



Spatial pattern in herb diversity and abundance of second growth mixed deciduous-evergreen forest of southern New England, USA

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ABSTRACT

This study was designed to answer questions about the patterns of understory diversity in managed forests of southern New England, and the factors that appear associated with those patterns. At the landscape-level, we used plot data to answer questions regarding the spatial distribution of forest understory plant species. Data from a combination of fixed area (understory vegetation) and variable radius (overstory trees) plot methods are combined with site variables for the analysis. Univariate and multivariate statistical methods are used to test for understory diversity relationships with overstory cover types and topography separately, and in combination. Analyses also test for relationships between specific understory species and cover types. In general the understory flora is dominated by four common clonal species that occur across the range of forest cover types: wild sarsaparilla (*Aralia nudicaulis* L.), Canada mayflower (*Maianthemum canadense* Desf.), star flower (*Trientalis borealis* Raf.), and partridgeberry (*Mitchella repens* L.). Results also show that over story composition and structure can be used to assess understory species richness. Species richness follows a general trend among cover types of: hardwood \geq regenerating forest, hardwood–pine, and pine \geq mixed \geq hardwood–hemlock > hemlock. Eastern hemlock (*Tsuga canadensis* L. Carriere) and mountain laurel (*Kalmia latifolia* L.) (which decreased in dominance from ridge to valley) both showed negative trends with understory species richness. Topographic position also appears associated with understory floristic patterns (particularly for the hardwood cover type), both in terms of species richness and compositional diversity which both increased from ridge, to midslope, to valley. However, overstory composition (cover type) appears to have a higher order influence on vegetation and mediates the role of topography. The results from this study provide foresters with a better understanding for maintaining floristic diversity and composition of the understory in managed forests.

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1. Introduction

Maintaining diversity in native ecosystems is now recognized as a critical factor for sustainable management for goods and services desired by society (UNEP, 1992; Brooks et al., 2006). Plants are a major component of diversity that is essential for maintaining and regulating ecosystem function (Bormann and Likens, 1979). The largest component of plant diversity in temperate forests is that found in the understory (Whigham, 2004). In temperate forests plant diversity and abundance in the understory plays an important role in contributing to leaf litter and mulch, facilitating decomposition, and in nutrient conservation (Bormann and Likens, 1979). Plants in the understory provide soil surface protection from erosive forces of precipitation and lethal temperatures from

radiation (Bormann and Likens, 1979). The understory also takes up nutrients from throughfall and decomposition (Peterson and Rolfe, 1982; Bormann and Likens, 1979; Roberts and Gilliam, 1995).

Forest managers are therefore increasingly concerned with maintaining understory plant diversity while developing and providing timber resources. Identifying indicators of understory plant diversity based on landform and forest cover types could provide managers with an efficient tool that can be combined with standard inventory methods. Such a tool could be used with stand-level inventories for mapping areas of high and low understory plant diversity and of particular species composition. Such stand scale maps can then be used in planning silvicultural operations that are compatible with protecting plant understory diversity and composition. Forest understory composition in central New England was shown to be influenced by both stand age and stand type (Whitney and Foster, 1988), while stand structure was an important factor in northern European deciduous forests

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(Thomsen et al., 2005). For eastern US forests, the relationships between slope position and soil moisture gradients (Huebner et al., 1995) and C/N ratios (Small and McCarthy, 2005) have been shown to affect understory plant community composition. The influences of microtopography (Bratton, 1976; Beatty, 1984) and site characteristics such as litter type and depth and coarse woody debris are also considered important factors in understory plant diversity (Brososke et al., 2001).

Stand-level variables (e.g. overstory basal area, density and species composition, topographic position) are considered to be the appropriate focus of this study, as the stand is the management unit most often identified when implementing silvicultural prescriptions (Roberts and Gilliam, 1995; Smith et al., 1997). However, very little work to date has looked at stand-level floristic associations between forest overstory and understory vegetation for southern New England mixed hardwood-coniferous forests. This study will identify forest stand variables that can be used to assess understory diversity for southern New England forests.

