

Understory plant responses to uneven-aged forestry alternatives in northern hardwood–conifer forests

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Abstract: The understory layer encompasses the majority of plant species diversity in forested ecosystems and may be sensitive to timber harvest disturbance. We hypothesize that (i) uneven-aged, low-intensity silvicultural systems can maintain understory plant diversity and support late-successional species following harvest disturbance; (ii) retaining and enhancing stand structural complexity can increase understory plant diversity in northern hardwood–conifer forests; and (iii) plant responses are influenced by interactions among canopy structure, soils, and climate processes. Experimental treatments include single-tree selection and group selection, both modified to increase structural retention, and a third technique designed to promote late-successional forest structure and function, structural complexity enhancement. Four replications of each treatment were applied to 2 ha units in Vermont and New York, USA. Understory vegetation was monitored 2 years pre- and 4 years post-treatment. Results show that over time, understory responses were strongly affected by overstory treatment and less influenced by soils and drought. All treatments succeeded at maintaining overall composition and diversity. However, late-successional diversity increased significantly in structural complexity enhancement units compared with group selection units. These results indicate that while conventional uneven-aged systems can maintain understory plant diversity, variations that retain or enhance structural complexity may be more effective at retaining late-successional species.

Résumé : La majeure partie de la diversité en espèces végétales des écosystèmes forestiers se retrouve dans le sous-étage qui peut être sensible aux perturbations causées par la récolte des arbres. Nous posons les hypothèses que (i) des systèmes sylvicoles de faible intensité et visant à obtenir une structure inéquienne peuvent maintenir la diversité végétale du sous-étage et supporter les espèces de fin de succession après la coupe, (ii) le maintien et l'amélioration de la complexité structurale du peuplement peuvent augmenter la diversité végétale du sous-étage de forêts mixtes composées de feuillus tolérants et de conifères et (iii) la réaction des plantes est influencée par des interactions entre la structure du couvert, le sol et les processus climatiques. Les traitements expérimentaux incluent le jardinage par pied d'arbre et par groupe, tous deux modifiés pour augmenter la rétention structurale, et une troisième technique, appelée amélioration de la complexité structurale, qui a été élaborée pour favoriser la structure et les fonctions des forêts de fin de succession. Quatre répétitions de chaque traitement ont été appliquées dans des unités expérimentales de 2 ha situées dans les États du Vermont et de New York, aux États-Unis. La végétation du sous-étage a été inventoriée 2 ans avant et 4 ans après l'application des traitements. Les résultats montrent qu'avec le temps, la réaction de la végétation du sous-étage a été fortement affectée par les traitements du couvert dominant et moins influencée par le sol et la sécheresse. Tous les traitements ont réussi à maintenir l'ensemble de la composition et de la diversité. Cependant, la diversité des espèces de fin de succession a augmenté significativement dans les unités où l'amélioration de la complexité structurale a été appliquée comparativement au jardinage par groupe. Ces résultats indiquent que même si les systèmes conventionnels visant à conserver une structure inéquienne peuvent maintenir la diversité végétale du sous-étage, des ajustements permettant de conserver ou d'améliorer la complexité structurale peuvent être plus efficaces pour conserver les espèces de fin de succession.

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Introduction

Understory vegetation comprises the majority of plant species diversity in forested systems and affects ecosystem-level processes, such as nutrient cycling and energy exchange (Roberts 2004). Intensive silvicultural systems can

alter the composition and diversity of understory communities by influencing the availability of light and nutrients, creating soil disturbance, and introducing vigorous competitors (Meier et al. 1995). Species adapted to late-successional forest stand structure or with limited modes of dispersal may be particularly sensitive to harvest disturbance (Halpern and

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Spies 1995; Roberts 2002). There is considerable previous research on understory responses to conventional even- and uneven-aged silvicultural treatments in northern hardwood forests (e.g., Jenkins and Parker 1999; Scheller and Mladenoff 2002). These studies have primarily compared silvicultural systems with relatively dramatic differences in postharvest canopy retention. Recent silvicultural research is exploring more subtle differences in postharvest canopy structure associated with variable levels of retention (Franklin et al. 1997; Aubry et al. 1999) and uneven-aged approaches modified to enhance structural retention (Seymour 2005; Keeton 2006). Understory responses to these approaches are less well understood.

Management strategies for forested ecosystems are increasingly focused on promoting biodiversity conservation and ecosystem functioning while sustaining economic productivity (Lindenmayer et al. 2006). To meet this objective, silvicultural models that attempt to mimic the natural disturbance regimes and structural complexity of forested ecosystems are being developed (Franklin et al. 2002; Seymour et al. 2002). In Vermont, researchers from the Forest Ecosystem Management Demonstration Project (FEMDP) are testing a technique that utilizes disturbance-based forestry principles (see Mitchell et al. 2002) to accelerate development of late-successional structural characteristics, termed structural complexity enhancement (SCE) (Keeton 2006; McKenny et al. 2006). The FEMDP study compares SCE against conventional uneven-aged approaches also modified to increase postharvest structural retention. A central question of this research is whether different types of uneven-aged prescriptions can be modified to achieve similar biodiversity objectives, or if even slight modifications in the type, magnitude, and spatial configuration of structural retention will alter biodiversity responses. New silvicultural systems are often specifically designed to minimize impacts on biodiversity; effects on plant communities can be a key indicator of their effectiveness in this regard.

Studies evaluating the response of understory plants to silvicultural manipulations in northern hardwood forests have commonly found understory vegetation to be very resilient (Hughes and Fahey 1991; Scheller and Mladenoff 2002). Species richness and diversity are often maintained and even increase following harvest disturbance (Metzger and Schultz 1984; Jenkins and Parker 1999). However, diversity as a measure of community response can be deceiving if there are compensatory increases and decreases in different plant groups. For example, the loss or decline of late-successional species, defined here as species that reach maximum abundance in mature, closed-canopy, interior forests, may be obscured by increases in ruderal species (Halpern and Spies 1995; Battles et al. 2001). In many forest types, decreased abundance or local extirpation of late-successional species has been observed following intensive harvest disturbance, indicating that certain species may be sensitive to overstory removal and soil disturbance (Halpern et al. 2005; Ramovs and Roberts 2005).

Postharvest composition of the understory layer is influenced by the interaction of disturbance intensity, timing, and extent, as well as the life history characteristics of persisting and colonizing species (Halpern 1989; Ramovs and Roberts 2005). Similar complex interactions affect recovery

dynamics and regeneration responses following natural disturbances (Carlton and Bazzaz 1998; Franklin and MacMahon 2000). Environmental site factors such as climate, elevation, topography, light, and soil resources can also shape the composition and diversity of the understory layer (Huebner et al. 1995; Roberts 2004). In particular, the influence of overstory structure on understory vegetation has been demonstrated in many forest types (e.g., Moola and Vasseur 2004; Halpern et al. 2005), including northern hardwood-conifer forests (Huebner et al. 1995; Brosofske et al. 2001). Disturbance can alter overstory characteristics and microtopographic features, such as coarse woody debris, that influence microsite conditions for plant species (Beatty 1984; Gilliam 2002). Similarly, relationships between understory vegetation and climatic and edaphic factors have been established (Pregitzer et al. 1983; Graves et al. 2006). Fratterigo et al. (2006) demonstrated that disturbance history influences patterns of soil nutrient availability in cove hardwood forests, which in turn affect the spatial heterogeneity of understory plants. Plant community composition is also affected by moisture availability (Davis et al. 1998; Hutchinson et al. 1999); extended periods of drought have been shown to induce declines in plant species richness and cover (Yurkonis and Meiners 2006). While these findings have contributed to a broad understanding of the factors controlling plant responses, few studies have investigated the relative importance or interaction of belowground (e.g., soil nutrient availability) and aboveground (e.g., canopy structure) influences on postharvest understory composition and diversity (Brosofske et al. 2001; Macdonald and Fenniak 2007).

The most common technique used to evaluate the impact of silvicultural treatments on understory vegetation is chronosequencing, which involves sampling vegetation in stands that are in varying stages of postharvest recovery. This approach assumes comparable initial site conditions, harvesting techniques, and postharvest disturbance history, and may not capture the dynamics of short-lived species or populations with episodic fluctuations (Halpern 1989). In northern hardwood-conifer forests, few studies of understory vegetation response have utilized preharvest data combined with postharvest data from more than 1 year (e.g., Metzger and Schultz 1984). Here we report on a data set spanning 6 years, including 4 years of post-treatment monitoring, which provides a comparatively longer time period over which to assess recovery dynamics, such as lagged responses. Furthermore, there is little information available on plant responses to low-intensity, uneven-aged systems with variable levels and spatial patterns of postharvest structural retention. Assessing initial understory responses to these variations may help to identify which combinations are capable of meeting criteria for biodiversity conservation, and if there is a critical canopy retention threshold for the local persistence of certain plant species (Halpern et al. 2005).

