Long-term compositional dynamics of Acadian mixedwood stands under different silvicultural regimes

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Abstract: Pathways of forest compositional dynamics over five decades (1953–2005) were reconstructed using measurements from permanent sample plots in a long-term silviculture experiment in a central Maine mixedwood forest. The objective of this study was to elucidate the dynamics of tree species composition at the sample plot level in relation to the initial composition when the experiment was established (1953–1957) and harvest disturbance history following a wide range of even-aged and uneven-aged silvicultural treatments. Cluster analysis revealed three groupings of sample plots based on pretreatment composition and harvest disturbance history, or nine subclusters (i.e., three harvest disturbance histories nested within each pretreatment composition). From 1953 to 2005, the silvicultural treatments generated an array of compositional outcomes at the plot level. Hardwood dominance increased following a history of heavy and infrequent harvests, while northern conifer dominance was maintained where harvests were lighter and more frequent. The importance of balsam fir (Abies balsamea (L.) Mill.) changed little across a range of harvest intensities. A ubiquitous decline in northern white-cedar (Thuja occidentalis L.) was found among silvicultural treatments, suggesting that additional intervention may be needed to promote cedar recruitment. Plot-level compositional dynamics indicated that neighborhood-scale stand dynamics were associated with variability in harvest disturbance overlain on plot-to-plot variability in tree species composition at the time the experiment was established.

Résumé : Les trajectoires de la dynamique de composition forestière au cours de cinq décennies (1953–2005) ont été reconstituées à l’aide de mesures provenant de placettes échantillons permanentes établies dans le cadre d’une expérience sylvicole de longue durée dans une forêt mixte du centre du Maine, aux États-Unis. L’objectif de cette étude était de déterminer la dynamique de la composition en espèces d’arbre à l’échelle de la placette échantillon en tenant compte de la composition initiale lorsque l’expérience a été établie (1953–1957) et de l’historique des coupes soumises à une large gamme de traitements sylvicoles associés à des régimes équivalents et inéquivalents. Une analyse de groupement a identifié trois groupes de placettes échantillons basés sur la composition avant le traitement et sur l’historique des coupes, ou neuf sous-groupes (c.-à-d. trois groupes historique des coupes imbriqués dans chaque composition avant le traitement). De 1953 à 2005, les traitements sylvicoles ont produit une gamme de compositions à l’échelle de la placette. La dominance des feuillus augmentait à la suite d’un historique de coupes sévères et peu fréquentes, alors que la dominance des conifères nordiques était maintenue là où les coupes étaient légères et plus fréquentes. L’importance du sapin baumier (Abies balsamea (L.) Mill.) a peu changé en fonction de l’intensité des coupes. Un déclin généralisé du thuya occidental (Thuja occidentalis L.) a été observé dans tous les traitements sylvicoles, ce qui indique que des interventions supplémentaires peuvent être nécessaires pour favoriser le recrutement du thuya occidental. La dynamique de composition à l’échelle de la placette indique que la dynamique des peuplements à l’échelle des arbres voisins était associée à la variabilité de l’intensité de coupe par le biais de la variabilité de la composition en espèces d’arbre entre les placettes au moment où l’expérience a été établie.

Introduction

Forest management is based on understanding the dynamic responses of forests to natural disturbances and silvicultural treatments over long time periods (Irland et al. 2006). Long-term measurements from controlled silviculture experiments are especially useful in helping advance our understanding of the influence of forest management on stand dynamics, since the measurements provide the appropriate temporal frame for capturing forest vegetation responses to management practices.

A major challenge for forest managers relying on natural regeneration is in forecasting future forest composition under various levels of harvest intensity (Miina and Heinonen 2008; Taylor et al. 2009). In naturally regenerated, mixed-species stands, uncertainty in forecasting species composition frequently arises because of the wide range of successional outcomes that can result from harvest treatments (Abrams et al. 1985; Gould et al. 2005). Secondary succession in mixed-species forests is often associated with
variability in local stand composition and structure (i.e., neighborhood), as well as disturbance history (Canham et al. 1994; Frelch 2002; Canham and Uriarte 2006). Spatio-temporal variation in neighborhood and disturbance factors can produce multiple pathways of succession within a single stand (Frelch et al. 1998).