The objectives of this study are to: (1) identify differences in understory species richness and composition that are associated with overstory composition and basal area, and (2) identify differences in understory species composition that are associated with the combination of overstory composition and topographic variation.

What this study does not do is compare floristic diversity in a managed forest with diversity in unmanaged forests where little to no human impacts have occurred. There is also some limitation to the study, as it was originally designed to monitor long-term floristic changes, rather than to test any specific hypothesis. However, we believe the high number of plots sampled and the sparse amount of information of this type available for southern New England forests overcomes any limitations in original design.

2. Site description

This study was conducted at the Yale-Myers Forest in Windham and Tolland Counties, Connecticut, USA (41°55'N 72°05'W). Yale-Myers Forest covers 3213 hectares in the towns of Ashford, Eastford, Westford, and Union, and is owned by Yale University and managed by The Yale School of Forestry and Environmental Studies for timber production, research, and educational activities.

Growing season for the region averages about 163 days a year, with an annual average daily temperature of 8.7 °C, and about 1090 mm of precipitation relatively evenly distributed throughout the year (USDA, 1981). The coldest month of the year is January, with mean daily high of 2 °C and mean daily low of -11 °C. July is the warmest month, with mean daily high of 28 °C and mean daily low of 14 °C (USDA, 1981).

The Yale-Myers Forest is located in the Eastern Highlands Region of Connecticut, with a landscape and surficial geology that is defined by Pleistocene glaciation (MacFaden and Ruth, 1972). Elevation at the forest ranges from 170 to 320 m with a rugged topography of broad, flat-topped ridges with many rock outcrops and narrow, often swampy valley bottoms (Meyer and Plusnin, 1945). The dominant soil types are Gloucester fine sandy loam, Brookfield fine sandy loam, Hinckley fine sandy loam, and Charlton. These soils are Typic and Lythic Dystrichrepts of till-derived material over granite-gneiss and schist, with bedrock lying at an average of 1–6 m, and have relatively high potential for forest production (Meyer and Plusnin, 1945; USDA, 1981).

Yale-Myers Forest falls within the Central Hardwoods–Hemlock–White Pine zone as described by Westveld et al. (1956). Dominant tree species include red oak (*Quercus rubra* L.), black oak (*Quercus velutina* Lam.), eastern hemlock (*Tsuga canadensis* (L.)

Carriere), black birch (*Betula lenta* L.), sugar maple (*Acer saccharum* Marsh), red maple (*Acer rubrum* L.), eastern white pine (*Pinus strobes* L.), white ash (*Fraxinus americana* L.) and pignut hickory (*Carya glabra* (Mill.) Sweet). The forest has a relatively rich understory flora composed of many of the shrubs, herbs, and ferns typical of central and northern Connecticut. Mountain laurel (*Kalmia latifolia* L.) is the dominant shrub. Hay-scented fern (*Dennstaedtia punctilobula* (Michx.) T. Moore) and New York fern (*Thelypteris noveboracensis* (L.) Nieuwl. are the dominant ferns. Common upland forest herbs include Canada mayflower (*Maianthemum canadense* Desf.), wild sarsaparilla (*Aralia nudicaulis* L.), star flower (*Trientalis borealis* Raf.), partridgeberry (*Mitchella repens* L.), violets (*Viola* spp.), wintergreen (*Gaultheria procumbens* L.), and sessile-leaf bellwort (*Uvularia sessilifolia* L.).