Our research objective was to evaluate changes in the diversity, composition, and abundance of understory plant communities following three uneven-aged forestry practices modified to increase postharvest structural retention: single-tree selection, group selection, and SCE. Pre- and post-disturbance understory communities were monitored to assess initial compositional changes including species persis-

tence and colonization, as well as local extirpations of sensitive species. To further understand the factors driving changes in the understory, we explored the relationships between plant responses and overstory structure, soil properties, and drought stress. We hypothesize that (i) variants of uneven-aged, low-intensity silviculture can maintain understory plant diversity and support late-successional species through harvest disturbance; (ii) retaining and enhancing stand structural complexity can increase understory plant diversity in northern hardwood–conifer forests; and (iii) plant responses are influenced by interactions between canopy structure, soils, and exogenous climate processes.

Methods

Study areas

The study was conducted at three study areas: the Mount Mansfield State Forest, the University of Vermont's Jericho Research Forest, and the Forest Ecosystem Research Demonstration Area (FERDA) in Paul Smiths, New York. The FERDA is a collaborative research effort among the Northern Research Station of the USDA Forest Service, Paul Smith's College, and the Adirondack Park Agency Visitor Interpretive Center. The Vermont Forest Ecosystem Management Demonstration Project (FEMDP) established the experimental treatments and long-term monitoring project at Mount Mansfield State Forest and the Jericho Research Forest. All three sites are mature (ca. 70–100 years), multiaged northern hardwood–conifer forests with a documented history of timber management. Mount Mansfield State Forest is situated on the western slopes of Mount Mansfield in northern Vermont at elevations ranging from 470 to 660 m; soils are primarily Peru extremely stony loams. The Jericho Research Forest is located in the foothills of the northern Green Mountains of Vermont at 200 to 250 m; soils are Adams and Windsor loamy sands or sandy loams. The FERDA sites are located at approximately 500 m elevation in the northwestern section of the Adirondack Park in New York. The soils are Adams loamy sands. At all three study sites, the dominant overstory species include sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britt.). At the Jericho Research Forest, eastern hemlock (*Tsuga canadensis* (L.) Carrière) is also co-dominant, and there are minor components of red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.). Red spruce (*Picea rubens* Sarg.) is a minor element of the canopy at Mount Mansfield State Forest. Minor components of eastern hemlock, red maple, balsam fir (*Abies balsamea* (L.) Mill.), and red spruce are present at the FERDA.

Experimental design

Four replicates of each treatment and eight untreated controls were established across the three study areas. Treatments included two conventional uneven-aged manipulations, single-tree selection (STS) and group selection (GS), and structural complexity enhancement (SCE). Experimental units were 2 ha in size and separated by 50 m (minimum) unlogged buffers to minimize cross-contamination of treatment effects. All three treatments were designed to retain a high degree of postharvest forest stand structure. However,

the treatments have different effects in terms of spatial patterning, level of retention, and the specific type of features retained (see Keeton 2006).

At the FEMDP sites, logging was conducted on frozen ground in winter of 2003. Experimental units received one of three manipulative treatments or were designated as an untreated control. The conventional treatments were modified to increase postharvest structural retention. Modifications were based on a target residual basal area of 18.4 m²/ha, maximum diameter of 60 cm, and a q-factor of 1.3. This prescription was applied in a dispersed (single-tree selection) or aggregated (group selection) spatial pattern (Keeton 2006). The approximate size of individual group selection patches (0.05 ha) was based on estimates of average fine-scale natural disturbance pattern in New England (Seymour et al. 2002) and resulted in eight to nine groups per 2 ha experimental unit. There was no additional cutting in matrix areas surrounding group selection openings.

SCE is designed to promote late-successional structural characteristics, including vertically differentiated canopies, elevated large snag and coarse woody debris volumes and densities, variable horizontal density (including small canopy gaps), and reallocation of basal area to larger size classes. FEMDP researchers used several silvicultural methods to accelerate development of these attributes as described in Keeton (2006). A target basal area (34 m²/ha) and maximum diameter at breast height (90 cm) characteristic of old-growth structure were used to develop a target diameter distribution to which stands were cut (Keeton 2006). The diameter distribution was also based on a rotated sigmoid form, which is typical of some eastern old-growth forests, depending on disturbance history, species composition, and other variables (Goodburn and Lorimer 1999). The sigmoidal distribution was applied as a nonconstant q-factor: 2.0 in the smallest size classes, 1.1 for medium sized trees, and 1.3 in the largest size classes. Accelerated growth in larger trees was promoted with full and partial crown release. Downed coarse woody debris volumes were enhanced 140% on average over preharvest levels. In two of the four SCE units (one per study area), coarse woody debris enhancement involved uprooting trees to mimic the pit and mound topography characteristic of natural disturbance in late-successional northern hardwood–conifer forests (Dahir and Lorimer 1996).

The FERDA consists of fourteen 2 ha units treated with a variety of even-aged, multiaged, and uneven-aged silvicultural methods during the winter of 1999–2000 (Rechlin et al. 2000). Data from eight units (two single-tree selection, two group selection, and four controls) were included in this study. Approximately 30% of tree volume was removed, leaving approximately 18 m²/ha in the treatment units, slash was left on site and treated to keep all branches below 1.3 m, and all standing dead trees were retained. In the group selection sites, approximately 10 openings were created within each 2 ha experimental unit. Individual patches were approximately 0.04 ha in size (Wade et al. 2003); very light thinning occurred in some matrix areas surrounding openings. Structural retention and spatial pattern of single-tree selection and group selection units at the FERDA and FEMDP sites were similar; as a result, data from these treatment types were combined in the analyses.

Data collection

In the FEMDP study areas, five randomly placed 0.1 ha permanent sampling plots were established within each 2 ha treatment unit, buffered by a 15 m minimum distance from the edge of the unit. We inventoried overstory structural characteristics by permanently tagging all live and dead trees (>5 cm dbh and >1.37 m tall) within the sampling plots. Species and diameter were recorded for each tagged tree. Thirteen 1 m² quadrats were established systematically along transects running north–south and east–west within each plot. Percent cover of all vascular and nonvascular species was estimated within the quadrats. Data were collected annually during the month of June in an attempt to capture the maximum diversity of spring ephemerals and later developing species. Two years of pretreatment and 4 years of post-treatment data are included in this study.

In the FERDA study areas, eight 0.04 ha permanent plots for sampling overstory structure were systematically located within each 2 ha treatment unit. Four 1 m² quadrats were established within each permanent plot for monitoring understory vegetation. Percent cover of all vascular species was estimated in each quadrat during May–June for 2 years pretreatment and 3 years post-treatment. At all of the study areas, we performed visual estimates of percent cover using a graduated scale; estimates were made in increments of 0.1 from 0.1%–1.0%, 1 from 1%–10%, 10 from 10%–90%, 1 from 90%–99%, and 0.1 from 99.1%–100%. This protocol was designed to reduce error associated with variable precision in visual estimation at different scales.

Soil macronutrients were sampled from four 2 m² subplots within each monitoring plot at the FEMDP study sites. A randomly located core of the O and A horizons was extracted to a maximum of 10 cm depending on strata depth. Samples were kept cool and prepared for processing within 24 h. Soil analyses were conducted at the University of Vermont Agricultural Testing Lab according to the methods described in Wolf and Beegle (1995). Soil samples were dried at 55 °C, ground in a mortar and pestle, and sieved through a 2 mm sieve. Available nutrients and reactive aluminum were extracted with modified Morgan solution (ammonium acetate at pH 4.8, with a 5:1 solution:soil ratio, shaken for 15 min). Available P was determined colorimetrically (molybdate blue, reduced with SnCl₂); major cations (Ca, K, Mg, Na, Al) and micronutrients (Fe, Mn, B, Cu, Zn, S) were determined by inductively coupled plasma spectroscopy (ICP). Total % C and % N were determined by combustion analysis (Thermo Finnegan FlashEA Analyzer, Milan, Italy) as described in Bremner (1996). For ammonium (NH₄⁺) and nitrate (NO₃⁻), 5 g dried and sieved soil was extracted with 1 mol/L KCl. Analysis was by automated colorimetric analyzer (NH₄⁺ by salicylate, NO₃⁻ by cadmium reduction followed by diazotized sulfanilamide). Organic matter (OM) was estimated by mass loss on ignition (2 h at 375°C); pH was measured in a 2:1 suspension.

Climate data were obtained from the National Climatic Data Center (NCDC 2007). We utilized Palmer drought severity index (PDSI) data for Vermont climate division 1 (western) and for New York division 8 (St. Lawrence Valley). The Palmer drought severity index is a time bias corrected monthly value that indicates prolonged moisture deficiency or excess for a region and has been shown to

reflect fluctuations in soil moisture (Mika et al. 2005). Temperature, evapotranspiration, soil moisture loss, soil moisture recharge, runoff, and precipitation are parameters used to calculate the index (Oliver and Fairbridge 1987). Use of a single index rather than multiple climatic parameters allowed us to reduce the number of explanatory variables, simplifying analyses and increasing statistical power.