Even when applied with the objective of creating homogeneity at the stand level, silvicultural treatments often fail to entirely eliminate substand heterogeneity (Pietarre et al. 2009) and may initiate a range of successional outcomes within a single stand that reflects smaller scale variability in harvest intensity. For long-term silviculture experiments where treatments are applied at the stand level, this range of substand dynamics can serve as a platform for investigating lines of inquiry beyond the scope of their intended design (Saunders and Wagner 2008; Pietarre et al. 2009).

Using over five decades (1953-2005) of measurements from a long-term experiment in central Maine, the objective of this study was to document the pathways of compositional development in Acadian mixedwood stands under a wide range of silvicultural regimes. However, rather than simply retracing stand dynamics by averaging sample plots as is traditionally done, we used plot-to-plot variability intrinsic to large-scale experiments to investigate the combined effects of initial species composition and harvest disturbance history on long-term compositional dynamics. A specific objective was to document the persistence of conifer species in conifer-dominated mixedwood stands that were exposed to a wide range of harvest disturbance intensities.

Methods

Study site

This study took place on the Penobscot Experimental Forest (PEF) near the towns of Bradley and Eddington, Maine. The PEF is within the Acadian Forest, a conifer-dominated mixedwood ecosystem covering much of Maine and the Canadian Maritime provinces (Halliday 1937). The PEF is a 1680 ha forest owned by the University of Maine Foundation and is jointly managed by the University of Maine and the United States Forest Service, Northern Research Station.

The climate of central Maine is cool and humid. February (average temperature –7.1 °C) and July (average temperature 20.0 °C) are the coldest and warmest months, respectively. The average precipitation is 107 cm. The growing season at the PEF is approximately 160 days long. Soils on the PEF are predominately loams formed from glacial till (Sendak et al. 2003). Contained within the PEF is a broad gradient of drainage and moderate to low productivity.

Soil types on the PEF are predominantly mixedwood types. The dominant conifer species on the PEF include balsam fir (Abies balsamea (L.) Mill.), eastern hemlock (Tsuga canadensis (L.) Carrière), red spruce (Picea rubens Sarg.), white spruce (Picea glauca (Moench) Voss), northern white cedar (Thuja occidentalis L.), and white pine (Pinus strobus L.), while the common hardwood species include red maple (Acer rubrum L.), paper birch (Betula papyrifera Marsh.), gray birch (Betula populifolia Marsh.), trembling aspen (Populus tremuloides Michx.), and bigtooth aspen (Populus grandidentata Michx.) (Sendak et al. 2003).

The history of the PEF prior to 1950 is not well documented, but the forest structure was probably irregular and uneven-aged as a result of periodic harvesting and natural disturbances (Sendak et al. 2003). Throughout much of the 1800s, a sawmill operated within the boundaries of PEF, which likely used pine and spruce preferentially over much of the forest during this period (Saunders and Wagner 2008). The 1913–1919 outbreak of the eastern spruce budworm (Choristoneura fumiferana Clem.) also had a significant influence on forest structure and composition before the PEF was established in the early 1950s (Seymour 1992; Saunders and Wagner 2008).

Long-term experiment

The US Forest Service (USFS) installed a replicated study between 1952 and 1957 to investigate the influence of silvicultural (even-aged and uneven-aged) and exploitative harvesting practices on the composition, structure, growth, and yield of mixed northern conifer stands in the northeastern US (Sendak et al. 2003). At the start of the experiment, two replicates of nine treatments were randomly assigned to sixteen 7–18 ha treatment units: 5-, 10-, and 20-year single-tree selection methods; two- and three-stage shelterwood methods; fixed and modified diameter-limit harvests; commercial clear-cutting; and an unharvested, natural area (control). In the early 1980s, both replicates of the three-stage shelterwood treatment were divided to investigate the influence of precommercial thinning (PCT) on mixed northern conifer stand development. As an amendment to the original experiment, the natural area, which was established as an unharvested control, was eventually divided to create two “pseudo-controls”. The addition of the PCT and pseudo-control units to this experiment increased the number of treatment units from 17 to 20. For more information about the treatment prescriptions see Sendak et al. (2003).

