* seedlings does not change substantially. There are few oak saplings, and no increase (or decrease) in oak saplings, in harvested versus unharvested sites. In *Pinus*-dominated stands, there is no indication of a significant change in *P. strobus* abundance in the seedling or sapling layers in response to harvesting. Harvested sites (average stump BA: 19.8 m²/ha) have no more seedlings than not/lightly harvested sites (average stump BA: 5.8 m²/ha), and because the total number of seedlings is greater on harvested sites, *P. strobus* seedlings are actually lower in relative abundance in harvested plots.

When we examine total seedling and sapling abundance across all plots, we find that sapling and seedling densities change after harvest in predictable ways (Fig. 3): initial increases are followed by declines in density over time, presumably due to density-dependent thinning. As expected, the increase in sapling and seedling densities is positively correlated with intensity of harvests (Table 3). Additionally, in both cases there is a negative interaction between harvest intensity and years since harvest, indicating that densities decrease over time, presumably due to density-dependent thinning from canopy closure. Note that the fixed Plot factor explains a large proportion of the deviance, implying large differences in mean density due to site-specific factors.

Despite the increase in the number of stems in the sapling layer after a harvest, when we analyze our complete dataset there appears to be no substantial change in the relative composition of the sapling layer after harvest (MRPP analysis, $A = 0.00277$, $P = 0.38$). Patterns of sapling composition are highly correlated with tree (i.e., overstory + midstory BA) composition (Mantel test, $r = 0.38$, $P < 0.001$). There is, however, a significant effect of harvest intensity (>10 m²/ha) on seedling composition (MRPP analysis, $A = 0.0157$, $P = 0.015$), with *B. lenta* ($IV = 54.5$, $P = 0.001$), *P. strobus* ($IV = 46.8$, $P = 0.06$), and *Quercus velutina* ($IV = 36.7$, $P < 0.001$) increasing in abundance and frequency on more heavily harvested sites. Except for the increases in these taxa, seedling composition is highly correlated with tree composition (Mantel test, $r = 0.43$, $P < 0.001$), as might be expected given localized seed dispersal.

Turning to an analysis of the full vascular flora, ordination results suggest that vascular plant composition varies gradually over several compositional axes. Axis 1 represents 41.3% of the variation in plant composition, and is most strongly correlated with both growing degree days and C:N ratio. Sites with low scores on axis 1 (lower C:N ratio and lower growing degree days) have a greater abundance of such taxa as *Trillium erectum*. Conversely, sites with higher Axis 1 scores (higher C:N ratios and higher growing degree days) have a greater abundance of such taxa as *Vaccinium* spp. and *Gaylussacia baccata*. Axis 2 represents 16.1% of