Data analysis

Understory responses

Quadrat-level sample data for preharvest and postharvest years at all three study sites were input into a Microsoft Access relational database. The final data set spanned 6 years and included over 16 000 observations. Quality control involved evaluating each observation to ensure positive identifications and consistency across the years. Several species with traits that were difficult to distinguish under field conditions were collapsed to genera. Individual species were classified into habitat guilds defined by habitat preference classes described by Ramovs and Roberts (2005). We equate their “forest class” with late-successional and their “disturbed class” with early-successional species as employed in this analysis. Habitat guilds include late-successional (species reach maximum abundance in mature, closed-canopy, interior forest), intermediate (species occupy young to mature, open- or closed-canopy forest but not excessively disturbed habitats), and early-successional species (species reach maximum abundance in open-canopy, disturbed areas). Habitat preferences were determined according to Gleason and Cronquist (1991).

Species were also classified according to their status as native or non-native. Seven non-native species were identified in the monitoring plots; these include *Cirsium vulgare*, *Epipactis helleborine*, *Galeopsis tetrahit*, *Geranium robertianum*, *Rorippa sylvestris*, *Taraxacum officinale*, and *Veronica officinalis*. Abundance of non-natives both before and after treatment was very low (ranging from 0.01% to 0.06% of total vegetative cover per experimental unit), and none exhibited invasive tendencies during the course of the study. As a result, no further analyses focused on this characteristic were performed.

We calculated plot level means for Hill’s (1973) series of diversity indices, which includes species richness (N_0), the exponential Shannon–Weiner index (N_1), and the reciprocal Simpson index (N_2) (Hill 1973). The sequence progressively downweights rare species; diversity measures are arranged according to their tendency to emphasize either species richness (weighting towards uncommon species) or dominance (weighting toward abundant species) (Magurran 2004). The indices are calculated as follows: N_0 = no. of species per quadrat, $N_1 = \exp(-\sum p_i \log p_i)$, and $N_2 = 1/\sum p_i^2$, where p_i is the proportional abundance of the i th species. The series of indices, as well as percent cover, were calculated for all species and for the habitat guilds. Treatment level means of the diversity and abundance response variables were calculated for preharvest and postharvest years within each of the habitat guilds (Table 1).

Analyses of treatment effects

Multivariate analyses were used to determine if treatment

Table 1. Diversity and abundance response variables by treatment for all species and for habitat guilds.

		GS		STS		SCE		CON	
		Pre	Post	Pre	Post	Pre	Post	Pre	Post
All species	N_0	7.12 (0.68)	7.88 (0.94)	8.04 (0.66)	10.15 (0.76)	8.35 (1.02)	13.85 (1.13)	8.27 (0.58)	7.87 (0.57)
	N_1	3.63 (0.32)	4.60 (1.17)	3.64 (0.68)	5.60 (1.14)	3.75 (0.68)	6.94 (0.82)	4.12 (0.43)	3.61 (0.54)
	N_2	2.99 (0.24)	3.83 (0.92)	2.91 (0.55)	4.71 (0.93)	3.22 (0.42)	5.53 (0.65)	3.37 (0.3)	2.90 (0.36)
	% cover	15.35 (2.76)	18.29 (6.60)	22.35 (4.87)	19.41 (4.14)	11.77 (4.40)	19.84 (5.90)	19.32 (0.68)	14.84 (3.11)
Late-successional species	N_0	11.50 (0.65)	9.75 (1.80)	10.75 (1.60)	17.00 (2.04)	12.50 (2.02)	17.00 (2.04)	12.13 (1.49)	12.25 (1.44)
	N_1	2.95 (0.33)	2.89 (0.70)	2.93 (0.57)	3.61 (0.88)	2.80 (0.61)	3.98 (0.67)	3.01 (0.32)	2.64 (0.36)
	N_2	2.52 (0.23)	2.72 (0.63)	2.50 (0.48)	3.37 (0.84)	2.47 (0.46)	3.62 (0.40)	2.70 (0.28)	2.32 (0.32)
	% cover	12.24 (1.57)	7.92 (0.96)	18.65 (2.27)	11.74 (1.69)	6.69 (1.39)	10.33 (1.88)	18.13 (2.57)	12.63 (1.5)
Intermediate species	N_0	1.75 (0.25)	2.00 (0.41)	2.75 (0.63)	3.25 (0.48)	3.25 (0.85)	3.75 (0.95)	3.00 (0.50)	3.00 (0.53)
	N_1	1.00 (0.00)	1.03 (0.03)	1.11 (0.05)	1.15 (0.05)	1.21 (0.09)	1.35 (0.12)	1.24 (0.07)	1.19 (0.06)
	N_2	0.47 (0.05)	0.56 (0.10)	0.78 (0.12)	0.79 (0.13)	0.86 (0.20)	1.12 (0.18)	1.01 (0.15)	0.97 (0.12)
	% cover	0.56 (0.32)	0.15 (0.03)	1.5 (0.95)	0.85 (0.52)	0.91 (0.34)	1.75 (0.73)	1.61 (0.59)	1.49 (0.54)
Early-successional species	N_0	2.00 (0.41)	3.00 (0.58)	1.50 (0.65)	3.25 (0.48)	2.00 (0.00)	3.50 (0.29)	1.88 (0.48)	1.50 (0.27)
	N_1	1.03 (0.02)	1.50 (0.24)	1.07 (0.05)	1.42 (0.18)	1.04 (0.02)	1.44 (0.10)	1.13 (0.05)	1.02 (0.02)
	N_2	0.59 (0.08)	1.21 (0.35)	0.34 (0.17)	1.31 (0.19)	0.63 (0.19)	1.30 (0.17)	0.45 (0.14)	0.44 (0.14)
	% cover	1.32 (0.62)	5.85 (3.46)	0.44 (0.23)	3.60 (1.13)	2.50 (1.75)	3.19 (1.90)	0.48 (0.26)	0.39 (0.18)

Note: Diversity response variables include species richness (N_0), the exponential Shannon–Weiner index (N_1), and the reciprocal Simpson index (N_2). Abundance is expressed as % cover. Treatments include group selection (GS), single-tree selection (STS), structural complexity enhancement (SCE), and untreated controls (CON). Values expressed are treatment means (± 1 SE) for 1 year before harvest (pre) and 3 years after harvest (post). Sample sizes: CON, $n = 8$; SCE, GS, and STS, $n = 4$.

had an effect on trends in the understory response variables over time. We used a linear mixed effects model in SAS version 9.1 (SAS Institute Inc. 2003) to model diversity response variables for all species and the habitat guilds. Treatment, site, and year were modeled as fixed effects, and plots and units were modeled as random effects. Plots were nested within units, and units were nested within sites. The model output includes parameter estimates for the fixed effects (e.g., treatment*year interaction) and covariance estimates for the random effects.

Analysis of variance (ANOVA) models were used to further explore the effect of treatment on understory response variables. The first hypothesis, that late-successional species can persist through low-intensity treatments, was tested by calculating unit-level means of the diversity and abundance response variables for the late-successional guild and running ANOVAs on the percent change of each variable from preharvest to postharvest years. We tested for differences between the two preharvest years to determine if there was significant interannual variability in the pretreatment baseline data. Because there were no significant differences between the two preharvest years, we defined preharvest as 1 year before harvest. Post-treatment was defined as 3 years after harvest, the longest time period available for all study areas. If significant treatment effects were detected, ANOVAs were followed by Tukey multiple comparison tests. The same technique was applied to the diversity and abundance response variables for species of all habitat guilds combined to determine if treatments maintained species diversity and to test the second hypothesis, that SCE increases understory plant diversity. This method was repeated for the early-successional and intermediate habitat guilds to identify other notable pre- to post-treatment trends.

We used the multi-response permutation procedure (MRPP) in PC-ORD version 4.41 (McCune and Mefford

1999) to test for differences in overall species composition among treatments and between preharvest and postharvest years within treatments using the Sørensen distance measure. Nonmetric multidimensional scaling (NMS), a non-parametric ordination method, was also applied in PC-ORD to interpret compositional patterns among the treatment units. The main advantages of NMS are the following: (i) it avoids the assumption of linear relationships among variables, (ii) it allows the use of any distance measure, and (iii) its use of ranked distances tends to linearize the relationship between distances in environmental space, relieving the “zero-truncation problem” in most ordination methods. For these reasons, NMS is considered the most effective ordination method for ecological community data (McCune and Grace 2002). We ran NMS on a species-by-sample matrix for pre- and post-treatment data with random starting configurations. Both ordinations used a Sørensen distance measure, and each included 20 runs of real data. Dimensionality of the data was assessed using the Monte Carlo permutation procedure in PC-ORD with 30 runs of randomized data.

To determine if any species were declining or absent from treatment units in postharvest years, presence or absence and abundance of individual species were evaluated throughout the study period. Species initially present in low frequencies (<2 quadrats) or at low densities (<0.5%) were not included in this assessment.

Subanalysis of overstory structure and soil properties

As an indicator of preharvest and postharvest stand structure, we calculated relative density (RD) following Curtis (1982). This form of relative density integrates quadratic mean diameter and stem density, and is thus indicative of multiple attributes of overstory structure, such as total occupation of growing space based on both tree density and size. The index is appropriate to both even- and uneven-aged stands (Curtis 1982). We used relative density as a surrogate

for treatment effects on canopy retention in this subanalysis. Plot and unit-level means for the required component forest inventory metrics were generated using the Northeast Ecosystem Management Decision model (NED-2) (Twery et al. 2005).