Within each treatment unit, tree inventories have been conducted on a systematic grid of 13–23 permanent sample plots before and after each harvest entry and approximately every 5 years after harvest. Stem diameter at breast height (DBH = 1.35 m) and the condition of all trees >11.5 cm DBH were recorded by species and species groups within 0.08 ha circular plots; saplings between 1.2 and 11.4 cm DBH were recorded within nested, 0.02 ha circular plots.

Study approach

The focus of this study was on the compositional dynamics of Acadian mixedwoods based on plot-level measurements from the long-term USFS silviculture experiment on the PEF. Thus, the sample plot served as the experimental unit for this analysis. Forest composition was estimated from individual tree measurements (stems ≥1.2 cm DBH) recorded on 231 permanent sample plots from 16 of 20 treatment units collected over six time periods spanning five decades (1953–2005). Both replicates of the natural area (untreated controls) were not included in this analysis because they have not received a harvest entry since the start of the experiment and therefore are outside of the scope of this investigation. The long-term dynamics of these unharvested stands were recently reported in Saunders and

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Wagner (2008). Two other treatment units, one replicate each of the fixed diameter-limit and commercial clear-cutting treatments, were also not included in this analysis, since they were not inventoried before the establishment of the original experiment and, therefore, lacked measurements of pretreatment forest composition. The six time periods (T) examined were (1) T0, 1953–1957 (pretreatment sample); (2) T1, 1960–1964; (3) T2, 1969–1974; (4) T3, 1980–1983; (5) T4, 1990–1994; and (6) T5, 1999–2005. Time periods were selected that captured at least one inventory on all plots and the last inventory before a harvest occurred.

Plot-level importance values (IVs) of six tree species and species groups, hereafter referred to as species, were used to represent the relative ecological importance of tree species to forest composition at the plot level (sensu Curtis and McIntosh (1951)). The six species variables were (1) fir (balsam fir), (2) cedar (northern white cedar), (3) hemlock (eastern hemlock), (4) HMWD (hardwood-dominated mixedwood, composed of paper and grey birch, American beech, sugar maple, trembling and bigtooth aspen, white red pine, and eastern larch), (5) maple (red maple), and (6) spruce (red, black, and white spruce). For each plot at each time period, IV was calculated by species as the mean of two percentages: percentage of total basal area and stem density.

Causes of tree mortality over the entire experiment were not recorded until the 1990s, which meant tree losses due to harvesting could not be quantified in each plot for the full five-decade period. However, sample plots in all compartments that received harvesting were inventoried immediately before and after each harvest entry. Based on these pre- and post-harvest inventories, four variables describing the harvest disturbance were generated using the reduction in basal area (BA) for all plots from harvested units over the five-decade period: (1) total BA reduction (TBAr), calculated as the sum of the differences in plot-level BA between all pre- and post-harvest inventories; (2) mean percent BA reduction (MBAr), calculated as the percentage decrease in plot-level BA between pre- and post-harvest inventories divided by the total number of recorded basal area reductions; (3) frequency of BA reduction (FRQr), representing the total number of recorded BA reductions; and (4) total hardwood BA reduction (THDr), calculated as the sum of the differences in plot-level hardwood BA between all pre- and post-harvest inventories. Since favoring the regeneration of northern conifer species was and continues to be a primary objective of this experiment, THDr was included to account for any bias toward removing hardwoods.

Statistical analysis

To account for the effects of initial forest composition and harvest disturbance on plot-level compositional dynamics, permanent sample plots were grouped according to pretreatment tree composition and five decades of silvicultural treatment. Two rounds of agglomerative, hierarchical cluster analysis were performed in PC-ORD (version 4.07; McCune and Mefford 1999) starting with all 231 plots to group plots based on (1) IV of tree species and (2) harvest disturbance variables. Combinations of distance measures and linkage methods were tested on both data sets to find an optimal cluster solution for each data set (i.e., compromise between number of clusters and information retained). Preliminary analysis of cluster analysis results indicated that THDr was not useful for distinguishing harvest disturbance clusters; therefore cluster analysis was rerun on harvest disturbance variables without THDr. Pretreatment clusters (PTCs) were formed using correlation distance and flexible beta linkage ($\beta = -0.85$), and harvest disturbance clusters (HDCs) were formed using Euclidean distance and flexible beta ($\beta = -0.65$).