Approximately 70% of Yale-Myers Forest is under active timber management, with the remaining area held as early or late successional reserves, forested wetlands, roads, or other non-timber production classification. Typical for central and southern New England, the majority of the land was cleared for agriculture or grazing between the mid-18th and mid-19th centuries (Smith, 1989; Foster, 1992). After land abandonment at the end of the 19th century, natural reforestation began with old-field white pine stands that later gave way to the current mixed-hardwoods–hemlock forest type. Most current stands originated at the turn of the 20th century, or after the hurricane of 1938 (Smith, 1989). Crown thinning and shelterwood systems are the most common treatments with an emphasis on the promotion of natural advance regeneration.

3. Materials and methods

Plot data was used to analyze floristic patterns at the Yale-Myers Forest. All understory and overstory data was collected between June 28, 2004 and August 14, 2004. All topographic data was collected during the summer of 2003.

Plots used for this study were originally mapped at the Yale-Myers Forest in 1978. Thirty transects were randomly located at the forest, with 10 circular, 4-m radius fixed area (50 m²) plots systematically spaced at 20 m along each transect. In 1996, 10 additional transects were added following the same methods, for a total of 40 transects containing 400 plots, 386 of which were used for this study. Transects fall within a variety of forest cover types, with the majority being contained in areas zoned as production forest by current land-use designation. The locations of all plots have been recorded using global positioning satellites and are stored in a permanent database with The Yale School Forest records. Data from the original transects have been used for several other studies including seedling regeneration patterns (Kittredge and Ashton, 1990) and deer browse impacts (Kittredge and Ashton, 1995).

At each 50 m² fixed plot, data was collected on all vascular understory plants including herbs, ferns and woody vines and shrubs. Plots were divided into four equal quadrants divided by cardinal direction, and each understory species present within a plot was tallied according to the number of quadrants it occurred in, regardless of the number of individuals present. Three common, native species considered to be strong competitors for understory growing space, mountain laurel, hay-scented fern and Pennsylvania sedge (*Carex pensylvanica* Lam.) were recorded by ocular estimation of percent cover of total plot area.

Using the center point of each fixed area plot, point sampling was used to tally overstory basal area for each plot (Avery and Burkhart, 1993). Overstory trees ≥ 5 cm DBH were tallied by species using a 2.5 BAF metric prism. Occurrences and basal area for all snags ≥ 10 cm DBH were recorded following the same method.

Topographic data was collected for each plot including slope position and slope aspect. Slope position and aspect was assessed in the field and verified using ArcMap v.9.0 (ESRI, Redlands, CA).

4. Data analysis

4.1. Analyses of species richness and within plot frequency

Plots were grouped into forest cover types according to the proportions of total basal area consisting of hardwood species (broad-leafed angiosperms), pine species (eastern white pine and red pine (*Pinus resinosa* Aiton.), and eastern hemlock. Groupings were then tested through cluster analysis using Ward's linkage method and Euclidean distance in PC-ORD v.4.1 (McCune and Meffords, 1999).

Species diversity was calculated as mean richness per 50 m² plot and total richness by forest cover type (Palmer, 1990). The quadrant system for tallying species occurrences provided limited options for calculating species abundances. A within plot frequency calculation was made to assess the mean species cover for each plot, and is considered an indirect measure of a plot's potential to support various levels of understory plant abundances. Within plot frequency was calculated as:

$$\frac{(\sum \text{each species quadrant totals})}{(\text{total plot richness})}$$

The greatest attainable within plot frequency value would be four, meaning that all species within the plot occurred in all quadrants. Limitations on species abundance data also negated the utility of using traditional diversity indices such as Shannon's Diversity or Simpson's Evenness which combine presence-absence data with abundances (Magurran, 1988). These indices obtain their robustness from species abundances that can range from 1 to ∞ , making the quadrant method (range 1–4) highly limiting for comparisons. In fact, a regression of richness versus Shannon's index for the data results in an extremely high correlation ($r^2 = 0.89$, $p < 0.0001$), indicating that little would be gained by using the more complex index instead of species richness.