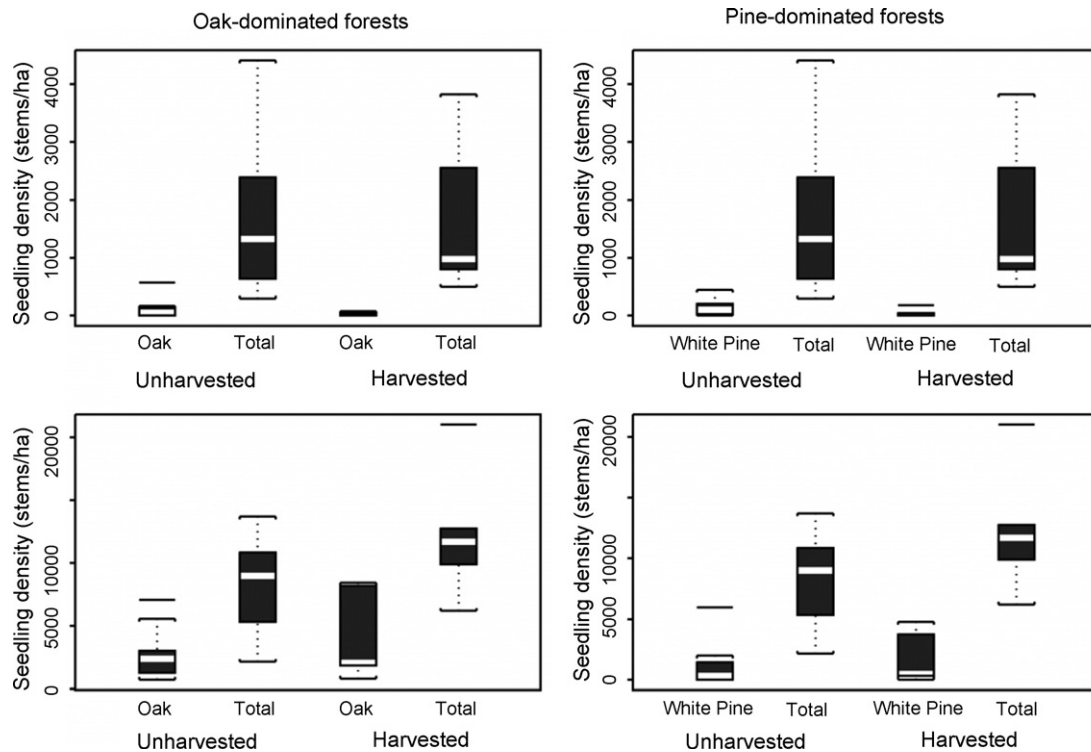


Fig. 2. The effect of harvesting on regeneration of the dominant taxa in oak-dominated forests (left column) and pine-dominated forests (right column). The top row shows sapling densities, while the bottom row shows seedlings densities. See text for details.

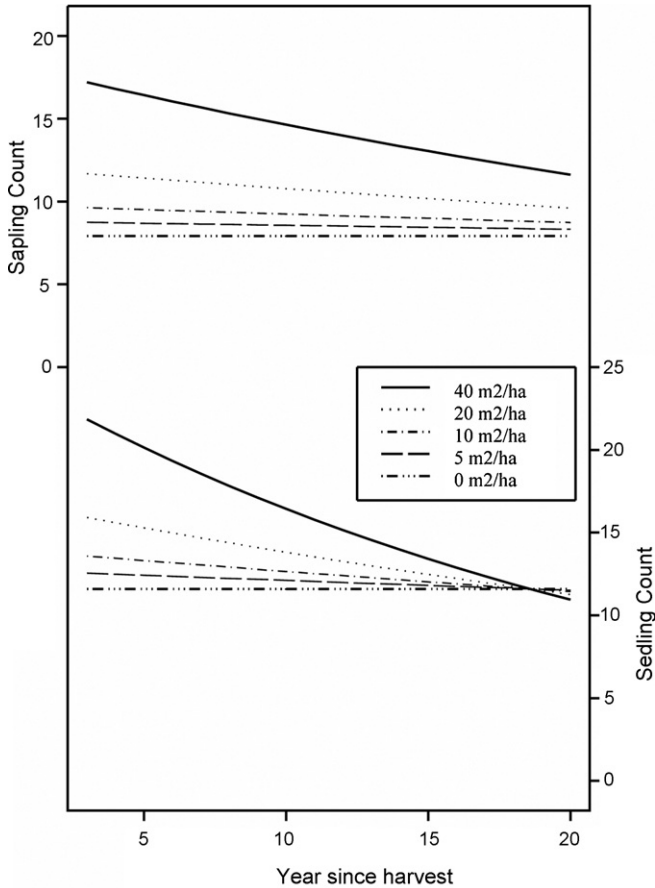


Fig. 3. The response of sapling and seedling count (#/ha) to harvesting events of different intensities (m²/ha basal area removed). Note the different y-axes for each of the strata. See text for details of the regression analysis that estimated these curves.

the total variation in species composition, and is primarily correlated with growing degree days and precipitation. Sites with a low score on this axis (lower growing degree days and more precipitation) have greater abundance of such taxa as *Picea rubens* and *Abies balsamea*. Conversely, sites with higher scores on this axis (greater growing degree days and less precipitation) have greater abundances of *Quercus* sp. and *Carya* sp. Axis 3 represents 22.2% of the variation in plant composition, and is correlated with

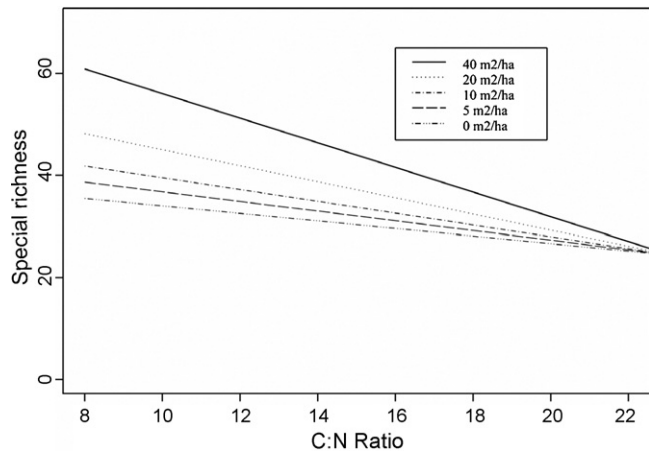


Fig. 4. Species richness in relation to harvest intensity (m²/ha basal area removed) and soil C:N ratio. See text for details of the regression analysis that estimated these curves.