Parametric and nonparametric statistics were used to test for differences among groups formed by cluster analysis. PTCs were compared using one-way analysis of variance (ANOVA) to test for differences in mean IV within species among clusters. HDCs were classified using both parametric and nonparametric statistics. ANOVA was used to test for differences in mean TBAr and MBAr among clusters. Mann–Whitney tests (nonparametric) were used to determine if HDC differed based on harvest frequency (FRQr). Means were separated when ANOVA detected significant differences using Tukey’s honestly significant difference test, while Mann–Whitney test results were used to separate median FRQr by HDC. All post-hoc testing was performed using R version 2.8 (R Development Core Team 2008) and significance was assessed at $\alpha = 0.05$.

The five-decade dynamics of subclusters (i.e., HDCs nested within PTCs) were retraced to document species-level trends in basal area, density, and relative importance. Mann–Whitney tests were used to compare mean IVs at T0 and T5 for each species separately within subclusters to determine if species importance changed significantly over the study period ($p < 0.05$). Nonmetric multidimensional scaling (NMS) was run in PC-ORD (version 4.07; McCune and Mefford 1999) to ordinate subclusters across the six time periods in compositional space defined by species’ IVs. Prior to NMS, IVs at each inventory period were averaged by subcluster. Following the recommendation of McCune and Grace (2002), multiple runs of NMS were performed to find an appropriate solution. The best two-dimensional solution was obtained using the “slow and thorough” autopilot setting with Euclidean distance, which stabilized after 105 iterations. Final stress and instability for the two-dimensional solution were 12.06 $\times 10^{-6}$ and 8.98 $\times 10^{-6}$, respectively. A Monte Carlo test based on 50 runs with randomized data found a 1.96% probability that a similar solution could have been obtained by chance. NMS coordinates of subclusters at each inventory period were used to retrace compositional dynamics in NMS space over five decades. Compositional dynamics of subclusters in relation to silvicultural treatments were interpreted from the NMS ordination using Pearson correlations of species and harvest disturbance variables with NMS axes.

Results

Cluster analysis and classification

Cluster analysis revealed three PTCs and HDCs among the sample plots. Clusters were identified by pruning dendrograms at long stems, which retained 73% and 81% of information from original pretreatment and disturbance pattern data sets, respectively. Based on these results, nine subclusters (i.e., three HDCs nested within each of three PTCs)
could be formed to retrace compositional dynamics over five decades (Table 1).

ANOVA results for comparisons of pretreatment mean IVs within species among clusters are presented in Table 2. Mean IV for hemlock (33.9%) was highest in PTC A ($p < 0.05$). Although the mean IV of fir was lowest in PTC A, fir on average still accounted for 29.2% of pretreatment species composition. Species composition of PTC A was dominated by hemlock and fir (i.e., fewest species needed to account for >50%). PTC B was dominated by fir and cedar (38.2% and 28.5%, respectively), which was the highest IV attained by cedar among PTCs. Fir dominated the species composition of PTC C (52.8%), which was the highest mean IV for fir across PTCs. Because of relatively low importance, spruce, HMWD, and maple were not used to type clusters. In the case of maple and HMWD, IV was <10% across clusters and maple IV was not significantly different among clusters.

ANOVA and Mann–Whitney tests detected differences ($p < 0.05$) in harvest disturbance variables among HDCs (Table 3), which were consistent with the membership of plots within silvicultural treatments (Table 4). HDC B had
lower mean TBAr and MBar and higher FRQr than the other HDCs (9.3 m², 20.2%, and 5, respectively); a pattern consistent with HDC B composed mainly of plots from selection harvest treatments. In contrast, HDC C had the highest mean TBAr and MBar and lowest FRQr (25.4 m², 60.3%, and 2, respectively), which reflected the higher proportion of plots from treatments associated with heavy overstory removal (i.e., commercial clear-cutting, two-stage shelterwood, and both diameter-limit treatments). Harvest disturbance variables for HDC A were intermediate between the other two HDCs (mean TBAr and MBar and median FRQr of 15.1 m², 35.2%, and 3, respectively). The difference in median FRQr between HDCs B and C was nonsignificant. Collectively, plots within HDC A were more of a mixture of even- and uneven-aged silvicultural treatments than the others. For convenience, HDCs A, B, and C will be referred to as medium intensity, low intensity, and high intensity, respectively. Additionally, plots separated out by HDC in a three-dimensional space defined by the harvest disturbance variables (Fig. 1), further substantiating our harvest disturbance classification.