A subset of the data from the FEMDP sites was used to evaluate the effects of soil properties on understory response variables and to determine whether local differences in soil characteristics may have confounded treatment effects. Five soil chemical characteristics thought to be important to understory vegetation were selected based on earlier studies (Pregitzer et al. 1983; Kolb and Diekmann 2004). These were percent OM, total percent N, Ca, available P, and pH. Because of a strong relationship in the data set between Ca and pH ($p < 0.001$, $r^2 = 0.339$), pH was not included in the analyses. Percent OM was included because it can be reflective of local soil moisture and cation exchange capacity (Johnson et al. 1997). Soil cation concentrations, particularly Ca, have been shown to control distributions of understory plants (Gilliam and Turrill 1993; Graves et al. 2006), and plant growth is commonly limited by availability of N and P (Marschner 1995). Samples from the organic layer (first 10 cm) were used, as this layer encompasses the bulk of the rooting zone of the understory. Plot and unit-level means were generated for each soil variable.

Preharvest to postharvest percent change was calculated for all variables, and a correlation matrix was used to identify relationships among the soil variables, relative density, and the diversity and abundance response variables for all species and for the habitat guilds. The linear mixed effects model was run for each response variable with treatment, site, and year as fixed effects, unit and plot as random effects, and soil characteristics as covariates.

The effects of site variables on overall species composition were assessed using the NMS ordination in PC-ORD. We calculated the percent of variance explained by each ordination axis and generated Kendall's tau correlations to identify associations between ordination scores and overstory and soil characteristics, both before and after treatment. Overlays were created in PC-ORD to interpret the results.

Analysis of moisture stress

Moisture stress in the study areas was assessed using the Palmer drought severity index (PDSI). The value of the index indicates periods of moisture excess (greater than 0.5) or deficiency (less than -0.5). Monthly drought index values were averaged into two time periods when moisture stress would likely influence understory vegetation. The prior year drought index represents a mean monthly value for July–September of the year preceding sampling. The current year drought index represents a mean monthly value for April–June of the sampling year. For diversity and abundance response variables (all species and habitat guilds), pretreatment data were removed, and unit means were standardized to \pm mean for each treatment and (or) site. For each treatment, simple linear regressions were used to identify relationships between the prior and current year drought indices and standardized annual means of the response variables.

Results

Treatment effects

Analysis of understory response trends over time using the linear mixed effects model showed a significant treatment*time interaction on diversity and abundance response variables for all species (N_0 , $p < 0.001$; N_1 , $p < 0.001$; N_2 , $p = 0.004$; % cover, $p < 0.001$). The same interaction effect was found for late-successional and early-successional species, but not for intermediate species (Table 2). Further exploratory analyses using ANOVA models revealed differences in diversity and abundance responses among treatments from 1 year before harvest (pre) to 3 years after harvest (post) (Fig. 1). Multiple comparison tests showed that for all species combined, percent change in richness ($p = 0.032$), diversity (N_1 : $p = 0.004$; N_2 , $p = 0.010$), and percent cover ($p = 0.031$) were significantly higher in SCE treatment units than in control units. Percent change in diversity for all species was also significantly higher in single-tree selection units than in the controls (N_2 : $p = 0.010$) (Table 3).

When responses were analyzed separately for habitat guilds, we found that SCE units maintained significantly higher richness than group selection units ($p = 0.010$), higher diversity than control units (N_1 , $p = 0.009$; N_2 , $p = 0.016$), and higher percent cover than group selection, single-tree selection, or control units for late-successional species ($p = 0.010$) (Fig. 2). Diversity responses of intermediate species were not different among treatments, but abundance increased significantly in SCE units compared with group selection or single-tree selection units ($p = 0.03$). All three treatments showed a minor increase in early-successional species diversity and abundance, but only the conventional treatments increased significantly (N_1 , $p = 0.011$; N_2 , $p = 0.006$; % cover, $p = 0.015$).

In the pretreatment data set, NMS found a three-dimensional solution (32 iterations; final stress of 9.17; Monte Carlo test, $p = 0.03$). The variation in species composition was explained by axis 1 (44.8%), axis 2 (33.2%), and axis 3 (12.0%); the three ordination axes accounted for 90% of the total variation. The first two axes are displayed in Fig. 3a. The NMS ordination and the results of the MRPP ($A = 0.009$, $p = 0.320$) indicated that there were no significant compositional differences among treatments. NMS also found a three-dimensional solution (23 iterations; final stress of 12.2; Monte Carlo test, $p = 0.03$) in the post-treatment data set. The three axes accounted for a total of 75.9% of the variation in species composition: 38.2%, 25.1%, and 12.6%, respectively. The first two axes are displayed in Fig. 3b. Although the ordination depicted stronger clustering of experimental units by treatment group, the results of the MRPP indicated that there was no significant difference in species composition among treatments ($A = 0.026$, $p = 0.142$). However, the average distance between SCE units ($\delta = 0.778$) was greater than the control ($\delta = 0.582$), group selection ($\delta = 0.560$) or single-tree selection ($\delta = 0.609$) units, reflecting the greater compositional heterogeneity among post-treatment SCE units. The results of the MRPP within treatments revealed no significant differences in overall species composition from preharvest to postharvest years in the control or treatment units (CON: $A = -0.046$, $p =$

Table 2. Linear mixed effects model results for diversity indices and percent cover for all species and by habitat guilds.

		Treatment × time		OM		Ca		N		P	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
All species	N_0	4.58	<0.001	2.66	0.104	0.04	0.838	1.90	0.169	1.76	0.186
	N_1	3.29	<0.001	0.07	0.791	0.00	0.971	1.15	0.284	0.00	0.948
	N_2	2.55	0.004	0.06	0.802	0.53	0.468	0.14	0.705	0.01	0.920
	% cover	3.36	<0.001	0.48	0.490	0.01	0.906	1.00	0.319	1.93	0.166
Late-successional species	N_0	2.73	0.002	0.00	0.976	0.00	0.946	0.02	0.876	0.47	0.496
	N_1	2.02	0.024	0.59	0.442	0.87	0.351	0.53	0.466	2.47	0.117
	N_2	1.81	0.047	0.08	0.778	0.23	0.629	0.13	0.721	0.50	0.478
	% cover	3.08	<0.001	0.46	0.498	1.83	0.177	5.25	0.023	0.93	0.336
Intermediate species	N_0	1.12	0.348	4.55	0.034	0.67	0.414	8.52	0.004	0.43	0.514
	N_1	1.52	0.117	11.32	0.001	0.01	0.905	11.26	0.001	0.87	0.351
	N_2	1.31	0.217	5.31	0.022	0.18	0.676	4.46	0.036	0.12	0.734
	% cover	0.98	0.467	0.22	0.640	0.28	0.597	1.62	0.204	1.22	0.271
Early-successional species	N_0	3.77	<0.001	0.12	0.733	0.00	0.987	0.01	0.909	3.22	0.074
	N_1	3.45	<0.001	1.19	0.276	0.22	0.637	0.05	0.830	2.46	0.118
	N_2	2.87	0.001	0.72	0.397	0.00	0.958	0.20	0.652	4.59	0.033
	% cover	3.50	<0.001	0.43	0.511	1.35	0.247	1.44	0.231	2.58	0.110

Note: Diversity indices include species richness (N_0), the exponential Shannon–Weiner index (N_1), and the reciprocal Simpson index (N_2). Soil covariates are % organic matter (OM), Ca, total % N, and P.

1.00; GS: $A = 0.028$, $p = 0.232$; STS: $A = 0$, $p = 0.458$; SCE: $A = -0.049$, $p = 0.855$).

In total, 108 vascular understory species were recorded in the pretreatment monitoring plots. Twenty of these were absent from one or more units in the post-treatment surveys. Of the 11 species that were absent from treatment units, excluding controls, all were classified as late-successional species and 10 had biotic (animal-mediated) modes of dispersal (Table 4). All treatment and control units experienced some local species losses. Group selection units lost a greater mean percentage of species (14.1%) than single-tree selection (7.3%), SCE (4.8%), or control (4.5%) units; however, there were no significant differences in mean percent species loss among treatments ($p = 0.07$).

Effect of overstory structure and soil properties

The effects of treatment and soil properties on overall trends in diversity responses over time were assessed with the linear mixed effects model. The interaction of treatment × time had a strong effect on understory response variables for all species, early-successional species, and late-successional species, while the effects of the soil covariates were not significant (Table 2). Conversely, for the intermediate species guild, the treatment × time interaction was not significant for any of the diversity or abundance response variables, while percent OM and total percent N did show significant effects (OM: N_1 , $p = 0.001$; N_2 , $p = 0.002$; N: N_0 , $p = 0.004$; N_1 , $p = 0.001$; N_2 , $p = 0.036$).