Table 3

Regression coefficients relating seedling and sapling densities to the intensity of harvest and the number of years since harvest

Variable	d.f.	Coefficient	Deviance	Pr(Chi)
Seedling: null deviance is 1995.6 on 1211 d.f., residual deviance is 1382.6 on 1084 d.f.				
Intercept	1	2.45	Null model	Null
Intensity	1	0.0189	5.8	0.016
Intensity:YearsPast	1	-0.00102	3.7	0.054
Site factor	125	Various	603.5	<0.001
Sapling: null deviance is 2421.9 on 1211 d.f., residual deviance is 1385.2 on 1084 d.f.				
Intercept	1	2.06	Null model	Null
Intensity	1	0.0211	25.3	<0.001
Intensity:YearsPast	1	-0.000576	1.5	0.23
Site factor	125	Various	1009.9	<0.001

A polygon-level site factor was included to account for unmeasured environmental differences among polygons. See text for details.

Table 4

Regression coefficients describing vascular plant richness as a function of soil C:N ratio, soil texture, historical land-use, harvest intensity, and years since harvest

Variable	d.f.	Coefficient	Sum of Sq	Pr(F)
Intercept		49.1		
C/N Ratio	1	-0.735	2485.8	<0.001
Landuse	2		679.5	0.028
Woodlot		Baseline		
Pasture		2.43		
Plowed		-0.362		
Percent Sand	1	-0.153	276.8	0.086
Intensity	1	0.701	285.0	0.082
C/N Ratio:Intensity	1	-0.0420	244.9	0.107
Intensity:YearsPast	1	0.0246	397.7	0.040

C:N ratio. It appears to separate out in ordination space some of the taxa that are most limited to low C:N ratio sites, including *Actaea* spp. and *Tiarella cordifolia*. Importantly, harvesting intensity does not correlate with any of the ordination axes, suggesting that the effect of harvesting accounts for a relatively small part of the overall variation in vascular plant composition.

Nevertheless, species richness increases with harvest intensity (Fig. 4), particularly in sites with low C:N ratios (richer soils). In the absence of harvesting, sites with lower C:N ratios (i.e., rich soils) have more species, and upon harvest these rich sites gain more species. There is a significant interaction between harvest intensity and years since the harvesting event (Table 4). Interestingly, the species gained after harvest apparently are retained on the site for at least a decade or more after harvest. There is also an effect on species richness of soil texture, with more sandy soils supporting fewer species, and prior land-use, with old pastures having more species than either continuously wooded sites or formerly plowed sites.

The effect of harvesting on vascular plant composition varies with soil richness. There is a significant difference in vascular plant composition among the four categories of C:N ratio and harvesting intensity (MRPP analysis, $A = 0.0954$, $P < 0.001$). Indicator species analysis indicates that few species are good indicators of high C:N sites (i.e., poor soils), whether logged or not (Table 5). Species that occur on these high C:N sites also occur on low C:N sites. In contrast, a large set of species are moderately indicative of low C:N sites (i.e., rich soils) that were not logged intensively, like *A. saccharum*. Similarly, a large set of species are associated with sites of low C:N and high intensity harvest (e.g., *B. lenta*, *Vitis* spp., and *Fraxinus americana*), including several invasive species (e.g., *Rhamnus frangula*, *Rosa multiflora*, *Berberis thunbergii*, and *Rhamnus cathartica*).