Basal area and density dynamics

Five-decade dynamics of basal area and density of the nine subclusters are presented in Figs. 2 and 3, respectively. Across PTC types, changes in total density and basal area were greatest in the high-intensity subclusters, intermediate in medium-intensity subclusters, and least in low-intensity subclusters. By the fifth decade, total density was higher and basal area was lower than preharvest levels for all subclusters. Over the study period, fir had the highest density in nearly all subclusters. Although hemlock and spruce basal area decreased over time in all subclusters, their densities tended to increase. HMWD and maple densities increased rapidly in high-intensity subclusters. Basal area and density of cedar decreased over time in all subclusters, while maple basal area and density tended to increase. Of all species, only cedar density decreased appreciably over the study period.

Compositional dynamics

Figure 4 shows five decades of compositional dynamics of subclusters in two-dimensional NMS space, coefficients of determination ($r^2$) for both axes, and vectors representing correlations of variables with NMS axes. According to $r^2$ values, NMS axes 1 and 2 accounted for 49.7% and 34.0%, respectively, of compositional variation in the data. Correlation vectors for species variables suggested that axis 1 captured a gradient defined largely by decreasing fir importance and increasing hemlock importance and, to a lesser extent, spruce importance moving from left to right in ordination.
space, while NMS axis 2 captured a gradient defined largely by decreasing cedar importance and increasing HMWD and maple importance moving from the bottom to the top of the ordination space. According to correlation vectors, harvest disturbance variables were more strongly correlated with NMS axis 2 indicating a gradient of increasing intensity of basal area reduction (TBAr and MBAr) moving from bottom to top, while the frequency (FRQr) increased from top to bottom.

Prior to the start of the silvicultural treatments (denoted as 0; T0), harvest disturbance subclusters sorted out in ordination space by PTC particularly along axis 1 (Fig. 4). After five decades, nearly all subclusters had migrated away from their starting positions in NMS space, with the exception of the low-intensity hemlock–fir cluster. The relative stability of the low-intensity hemlock–fir cluster also was reflected by minor changes in species importance over time (Fig. 5), and absence of significant differences in species-level IV between T0 and T5 (Table 5). Despite changes observed in ordination space, fir importance did not change significantly in any subcluster over five decades.

HDCs within PTC types were less clumped at T5 relative to T0, which indicated compositional divergence. Compositional divergence within PTC types was associated with increasing importance of HMWD, maple, or both as harvest intensity increased (Fig. 5). Divergence within PTC types was also associated with significant decreases in spruce importance observed in all high-intensity subclusters. With the exception of maple importance in the medium-intensity hemlock–fir cluster, mean IV for HMWD and maple was significantly greater at T5 than T0 in medium- and high-intensity subclusters (Table 5). The trend of increasing HMWD and maple importance was reflected by the vertical sorting of subclusters within PTC types at T5 along axis 2, which corresponded with increasing TBAr and MBAr and decreasing FRQr (Fig. 4). Vertical sorting was also likely associated with declining cedar importance over the five-decade period, which was significant in nearly all subclusters except the low-intensity hemlock–fir cluster. In the case of hemlock–fir subclusters, compositional divergence was also linked with significant decreases in the importance of hemlock, and spruce in the high-intensity cluster, as harvest intensity increased, a pattern consistent with upward and leftward shifts in NMS space.