The correlation matrices did not reveal any consistent relationships between preharvest to postharvest percent change in soil properties and understory response variables. At the plot level, soil variables were generally not associated with diversity and abundance responses, with a few exceptions. Change in percent OM was positively correlated with intermediate species richness ($r^2 = 0.174$, $p = 0.008$) and early-successional N_2 diversity ($r^2 = 0.205$, $p = 0.014$), and negatively correlated with early-successional N_1 diversity ($r^2 = 0.510$, $p = 0.009$). Negative correlations were found

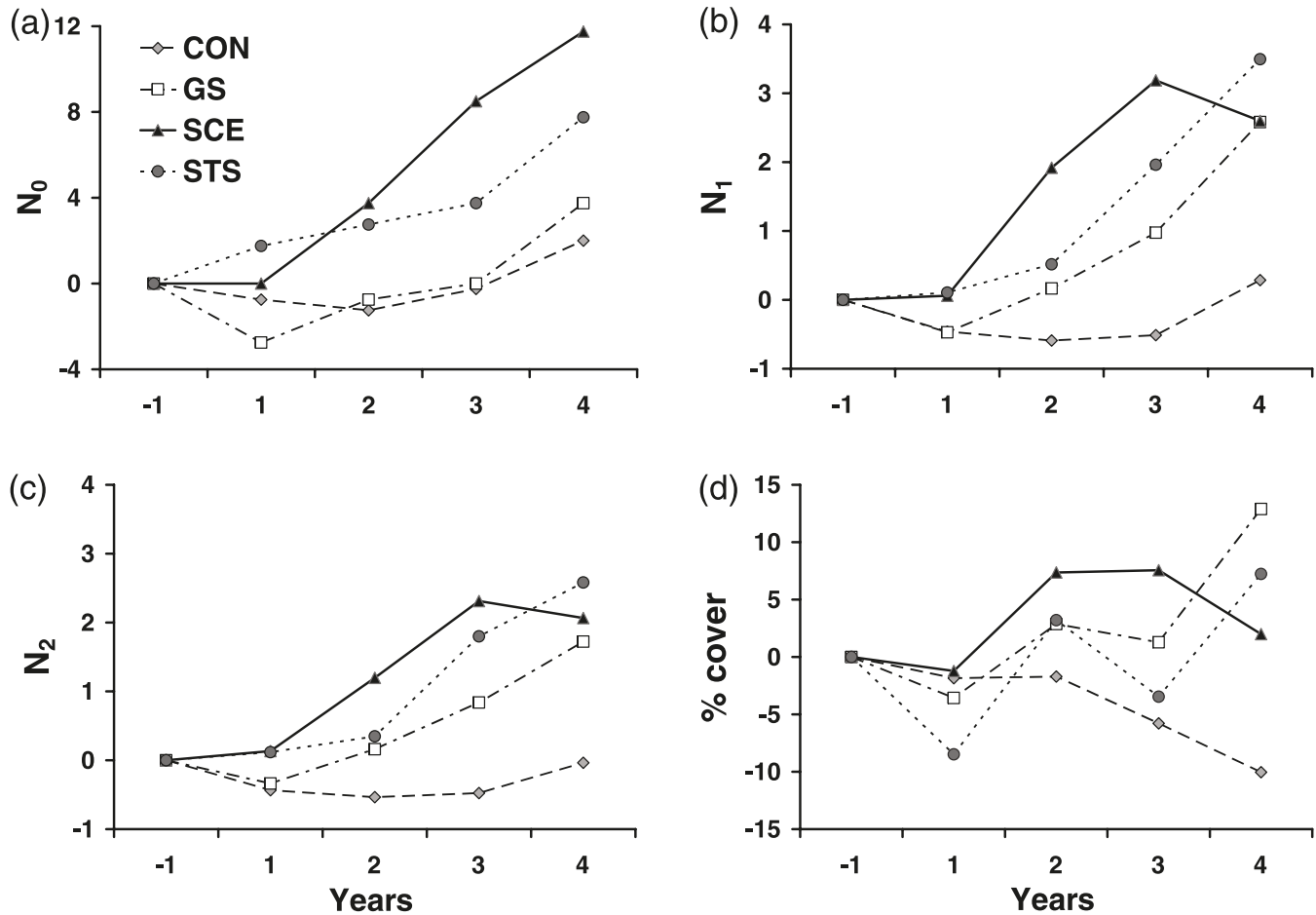
between change in total percent N and early-successional species richness ($r^2 = 0.180$, $p = 0.022$), and between change in Ca and late-successional N_2 diversity ($r^2 = 0.097$, $p = 0.022$). In contrast, overstory structure, represented by change in relative density, was negatively correlated with changes in all response variables at the plot level, excluding late successional species richness ($r^2 = 0.000$, $p = 0.976$). At the unit level, no preharvest to postharvest changes in soil nutrients were associated with the response variables. Change in relative density was also not correlated with response variables, with the exception of a negative association with changes in species diversity for all species (N_1 : $r^2 = 0.209$, $p = 0.043$; N_2 : $r^2 = 0.252$, $p = 0.024$).

Kendall rank correlation coefficients (τ) for the five selected overstory and soil variables on the NMS ordination axes before and after treatment are listed in Table 5. Before treatment, none of the variables were significantly correlated with axis 1, which accounted for most of the variation in species composition. Relative density ($\tau = 0.439$) and percent OM ($\tau = -0.336$) were strongly correlated with axis 2, and relative density was strongly correlated with axis 3 ($\tau = -0.435$) (Fig. 3a). After treatment, relative density ($\tau = 0.368$), percent OM ($\tau = -0.362$), and N ($\tau = -0.336$) were significantly correlated with axis 1, and all of the soil variables (OM, $\tau = 0.441$; Ca, $\tau = 0.520$; N, $\tau = 0.338$; P, $\tau = 0.494$) were significantly correlated with axis 2 (Table 5).

Effect of climate variability

Drought indices were not strongly correlated ($p = 0.09$ – 0.99) with standardized diversity response variables for all species or for the habitat guilds in the control units. In the treatment units, there were no significant correlations between the prior year drought index and diversity responses or between the current year drought index and diversity responses, with the exception of late-successional species richness. The current year drought index was positively correlated with late-successional species richness in units

Fig. 1. Change in treatment means of overall (a) species richness (N_0), (b) the exponential Shannon–Weiner index (N_1), (c) the reciprocal Simpson index (N_2), and (d) percent cover from 1 year preharvest to 4 years postharvest. Data are normalized to 1 year preharvest. Year 3 is used as postharvest in ANOVAs. Sample sizes are untreated controls (CON), $n = 8$ for all years; structural complexity enhancement (SCE), $n = 4$ for all years; group selection (GS) and single-tree selection (STS), $n = 2$ for year 4.



treated with group selection ($p = 0.012$, $r^2 = 0.747$), single-tree selection ($p = 0.018$, $r^2 = 0.703$), and SCE ($p = 0.024$, $r^2 = 0.602$).

Discussion

Understory plant responses to experimental treatments

General responses

The results of this study support our hypothesis that, in northern hardwood–conifer forests, understory plant species diversity can be maintained through uneven-aged forestry practices that retain or enhance stand structural complexity. Experimental units treated with group selection, single-tree selection, and structural complexity enhancement (SCE) all showed increases in diversity measures during the 4 years following harvest disturbance (Fig. 1). We observed a significant increase in diversity response variables in the SCE units from 1 year preharvest to 3 years postharvest, suggesting that enhancement of stand structural complexity may increase overall species diversity, at least during the initial postdisturbance recovery period. The lack of significant differences in postharvest species composition among treat-

ments and from preharvest to postharvest within treatments indicates that all three treatments were generally capable of preserving the integrity of the understory layer. In evaluating short-term responses, it can be difficult to discern the immediate effects of disturbance from the direct and indirect effects of residual overstory structure, which may become increasingly important over time (Halpern et al. 2005). Nevertheless, initial responses, such as the ability of certain species or guilds to persist through the disturbance, may be indicative of the intensity of silvicultural systems and could have important implications for biodiversity conservation.

Response of habitat guilds

Previous studies of postharvest forest understories have documented diversity increases immediately following silvicultural disturbance (Gilliam et al. 1995; Halpern and Spies 1995). These increases are often attributed to an influx of early-successional species as a result of changes in light and resource availability on the forest floor. Dominance of early-successional species is generally short-lived, but with periodic disturbance their presence may impact recovery of the understory (Scheller and Mladenoff 2002). We detected an increase in early-successional species diversity and abun-

Table 3. ANOVA results of changes in diversity and abundance response variables for all species and for habitat guilds from 1 year preharvest to 3 years postharvest.