Table 5

Indicator species analysis for vascular plant composition, as a function of harvest intensity and C:N

Low intensity harvest and high C:N			High intensity harvest and high C:N		
Species	IV	P	Species	IV	P
<i>Vaccinium angustifolium</i>	29.4	0.046	<i>Pteridium aquilinum</i>	25.8	0.032
			<i>Abies balsamea</i>	11.8	0.050
Low intensity harvest and low C:N			High intensity harvest and low C:N		
Species	IV	P	Species	IV	P
<i>A. saccharum</i>	47.0	0.002	<i>B. lenta</i>	46.1	0.031
<i>Carex</i> spp.	44.0	0.002	<i>Vitis aestivalis</i>	33.3	0.001
<i>Smilacina racemosa</i>	33.9	0.019	<i>F. americana</i>	31.2	0.023
<i>Carya cordiformis</i>	22.3	0.003	<i>Rubus</i> spp.	30.2	0.011
<i>Viburnum recognitum</i>	18.9	0.024	<i>Solidago</i> spp.	30.0	0.006
<i>Trillium erectum</i>	18.5	0.009	<i>Arisaema triphyllum</i>	28.1	0.009
<i>Celastrus orbiculatus</i>	17.4	0.011	<i>Potentilla simplex</i>	26.5	0.006
<i>Ostrya virginiana</i>	17.3	0.036	<i>Lindera benzoin</i>	26.0	0.001
<i>Prunus virginiana</i>	15.4	0.019	<i>Dryopteris marginalis</i>	25.9	0.006
<i>Lonicera morrowii</i>	13.8	0.029	<i>Rhamnus frangula</i>	25.7	0.003
<i>Populus tremuloides</i>	12.6	0.041	<i>Athyrium filix-femina</i>	23.1	0.009
<i>Spiraea</i> spp.	12.6	0.045	<i>Rubus allegheniensis</i>	22.8	0.050
<i>Carpinus caroliniana</i>	10.7	0.046	<i>Rosa multiflora</i>	20.8	0.006
			<i>Carex debilis</i>	19.7	0.018
			<i>Phegopteris connectilis</i>	18.6	0.011
			<i>Berberis thunbergii</i>	17.2	0.028
			<i>Rhamnus cathartica</i>	17.0	0.009
			<i>Sambucus</i> spp.	16.8	0.021
			<i>Solanum dulcamara</i>	14.9	0.014
			<i>Agrostis</i> spp.	14.8	0.015
			<i>Veronica officinalis</i>	13.4	0.038
			<i>Geranium maculatum</i>	11.6	0.023

For this and NMDS analyses, species in the genera *Actaea*, *Aronia*, *Circaea*, *Corylus*, *Galium*, *Glyceria*, *Oxalis*, *Panicum* (*Dichanthelium*), *Polypodium*, *Prenanthes*, *Rhododendron*, *Ribes*, *Sambucus*, *Spiraea*, *Ulmus*, *Veronica*, and *Viola* were lumped to genus. For *Aster*, we created three groups: *A. divaricatus*, *A. acuminatus*, and other. Similarly, for *Carex* we recognized four groups: *C. debilis*, *C. laxiflorae* spp., *C. pensylvanica*, and other; for *Solidago*, we recognized two groups: *S. rugosa* and other.

4. Discussion

In the past two decades, there has been increased recognition of the need for forest management to address biodiversity conservation goals, including the maintenance of native species richness, in addition to traditional timber production objectives (Halpern and Spies, 1995; Seymour et al., 2000; Elliott and Knoepp, 2005; Reier et al., 2005). Although numerous studies have evaluated the extent to which forest harvesting influences species richness of vascular plants, results are highly varied and may, to some extent, be system-specific (Roberts and Gilliam, 1995). For instance, substantial long-lasting declines in herb species richness have been reported as a result of clearcutting of southern Appalachian hardwood forests (Duffy and Meier, 1992; Meier et al., 1995), whereas limited response or rapid recovery of species composition and richness have been documented for a range of forest types and silvicultural systems (Albert and Barnes, 1987; Reader, 1987; Halpern and Spies, 1995; Scheller and Mladenoff, 2002; Kern et al., 2006). Several authors have suggested that shifts in composition and species richness are related to logging intensity (e.g., Reader, 1987; Bergstedt and Milberg, 2001; Zenner et al., 2006). Our study is consistent with other studies that show a limited change in species composition following relatively low-intensity logging.

Most prior studies have evaluated forest harvesting effects at the scale of individual stands, which corresponds with the scale at which harvests are conducted. However, because local responses to harvesting vary substantially, it is also critical to evaluate the overall landscape-scale impacts of harvesting on biodiversity (Bergstedt and Milberg, 2001). Few prior studies have been conducted at such broad spatial scales. In this study, we evaluated the extent to which forest harvesting influences vegetation composition and species richness across a region that is character-

ized by varied topography, elevation, and soils. Importantly, unlike most previous studies in North America that have been largely restricted to public lands, we evaluated harvesting effects across a region that is largely owned and managed by numerous non-industrial private forest (NIPF) landowners. Although such ownership patterns have resulted in dispersed, low to moderate intensity harvesting regimes across much of the eastern deciduous forest (Kittredge et al., 2003), we are aware of only one previous study that has explicitly evaluated harvesting impacts on the vascular vegetation of NIPF lands in the eastern U.S. (Fredericksen et al., 1999).