By T5, patterns of species importance are similar within fir–cedar and fir subclusters (Fig. 5), which was reflected by convergence in ordination space (Fig. 4). Compositional convergence, in this case, was associated with significant decreases in cedar and spruce importance in fir–cedar and fir subclusters, respectively, with similar trends in HMWD.
Fig. 4. Developmental pathways of low (dotted), medium (dashed), and high (solid) harvest intensity subclusters nested within hemlock–fir, fir–cedar, and fir subclusters in nonmetric multidimensional scaling (NMS) space over six time periods from 1953 to 2005. T0 and T5 are represented by circles and arrows, respectively. Vectors within the inset image (bottom right corner) depict Pearson correlations of tree species (solid vectors) and harvest disturbance variables (underlined labels, dashed vectors) with NMS axes. Species variable labels: FIR, balsam fir; CEDAR, northern white-cedar; HEM, eastern hemlock; HMWD, hardwood-dominated mixedwood; MAPLE, red maple; SPRUCE; spruce species. Harvest disturbance variable labels: TBAr, total basal area reduction; MBAr, mean percent basal area reduction; FRQr, frequency of basal area reduction.

Discussion

From 1953 to 2005, varied silvicultural treatments generated an array of compositional outcomes at the sample plot level that were associated with differences in both initial tree species composition and subsequent harvest disturbances. Compositional outcomes ranged from no change from pretreatment conditions to significant changes after five decades for subclusters with a history of high-intensity harvesting. The developmental pathways of subclusters tended to migrate away from pretreatment conditions and departures from pretreatment conditions increased with increasing harvest disturbance intensity.

A general trend identified in this investigation was that stand compositional changes were greatest in the high-intensity subclusters, intermediate in medium-intensity subclusters, and least in low-intensity subclusters. This trend across harvest intensities is consistent with an ecological release associated with increasing disturbance intensity (Pickett and White 1985). We use the term ecological release to describe a rapid increase in the importance of species that were previously subordinate. One way disturbance can trigger an ecological release is by increasing resource availability, which in turn creates recruitment opportunities for species with higher resource demands (Pickett and White 1985; Peterson and Pickett 1995; Davis et al. 2000).

At the start of this long-term experiment, permanent sample plots were largely dominated by northern conifer species with only a minor component of hardwood species. Compared with hardwoods, this group of northern conifers is more shade tolerant and capable of regenerating beneath closed canopies. Tolerance of understory conditions confers a level of compositional stability in the absence of major disturbances where understory-tolerant species are locally dominant (Whitmore 1989; Freligh 2002). The maintenance of northern conifer dominance in subclusters with a history of low-intensity harvesting (e.g., 5-year and 10-year single-tree selection) supported this hypothesis.

After five decades of various harvest treatments, the relative importance of hardwood species increased mainly in plots that received medium- and high-intensity harvesting (e.g., shelterwood, diameter-limit cutting, and commercial clear-cutting). Collectively, these hardwood species can sprout vigorously and are capable of rapid regrowth that enables them to quickly capture new growing space created following disturbance (Dietze and Clark 2008). Also, intense harvesting can cause substantial damage to northern conifer advance regeneration and, thus, favor hardwood development by reducing competition with shade-tolerant conifers (Westveld 1931; McInnis and Roberts 1991). The rapidly increasing densities of shade-intolerant hardwood species suggest that the ecological release observed in this study is likely the product of prolific hardwood sprout development, increasing resource availability, and perhaps, damage to competing conifer advance regeneration in plots where harvesting was historically more intense.

Our results indicated that balsam fir dominance was maintained over a wide range of silvicultural regimes applied during five decades. Of the shade-tolerant conifers native to the Acadian forest, balsam fir is arguably the most opportunistic (Place 1955; Greenwood et al. 2008). Balsam fir compensates for its short longevity through the prolific development of advance regeneration (Frank 1990; Seymour 1992). In a regeneration study using this same experiment, balsam fir regeneration was the most abundant among the silvicultural treatments (Brissette 1996). Not only does balsam fir gain a competitive advantage though prolific regeneration, but balsam fir height growth responds more quickly than co-occurring shade-tolerant conifers of similar size following overstory removal (Westveld 1931). The high relative density of balsam fir across subclusters observed in this study suggests that balsam fir dominance was maintained through prolific regeneration mediated by silvicultural treatments.