		MS	F	p	Multiple comparisons ($\alpha = 0.05$)
All species	N_0	2233	3.75	0.032	SCE > CON
	N_1	7175	6.63	0.004	SCE > CON
	N_2	5506	5.32	0.010	SCE, STS > CON
	% cover	6775	3.82	0.031	SCE > CON
Late-successional species	N_0	1842	5.06	0.012	SCE > GS
	N_1	1868	5.4	0.009	SCE > CON
	N_2	2201	4.67	0.016	SCE > CON
	% cover	5940	9.27	0.001	SCE > CON, GS, STS
Intermediate species	N_0	842	0.37	0.774	
	N_1	61.3	1.23	0.333	
	N_2	267	1.18	0.350	
	% cover	3479	3.84	0.030	SCE > GS, STS
Early-successional species	N_0	14389	1.92	0.167	
	N_1	969	5.12	0.011	GS > CON
	N_2	5694	6.06	0.006	STS > CON
	% cover	58694	4.75	0.015	STS > CON

Note: Diversity response variables include species richness (N_0), the exponential Shannon–Weiner index (N_1), and the reciprocal Simpson index (N_2). Abundance is expressed as % cover. Treatment types include group selection (GS), single-tree selection (STS), structural complexity enhancement (SCE), and untreated controls (CON).

dance in all three treatments; however, only the conventional treatments increased significantly. This may be due to increased light availability in the conventional treatment units, which retained significantly less overstory structure (e.g., canopy closure and leaf area index) than SCE treatment units (Keeton 2006). There was no difference in soil compaction among treatments, yet higher levels of scarification in the conventional treatment units (W.S. Keeton, unpublished data) may also have contributed to postharvest increases in early-successional species. Additionally, greater retention and enhancement of late-successional structural characteristics in the SCE treatment units (Keeton 2006) may have reduced the amount of early-successional habitat available for postharvest colonization.

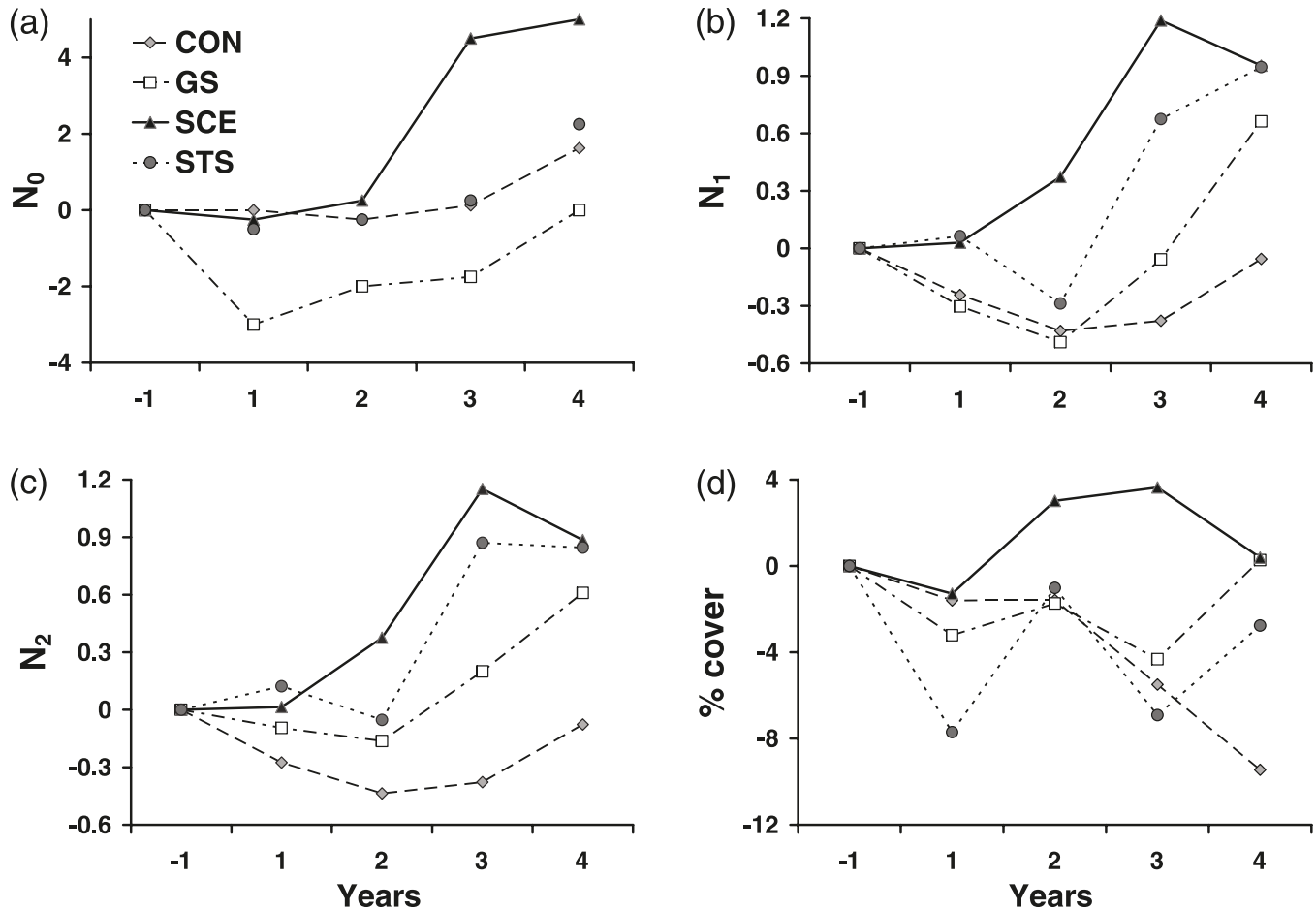
Understory diversity commonly increases with light availability (Brosfokske et al. 2001). The diversity increases in all three treatment types in this study support this relationship. However, SCE units experienced less overstory removal and showed greater increases in understory diversity than conventional treatment units, suggesting that heterogeneity may be more important for diversity response than total availability of light in the understory. The spatial heterogeneity of light created by small canopy gaps, as well as variability in other structural characteristics such as coarse woody debris, can enhance understory species richness and may be particularly important for late-successional species (Beatty 2003). A study by Scheller and Mladenoff (2002) on the spatial patterning of understory communities in northern hardwood forests showed that old-growth had smaller understory community patch sizes and greater patch heterogeneity than younger forests. Community patch size was correlated with both coarse woody debris and light heterogeneity (Scheller and Mladenoff 2002). The application of SCE in this study attempted to approximate the structural heterogeneity of old-growth forests (Runkle 2000; Keeton et al. 2007) by retaining large diameter trees, harvesting trees in a variable density pattern to create a range of small gap

sizes as well as undisturbed patches, creating pit and mound topography, and increasing levels of coarse woody debris (Keeton 2006). These changes may have increased microsite heterogeneity and reduced interspecific competition of understory plants after harvest, allowing a greater diversity of understory species to persist, particularly those that require late-successional habitat. Although overall changes in species composition were not significantly different among treatments, post-treatment increases in late-successional species richness, diversity, and cover were significantly higher in SCE treatment units than control units (Fig. 2). This trend could become more pronounced over longer time periods, as the primary influence on understory communities shifts from the initiating disturbance to the residual structure (Halpern et al. 2005). However, although late-successional richness continued to increase, the two measures of late-successional diversity decreased slightly from postharvest year 3 to year 4 in the SCE treatment units, suggesting that the initial increase may be unstable or transient. Alternatively, the slight decrease may represent interannual variability attributable to other environmental controls.

Local extirpations

Local extirpations of species that are sensitive to disturbance have been observed in intensively managed forests (Halpern et al. 2005; Ramovs and Roberts 2005). Species that reproduce clonally or have biotic dispersal mechanisms may be particularly sensitive to silvicultural disturbance (Meier et al. 1995; Mabry et al. 2000). In this study, the percentage of species lost in treatment units was not significantly different from the percentage lost in control units, although the identity and habitat preference of these species differed. Macdonald and Fenniak (2007) suggest that the threshold for a “lifeboating” effect of variable-retention harvesting must be between 20% and 75% retention of stand basal area. The levels of basal area retention in the treatments employed in this study were within or above this

Fig. 2. Change in treatment means of late-successional (a) species richness (N_0), (b) the exponential Shannon–Weiner index (N_1), (c) the reciprocal Simpson index (N_2), and (d) percent cover from 1 year preharvest to 4 years postharvest. Data are normalized to 1 year preharvest. Year 3 is used as postharvest in ANOVAs. Sample sizes are untreated controls (CON), $n = 8$ for all years; structural complexity enhancement (SCE), $n = 4$ for all years; group selection (GS) and single-tree selection (STS), $n = 4$ for years -1 through 3, $n = 2$ for year 4.