4.1. Tree regeneration on harvested versus unharvested sites

Our results indicate that the overall effect of widespread low to moderate intensity harvesting on woody plant composition is relatively small. Harvesting significantly changes the structure of the forest, producing canopy openings, and initially decreasing overstory density and basal area. Following a harvest there is a rapid increase in recruitment into the seedling and sapling layers, followed by growth of these young trees. However, harvesting exerts only slight changes in tree composition as recruitment is often similar in composition to the forest overstory, with some notable exceptions. For instance, *B. lenta* apparently increases in abundance and frequency on harvested sites regardless of overstory tree composition, and oak regeneration is limited, even in oak-dominated stands. The relatively modest post-harvesting difference in species composition that we observed may be due to the relatively low harvesting intensity in our study area, often less than one-fifth of stand volume (Kittredge et al., 2003; McDonald et al., 2006) which may limit the extent to which resource availability is altered, in contrast to more intensive harvests. Note

that land clearing and logging during the agricultural period were likely significantly more intense disturbances than current logging, and may have previously removed disturbance-sensitive species, both woody and herbaceous, from many forested sites (Donohue et al., 2000).

P. strobus regeneration seems moderately increased by harvesting overall, as indicated by our MRPP analysis. Closer inspection suggests that this result derives primarily from the moderate increase of *P. strobus* seedlings in harvested Mixed hardwood, *Quercus*, and *Tsuga*-dominated forests (Table 2). However, stocking densities in these forest types remain well below 1700 saplings/ha recommended for white pine production (Philbrook et al., 1973). Interestingly, white pine-dominated forests have substantial regeneration of white pine without harvest, and harvest does not seem to increase the relative abundance of white pine regeneration substantially in these stands. The abundance of white pine regeneration across both harvested and unharvested white pine stands appears adequate for its retention in these forests.

Harvesting on NIPF and other lands in the region does not increase oak regeneration substantially. Red oak regeneration predominately occurs in oak-dominated forests, suggesting possible dispersal or establishment limitations in other forest types. Harvesting in oak-dominated forests may increase the number of red oak seedlings, but our results suggest that few of these seedlings make it into the sapling layer. Similarly, although oak seedlings are more abundant in harvested versus unharvested white pine and hemlock forests, it is unclear how many of these will survive to become saplings. Recommended stocking densities in oak-dominated forests vary widely (Oliver, 1978; Desmarais, 1998), and it is thus difficult for us to assess whether current levels of oak regeneration are sufficient to maintain oak as a canopy dominant without information on the survivorship of oak seedlings and saplings over time. However, current patterns of logging clearly favor the establishment of other species far more than oak.

4.2. Harvesting effects on species composition and richness

For vascular plant composition as a whole, the response to harvesting varies depending on soil richness. On high C:N ratio sites (i.e., poor soils), there is little change in species richness after harvesting. However, low C:N sites (i.e., rich soils) may double in species richness after a harvest. There is a large suite of species that is indicative of harvests on rich sites. Many of these are successional species that will decline rapidly and also occur at low frequency in closed-canopy forests on rich soils, and are not of great conservation concern. However, several of them are non-native invasive species that are likely to persist indefinitely after harvest (McDonald et al., in press). We saw no evidence that species declined dramatically or disappeared following harvesting on rich or on poor sites. Thus, harvest on high C:N sites apparently results in little change in vascular plant composition, while harvests on low C:N sites seem to change vascular plant composition in ways that are likely to persist for a long period of time.

5. Conclusions

Variation in plant composition caused by harvesting seems far less in magnitude than that caused by climatic and edaphic gradients. This may be due to the relatively large scale of our study, which examined sites throughout central and western Massachusetts. It may also result from the low-intensity harvests in the region. Nonetheless, substantial change in species composition

occurs on sites with rich soils after harvest. Forest managers should attempt to limit soil disturbance on such sites, with particular attention to the sensitivity of rich mesic forests that support regionally uncommon species (Bellemare et al., 2005) and that may be susceptible to the establishment of invasive species after logging.