Recent studies on the long-term stand dynamics of Acadian mixedwoods over the last half century or more observed a decline in balsam fir in unmanaged mixedwood stand types, which was largely attributed to mortality induced by the eastern spruce budworm (Saunders and Wagner 2008; Amos-Binks et al. 2010). Saunders and Wagner (2008) observed higher balsam fir mortality in the unmanaged natural area of this experiment during the last outbreak of the 1970s and 1980s. Interestingly, the results from this study indicated that fir dominance persisted in harvested stands despite defoliation of nearby unmanaged areas of the PEF during the 1970–85 outbreak.
Cedar, hemlock, and spruce were the only species that showed a significant decline in importance over the five-decade period. Cedar showed a significant decline in all but one subcluster. Cedar decline is pervasive throughout its geographic range, which has been linked to three main causes: regeneration failures, poor recruitment into sapling and pole size classes, and harvesting levels that exceed growth (Hofmeyer et al. 2009). With decreases in both basal area and density observed in all subclusters, cedar decline in this study may be linked to all three causes. However, results from a recent investigation of cedar regeneration dynamics on the PEF suggests that cedar recruitment has been limited more by ingrowth of established trees (e.g., seedling to sapling stages) than by the establishment of new seedlings and that harvesting of merchantable trees also contributed to cedar decline (Larouche et al. 2010). Larouche et al. (2010) observed prolific deer browsing of cedar regeneration on the PEF, which has likely contributed to poor recruitment of ce-

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**Table 5.** Results of Mann–Whitney tests comparing median importance values at T0 and T5 by species for each subcluster.

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*HMWD, hardwood-dominated mixedwood composed of paper and grey birch, American beech, sugar maple, trembling and bigtooth aspen, white and red pine, and eastern larch.

**Note:** Positive and negative signs indicate whether importance values at T5 were significantly greater than (+) or less than (–) those at T0 (α = 0.05). Circles indicate no difference after five decades. L, M, and H are low-, medium-, and high-intensity harvest disturbance cluster types.
dar into larger size classes. Based on the findings of this study and that of Larouche et al. (2010), sustaining cedar recruitment may require additional silvicultural treatments beyond those tested in this experiment. For both spruce and hemlock, declines were associated with reductions in basal area since densities were higher at the end of the study period. This pattern was likely a result of removing overstory spruce and hemlock during harvesting, which simultaneously enhanced the recruitment of these shade-tolerant species through the release of advance regeneration, new seedling establishment, or both.

Using a similar approach, Gould et al. (2005) found that initial species composition at the time of harvest was an important determinant of stand developmental pathways following clear-cutting in central hardwood forests of Pennsylvania and concluded that multiple pathways are likely to be observed in stands containing species with different modes of regeneration (e.g., sprouting, advance regeneration, postdisturbance establishment) and a range of shade tolerances. Collectively, the tree species in this study comprise an array of autecological and life history attributes, which likely contributed to the variability in developmental pathways observed in this investigation. However, we were able to account for variation in both initial species composition and harvest disturbance history, which revealed that compositional dynamics at the plot level were linked to variability in both factors. Based on our findings, pathways of neighborhood-scale compositional dynamics were likely associated with variability in harvest disturbance history generated by the long-term silviculture experiment overlap on plot-to-plot variability in tree species composition at the time the experiment was established.

Long-term silviculture experiments provide opportunities to investigate the influence of harvesting practices on stand dynamics across the range of temporal scales relevant to forest management (Irland et al. 2006). Our findings support the widely held view about the effect of silviculture on tree species composition in forests dominated by species associated with later stages of secondary succession — that higher harvest intensity increases dominance by early-successional species (especially intolerant hardwoods), while lighter harvest maintenance maintains dominance by late-successional (primarily conifer) species (Oliver and Larson 1996; Frelitch 2002). In a recent analysis of the same long-term experiment, Saunders and Wagner (2008) observed a dominance shift from shade-tolerant northern conifers to shade-intolerant hardwoods in both commercial clear-cut and fixed diameter-limit treatments, while the 5-year selection treatment maintained a relatively stable species composition dominated by northern conifer species. Despite these compositional trends, we observed that dominance by balsam fir, a shade-tolerant northern conifer, was maintained across a wide range of harvest intensities, suggesting that the development of balsam fir has contributed to the persistence of a northern-conifer component under higher harvest intensities.

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