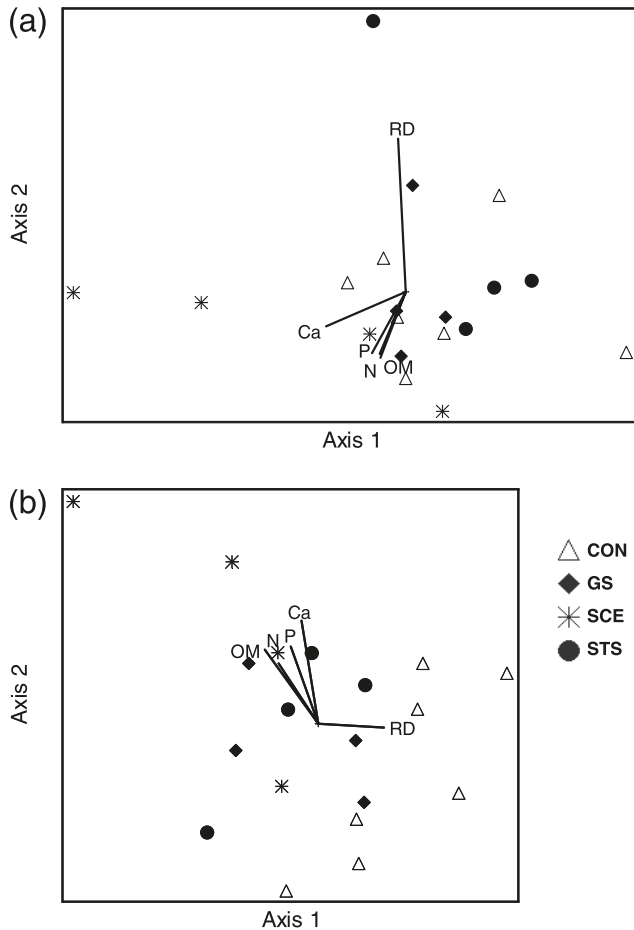
range (GS, STS: 64%–70% retained; SCE: 81% retained; see Keeton 2006). The greater mean percentage of species lost from conventional units (GS, 14.1%; STS, 7.3%) than SCE or control units (4.8% and 4.5%, respectively) indicates that the level of retention may influence the persistence of understory species. Reader (1987) also found that percent of understory species lost increased with cutting intensity in hardwood forests of southern Ontario. However, in contrast with our study, Reader (1987) demonstrated that size of the silvicultural openings did not influence loss of understory species. Based on our findings, the differences between group selection and single-tree selection units, while not significant, suggest that the spatial pattern of retention may also be important.

The majority of species locally extirpated from one or more experimental treatment units following harvest disturbance were late-successional, perennial herbs or shrubs with biotic modes of dispersal (Table 4). Three of these species, *Lonicera canadensis*, *Oxalis acetosella*, and *Trientalis borealis*, have been previously identified as sensitive to disturbance (Ruben et al. 1999; Wiegmann and Waller 2006). Many similar studies (e.g., Halpern and Spies 1995) have proposed that investigations of diversity responses alone

can obscure important compositional changes. Our study supports this viewpoint by demonstrating that although low-intensity, uneven-aged treatments can support late-successional understory plant diversity, populations of sensitive species may still be adversely impacted, even by timber harvests that retain very high levels of postharvest stand structure.

We recognize several uncertainties related to the observed loss of species from treatment units. The loss of species from control units suggests that irrespective of treatment, there are fluctuations in the presence and abundance of understory species. The mean preharvest abundances of impacted species were all very low (<9%), suggesting that species initially present in low densities are more likely to be affected by forest management practices. The absence of a particular species in postharvest years may be due to climatic variation, site conditions, plant life history characteristics, variable sampling techniques, or a combination of these factors. Species classified as locally extirpated may have been dormant or simply not detected in the 4 post-harvest sampling years. Others that persisted through the harvest disturbance may be gradually extirpated as a result of disturbance-related stress, inability to adapt to micro-

Fig. 3. Relationship of species composition to forest structure and soil variables using nonmetric multidimensional scaling: (a) pretreatment (% of variation in species data: axis 1 = 44.8; axis 2 = 33.2) and (b) post-treatment (% of variation in species data: axis 1 = 38.2; axis 2 = 25.1). Site variables include relative density (RD), % OM, Ca, total % N, and P. Treatment types include untreated controls (CON), group selection (GS), structural complexity enhancement (SCE), and single-tree selection (STS).



climate changes, and increased competition with ruderal species (Meier et al. 1995; Halpern et al. 2005). Finally, as recolonization from clonal expansion and seed dispersal proceeds at the sites, continued monitoring may indicate that local extirpations are short-term in nature.

Influence of overstory structure and soil properties

Composition and diversity of forest understories are known to be related to local environmental and edaphic factors and can vary at different spatial scales (Brosfokske et al. 2001). For instance, soil nutrient availability has been shown to influence patterns of understory vegetation (Kolb and Diekmann 2004; Fraterrigo et al. 2006). Plant distributions are affected by soil cation concentrations, particularly Ca (Gilliam and Turrill 1993; Graves et al. 2006). The soil characteristics evaluated in this study appeared to have some influence on understory responses, yet the relationships we detected were highly variable and did not reveal consistent trends. A negative relationship between Ca and late-successional diversity (N_2) was detected at a fine spatial

scale (0.1 ha or plot-level); however, there were no correlations between Ca and other response variables at the fine scale, or between Ca and response variables at a coarser spatial scale (2 ha or unit-level).

Total percent N and percent OM were also related to certain diversity responses for intermediate and early-successional species at the fine scale; however, the directionality of these associations was inconsistent, and they were not observed at the coarser scale. Previous studies have also documented negative relationships between nutrient availability and plant species diversity at fine scales (Brosfokske et al. 2001; Gilliam 2002). Tilman (1993) hypothesized that increased productivity as a result of greater nutrient availability suppressed diversity in grasslands by reducing germination sites available to colonizing species, an idea that may also be applicable to forested systems. In this study, the negative association between certain soil nutrients and plant species diversity may be attributed to effects of the silvicultural disturbance. Forest management activities often alter soil properties, although the intensity and duration of these changes vary with the soil and forest type, as well as the type of management employed (Grigal 2000). Depending on the intensity of harvest, soil nutrient availability can increase as a result of high OM inputs or decrease because of biomass removal and leaching (Johnson et al. 1997; Elliott and Knoepp 2005).

While forest management may lead to a short-term decline in soil nutrients, elimination of overstory competition may temporarily increase the availability of these nutrients (and light) to understory vegetation (Roberts 2004), leading to increased productivity and diversity. Calcium is one of the elements most susceptible to depletion following timber harvesting because of its high concentration in tree wood and bark (Schaberg et al. 2001). In this study, we observed decreases in soil Ca in both treated and control units, indicating that soil Ca depletion, a widespread phenomenon in northeastern forests linked to acid deposition (Federer et al. 1989; Likens et al. 1998), is occurring in the study areas irrespective of timber harvesting. Increases in plant species diversity were limited to treated areas, suggesting that the negative association between Ca and late-successional plant species diversity involves some interaction with treatment. Similar to our study, Gilliam et al. (2002) found a negative correlation between Ca and plant species diversity, but only in treated stands.

The relative strength of the influence of overstory structure versus soil properties on understory vegetation is unclear. Studies have demonstrated that both timber harvest and soil properties strongly influence the understory layer (Elliott and Knoepp 2005; Macdonald and Fenniak 2007). In some instances, soil properties exert a greater control on forest understories than stand structure (Gilliam 2002), while in others, the influence of overstory characteristics can override local site factors (Brosfokske et al. 2001). We observed strong relationships between preharvest to postharvest change in relative density and all response variables at the fine scale, and with change in both measures of diversity for all species at the coarser scale, indicating that changes in overstory structure were strongly related to understory response. Results of the linear mixed effects model support this conclusion; over time, understory response variables for

Table 4. Understory species recorded preharvest and absent postharvest.

Scientific name	Treatment				Growth form	Fruit type	Dispersal	Habitat preference
	GS	SCE	STS	CON				
<i>Actaea alba</i>		×			Perennial herb	Berry	Biotic	Late-successional
<i>Adiantum pedatum</i>				×	Fern	Spore	Abiotic	Late-successional
<i>Aralia nudicaulis</i>	×		×	×	Perennial herb	Drupe	Biotic	Late-successional
<i>Arisaema triphyllum</i>	×		×		Perennial herb	Berry	Biotic	Late-successional
<i>Asarum canadense</i>		×		×	Perennial herb	Capsule	Biotic	Late-successional
<i>Coptis trifolia</i>	×				Perennial herb	Follicle	Biotic	Late-successional
<i>Eupatorium rugosum</i>				×	Perennial herb	Achene	Abiotic	Intermediate
<i>Lonicera canadensis</i>	×		×		Shrub	Berry	Biotic	Late-successional
<i>Medeola virginiana</i>	×				Perennial herb	Berry	Biotic	Late-successional
<i>Osmunda claytoniana</i>	×		×		Fern	Spore	Abiotic	Late-successional
<i>Oxalis acetosella</i>		×			Perennial herb	Capsule	Biotic	Late-successional
<i>Panax trifolium</i>				×	Perennial herb	Drupe	Biotic	Late-successional
<i>Polygonatum pubescens</i>		×			Perennial herb	Berry	Biotic	Late-successional
<i>Polygonum cilinode</i>				×	Perennial herb	Achene	Biotic	Intermediate
<i>Pyrola elliptica</i>				×	Perennial herb	Capsule	Abiotic	Late-successional
<i>Sambucus racemosa</i>	×			×	Shrub	Berry	Biotic	Early-successional
<i>Smilacina racemosa</i>			×		Perennial herb	Berry	Biotic	Late-successional
<i>Trientalis borealis</i>	×				Perennial herb	Capsule	Biotic	Late-successional
<i>Trillium erectum</i>	×				Perennial herb	Berry	Biotic	Late-successional
<i>Viburnum alnifolium</i>		×			Shrub	Drupe	Biotic	Late-successional

Note: × indicates the species was absent from two or more units of this treatment type for all 4 postharvest years. Treatment types include group selection (GS), single-tree selection (STS), structural complexity enhancement (SCE), and untreated controls (CON). Life history characteristics were determined from Gleason and Cronquist (1991), Handel et al. (1981), and Mabry et al. (2000).