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References

- Abrams, M.D., 1998. The red maple paradox. *Bioscience* 48, 355–364.
- Abrams, M.D., 2003. Where has all the white oak gone? *Bioscience* 53, 927–939.
- Albert, D.A., Barnes, B.V., 1987. Effects of clearcutting on the vegetation and soil of a sugar maple-dominated ecosystem, western Upper Michigan. *Forest Ecol. Manage.* 18, 283–298.
- Bellemare, J., Motzkin, G., Foster, D.R., 2005. Rich mesic forests: Edaphic and physiographic drivers of community variation in western Massachusetts. *Rhodo* 107, 239–283.
- Belloq, M.I., Jones, C., Dey, D.C., Turgeon, J.J., 2005. Does the shelterwood method to regenerate oak forests affect acorn production and predation? *Forest Ecol. Manage.* 205, 311–323.
- Bergstedt, J., Milberg, P., 2001. The impact of logging intensity on field-layer vegetation in Swedish boreal forests. *Forest Ecol. Manage.* 154, 105–115.
- Beven, K.J., Kirkby, M.J., 1979. A physically based, variable contributing area model of basin hydrology. *Hydrol. Sci. Bull.* 24, 43–69.
- Brady, N.C., Weil, R.R., 2002. The nature and properties of soil, 13th edition. Prentice-Hall, Upper Saddle River, NJ.
- Chen, J.Q., Franklin, J.F., Spies, T.A., 1993. An empirical-model for predicting diurnal air-temperature gradients from edge into old-growth Douglas-Fir forest. *Ecol. Model.* 67, 179–198.
- Cottam, G., Curtis, J., 1956. The use of distance measures in phytosociological sampling. *Ecology* 37, 451–460.
- Cronon, W., 1983. Changes in the Land: Indians, Colonists, and the Ecology of New England. Hill and Wang, New York.
- Davies-Colley, R.J., Payne, G.W., van Elswijk, M., 2000. Microclimate gradients across a forest edge. *NZ J. Ecol.* 24, 111–121.
- Desmarais, K., 1998. Northern Red Oak Regeneration: Biology and Silviculture. University of New Hampshire, Department of Natural Resources, Durham, NH.
- Donohue, K., Foster, D.R., Motzkin, G., 2000. Effects of the past and the present on species distribution: land-use history and demography of wintergreen. *J. Ecol.* 88, 303–316.
- Duffy, D.C., Meier, A.J., 1992. Do Appalachian herbaceous understories ever recover from clearcutting? *Conserv. Biol.* 6, 196–201.
- Dufréne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 61, 53–73.
- Elliott, K.J., Knoepp, J.D., 2005. The effects of three regeneration harvest methods on plant diversity and soils characteristics in the southern Appalachians. *Forest Ecol. Manage.* 211, 296–317.
- Finley, A.O., Kittredge, D.B., 2006. Thoreau, Muir, and Jane Doe: different types of private forest owners need different kinds of forest management. *Northern J. Appl. Forest.* 23, 27–34.
- Foster, D., Aber, J. (Eds.), 2004. Forests in Time: The Environmental Consequences of 1000 Years of Change in New England. Yale University Press, New Haven.
- Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., Knapp, A., 2003. The importance of land-use legacies to ecology and conservation. *Bioscience* 53, 77–88.
- Foster, D.R., Motzkin, G., Slater, B., 1998. Land-use history as long-term broad-scale disturbance: Regional forest dynamics in central New England. *Ecosystems* 1, 96–119.
- Fredericksen, T.S., Ross, B.D., Hoffman, W., Morrison, M.L., Beyea, J., Johnson, B.N., Lester, M.B., Ross, E., 1999. Short-term understory plant community responses to timber-harvesting on non-industrial private forestlands in Pennsylvania. *Forest Ecol. Manage.* 116, 129–139.
- Gilliam, F.S., 2002. Effects of harvesting on herbaceous layer diversity of a central Appalachian hardwood forest in West Virginia, USA. *Forest Ecol. Manage.* 155, 33–43.

- Gleason, H., Cronquist, A., 1991. Manual of the Vascular Plants of the Northeastern United States and Adjacent Canada, 2nd edition. New York Botanical Garden, Bronx, NY.
- Gray, A.N., Spies, T.A., Easter, M.J., 2002. Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests. *Can. J. Forest Res.* 32, 332–343.
- Hall, B.G., Motzkin, G., Foster, D.R., Syfert, M., Burk, J., 2002. Three hundred years of forest and land-use change in Massachusetts, USA. *J. Biogeogr.* 29, 1319–1335.
- Halpern, C.B., Spies, T., 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecol. Appl.* 5, 913–934.
- Kern, C.C., Palik, B.J., Strong, T.F., 2006. Ground-layer plant community responses to even-age and uneven-age silvicultural treatments in Wisconsin northern hardwood forests. *Forest Ecol. Manage.* 230, 162–170.
- Kittredge, D.B., 1996. Decreasing woodlot size and the future of timber sales in Massachusetts: when is an operation too small? *Northern J. Appl. Forest.* 13, 96–101.
- Kittredge, D.B., Finley, A.O., Foster, D.R., 2003. Timber harvesting as ongoing disturbance in a landscape of diverse ownership. *Forest Ecol. Manage.* 180, 425–442.
- Mantel, N., 1967. The detection of disease clustering and a generalized regression approach. *Cancer Res.* 27, 209–220.
- McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software, Gleneden Beach, Oregon.
- McDonald, R.I., Motzkin, G., Bank, M., Kittredge, D.B., Burk, J., Foster, D., 2006. Forest harvesting and land-use conversion over two decades in Massachusetts. *Forest Ecol. Manage.* 227, 31–41.
- McDonald, R.I., Motzkin, G., Foster, D.R., in press. Assessing the importance of historical factors, contemporary processes, and environmental conditions on invasive species. *J. Torrey Bot. Soc.*
- Meier, A.J., Bratton, S.P., Duffy, D.C., 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. *Ecol. Appl.* 5, 935–946.
- Motts, W.S., O'Brien, A.L., 1981. Geology and Hydrology of Wetlands in Massachusetts. University of Massachusetts Water Resources Center, Amherst.
- Motzkin, G., Wilson, P., Foster, D.R., Allen, A., 1999. Vegetation patterns in heterogeneous landscapes: the importance of history and environment. *J. Veget. Sci.* 10, 903–920.
- National Climatic Data Center, 2006. Weather Station Data. National Climatic Data Center, Washington, DC.
- Newmark, W.D., 2001. Tanzanian forest edge microclimatic gradients: Dynamic patterns. *Biotropica* 33, 2–11.
- Oliver, C., 1978. The Development of Northern Red Oak in Mixed Stands in Central New England. Yale School of Forestry and Environmental Studies Bulletin No. 91, New Haven.
- Ollinger, S., Aber, J., Federer, C., Lovett, G., Ellis, J., 1995. Modeling Physical and Chemical Climate of the Northeastern United States for a Geographic Information System. U.S. Department of Agriculture, Forest Service, Radnor, PA.
- Philbrook, J.S., Barrett, J.B., Leak, W.B., 1973. A stocking guide for eastern white pine. USDA Forest Service, Research Note NE-168, Northeastern Forest Experiment Station, Upper Darby, PA.
- Reader, R.J., 1987. Loss of species from deciduous forest understory immediately following selective tree harvesting. *Biol. Conserv.* 42, 231–244.
- Reier, U., Tuvi, E., Partel, M., Kalamees, R., Zobel, M., 2005. Threatened herbaceous species dependent on moderate forest disturbances: a neglected target for ecosystem-based silviculture. *Scand. J. Forest Res.* 20, 145–152.
- Roberts, M.R., Gilliam, F.S., 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. *Ecol. Appl.* 5, 969–977.
- Saunders, S.C., Chen, J.Q., Drummer, T.D., Crow, T.R., 1999. Modeling temperature gradients across edges over time in a managed landscape. *Forest Ecol. Manage.* 117, 17–31.
- Scheller, R.M., Mladenoff, D.J., 2002. Understory species patterns and diversity in old-growth and managed northern hardwood forests. *Ecological Applications* 12, 1329–1343.
- Seymour, R.S., White, A.S., deMaynadier, P., 2000. Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. *Forest Ecol. Manage.* 155, 357–367.
- Smouse, P.E., Long, J.C., Sokal, R.R., 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Systematic Zool.* 35, 627–632.
- Zenner, E.K., Kabrick, J.M., Jensen, R., Peck, J., Grabner, J., 2006. Responses of ground flora to a gradient of harvest intensity in the Missouri Ozarks. *Forest Ecol. Manage.* 222, 326–334.