Table 5. Kendall's tau correlations (τ) between the ordination axes and site variables.

Site variable	Preharvest			Postharvest		
	Axis 1 (44.8%)	Axis 2 (33.2%)	Axis 3 (12.0%)	Axis 1 (38.2%)	Axis 2 (25.1%)	Axis 3 (12.6%)
RD	-0.099	0.439	-0.345	0.368	-0.135	-0.170
OM	-0.072	-0.336	0.072	-0.362	0.441	0.230
Ca	-0.230	-0.257	-0.112	-0.204	0.520	0.178
N	-0.086	-0.323	0.086	-0.336	0.388	0.283
P	-0.165	-0.323	-0.072	-0.283	0.494	0.151

Note: Site variables include relative density (RD), % organic matter (OM), Ca, total % N, and P. The preharvest ordination included data from 1 year before harvest, and the postharvest ordination contained data from 3 years postharvest. Bold values indicate a significant correlation ($p < 0.05$).

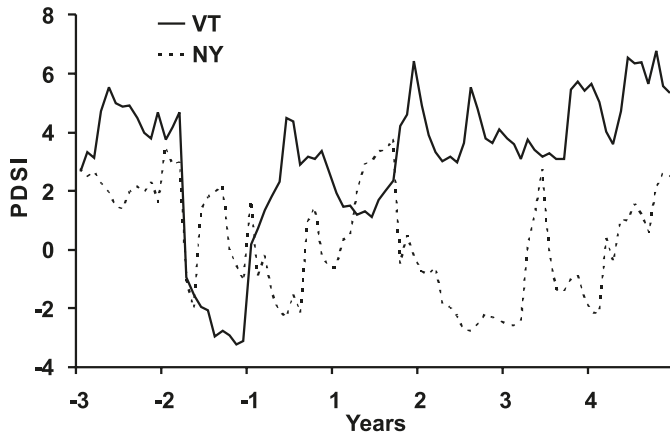
all species, early-successional, and late-successional species were strongly affected by treatment and less influenced by soil properties (Table 2). Model results also suggest that the influence of overstory structure is less important to intermediate species, which can occupy both open and closed canopy forests; for these species, soil covariates may be more important. The ordination indicates that both overstory and soil characteristics are useful in explaining some of the variation in species composition, although much of the variation is left unexplained. As in similar studies (e.g., Macdonald and Fenniak 2007), it is likely that plant species composition was also influenced by unmeasured factors, such as elevation and microtopography, as well as historical patterns of disturbance and recovery.

Effect of drought stress

Moisture availability is often cited as a significant factor influencing vegetation dynamics in forest understories (Hutchinson et al. 1999; Kolb and Diekmann 2004). In this study, periods of moderate to severe drought occurred dur-

ing the preharvest years at the sites in Vermont and in both preharvest and postharvest years at the sites in New York (Fig. 4). However, there were no significant relationships between the drought indices and understory response variables for all species or for the habitat guilds in the control units, indicating that independent of changes in overstory structure, drought stress did not have a strong influence on understory response. The relationships between late-successional species richness and the current year drought index observed in the treatment units suggest that by exposing the understory to higher light levels and desiccation, silvicultural disturbance may exacerbate the effects of drought stress on late-successional species. The relationships we observed between moisture stress and declines in late-successional species richness were stronger in conventional treatments that experienced a greater reduction in canopy closure compared with the SCE units. This indicates that these effects may vary with the size and spatial clustering of canopy openings. Uneven-aged practices like SCE that retain high levels of canopy closure and vertical canopy

Fig. 4. Fluctuations in the Palmer drought severity index (PDSI) in the Vermont (VT) and New York (NY) study areas from 3 years preharvest to 4 years postharvest. The PDSI value indicates periods of moisture excess (greater than 0.5) or deficiency (less than -0.5).



complexity (Keeton 2006) may expose understory plant communities to less postharvest moisture stress and associated changes in plant community composition.

Recovery from preharvest drought conditions is one possible explanation for the large postharvest increases in diversity and abundance in the SCE treatment units. However, to return to predrought levels, species richness would need to increase by 18.5%, and diversity would need to increase by 15.7% (N_1) and 10.2% (N_2). The increases we observed, 44.9% for richness, 42.6% for N_1 diversity, and 47.5% for N_2 diversity, were two to four times this level. This suggests that, while recovery from drought may have been partially responsible for the increases in understory response variables, the majority of the changes can be attributed to treatment effects. This conclusion is supported by the absence of significant relationships between drought indices and understory response variables in the control units.

Management implications

Sustainable forest management practices aim to maintain biodiversity and ecosystem functioning while providing opportunities for timber revenue generation. Experimental research at the scale of individual forest stands provides an opportunity to assess the contribution of these practices to broader, landscape-scale conservation efforts. Assessments of how plant species respond to silvicultural treatments increase our understanding of the aggregate representation of different elements of plant biodiversity (e.g., early vs. late successional) provided by the mix of treatments and stand conditions present at larger spatial scales. The results of our study will be useful in this context.

Our results generally support previous studies that demonstrate the capacity for uneven-aged silvicultural systems to maintain understory plant diversity in northern hardwood-conifer forests (e.g., Scheller and Mladenoff 2002; Kern et al. 2006). The treatments in this study were modified to retain or enhance postharvest structure, and it appears that even subtle differences in type, magnitude, and spatial configuration of the silvicultural prescription can result in varying understory vegetation responses. Techniques that enhance stand structural complexity may increase microsite

variability on the forest floor and, as a result, sustain higher levels of understory plant diversity. By retaining biological legacies (see Franklin et al. 2002) in the form of undisturbed patches of forest canopy and forest floor, these techniques may preserve late-successional species and those that are slow to recolonize formerly occupied sites.

Despite overall maintenance of diversity under all of the low impact treatments investigated in this study, including conventional selection systems, we did observe local extirpations of certain plant species, predominantly those with an affinity for late-successional habitat, within experimental units of all treatment types, including the controls. However, during the 4-year post-treatment study period, group selection units lost a greater percentage of species (14.1%) than single-tree selection (7.3%), SCE (4.8%), or control (4.5%) units. SCE involved less overstory removal than the conventional treatments; the only difference between the group and single-tree selection prescriptions was dispersed versus aggregated harvesting (see Keeton 2006). These results suggest that both the magnitude and spatial pattern of structural retention are important for retaining understory plant species through a harvest disturbance. This finding emphasizes the need to better predict compositional changes in understory plant communities following different types and intensities of silvicultural disturbance.

Where risks to plant populations, such as local extirpations of rare, threatened, or sensitive species, are deemed unacceptable, efforts can be made to minimize deleterious impacts on soils and plant communities. Choice of harvesting machinery as well as skidding and yarding practices are important considerations in this respect (Vossbrink and Horn 2004). Patch retention standards, no-entry zones around selected locations with sensitive plants, greater postharvest structural retention (i.e., reduced percent basal area removals), and logging during the dormant season are possible alternatives for minimizing impact (Berger et al. 2004). Other researchers have recommended that, in addition to best management practices for sustainable forestry, reserves may be necessary to conserve all elements of biodiversity, including sensitive plant species (Poiani et al. 2000).

Although we did not observe many strong relationships between soil properties and understory responses in this study, other studies have documented soil-vegetation relationships (Hutchinson et al. 1999; Graves et al. 2006). Forest management practices can indirectly affect understory plant communities by influencing the availability of soil nutrients (Gilliam 2002; Fraterrigo et al. 2006). For instance, intensive silvicultural disturbance can lead to loss of soil nutrients through biomass removal and leaching (Adams et al. 2000; Grigal 2000). Thus, management approaches similar to those employed in this study that involve increased retention of tree biomass, minimal soil disturbance, and even augmentation of coarse woody debris inputs may have important implications for nutrient cycling and site productivity.

Conclusions

In this study, changes in understory plant species diversity and abundance following timber harvest were primarily driven by changes in stand structure, rather than changes in soil properties or moisture availability. Species composition

was influenced by both overstory and soil characteristics and did not differ significantly among treatments 3 years after disturbance. Our results suggest that while conventional, uneven-aged treatments are capable of maintaining understory plant diversity, variations that retain or enhance structural complexity may be more effective in preserving late-successional species. Over time, increased microsite heterogeneity as a result of these techniques may also increase understory plant diversity.

This analysis reflects understory response over 4 years postharvest, and interpretations are therefore limited in scope to the initial recovery period. Continued monitoring of understory vegetation, particularly sensitive species, will help differentiate initial disturbance effects from the effects of residual structure, contributing to a more complete understanding of understory vegetation dynamics following modified uneven-aged forestry practices in northern hardwood-conifer forests.

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