Topographic data was grouped into two broad categories of slope position, and aspect. Slope position was used to group plots into: (i) ridge sites – xeric, shallow to bedrock soils; (ii) midslope sites – thicker, more mesic and productive soils; and (iii) valleys – mesic to hydric soil moisture conditions. Slope positions were delineated by plot position on a continuous elevation gradient approximately divided by upper 25% (ridge), central 50% (mid-slope), and lower 25% (valley).

Slope aspect was grouped into three categories based on the recognition that in the northern hemisphere slopes with north and northeastern aspects support higher forest productivity (Beers et al., 1966; Small and McCarthy, 2005). These three groups are: NE (northeast) 345.5°–104.5°, SW (southwest) 165.5°–284.5°, and INT (intermediate) 105°–165° and 285°–345°. Slope aspect was also calculated as a continuous variable following the Beers et al. (1966) method which gives the greatest weight to north and northeast slopes and scales evenly in both directions:

$$A' = \cos(A_{\max} - A) + 1$$

where A_{\max} is 45° and A is slope measured in azimuth degrees clockwise from north.

One-way analysis of variance (PROC GLM) in SAS v.9.1 (SAS Institute, Cary, NC) was used to test for significant relationships between topography and cover type variables and understory species richness and within plot frequency. Variables that were determined to be significant at the $p < 0.05$ level were then entered into a two-way ANOVA (PROC GLM) with forest cover type as the main effect to determine importance of topography within

forest cover types. Pair wise comparisons of all means were made using the Tukey–Kramer adjusted multiple comparison test with significance tested at the $p < 0.05$ level (SAS v.9.1).

Stepwise multiple regression analysis (SAS v.9.1) was used to analyze understory richness and within plot frequency relationships with forest structure variables. Analysis was run on all plots combined testing the following forest structure variables: percent cover of mountain laurel, hay-scented fern, and Pennsylvania sedge basal area of pine, hardwood and hemlock, percent total transmitted light, and Beers aspect. A second stepwise multiple regression analysis was run independently on the hardwood cover type to test for the effects of the above variables plus basal area of individual overstory species. For all models, variables were included if significant at the $p < 0.05$ level.

4.2. Analyses of compositional diversity

Mantel tests in PC-ORD v.4.1 were used to test for associations between plot variables and species composition. The Mantel test tests the significance of correlation between two distance matrices originating from the same sample units and produces the standardized mantel statistic, r , and is equivalent to Pearson's correlation coefficient (Sklenar and Jorgensen, 1999; McCune and Grace, 2002). Sorenson's (Bray–Curtis) distance measure was used to produce distance matrices and significance was tested using the Monte Carlo randomization test option. As the plot variables tested are assumed to vary in both the degree and type of influence exerted on species composition, separate tests were run comparing the understory presence-absence matrices to corresponding plot variable matrices, and independent r statistics are reported (Burgman, 1987; Brososke et al., 2001). Mantel tests were run for all plots combined and for the hardwood cover type.

Species importance values were calculated to determine associations between common understory species and forest cover types. Importance values are reported as an index combining presence-absence and frequency of occurrence data for each species, and were calculated as:

$$\frac{(\# \text{ of plots in which species occurs} / \text{total} \# \text{ of plots for cover type}) + (\# \text{ of quadrants in which species occurs} / \text{total} \# \text{ of quadrants for cover type})}{2} \times 100$$

Understory species were considered common and importance values reported if they attained a value of ≥ 10 in at least one cover type. Due to the fact that the number of plots differs for each forest cover type, understory species importance values are relative only within individual cover types, and should not be compared across cover types.

Topographic species associations were also determined by slope position within the hardwood cover type. Mean basal area, percent cover of mountain laurel, plot-level richness and total richness were calculated for each position. Indicator species analysis (Dufrene and Legendre, 1997) was used in PC-ORD v.4.1 to identify understory species associations with slope positions. Significance was determined using the Monte Carlo test based on 1000 randomizations (McCune and Grace, 2002).

5. Results

5.1. Forest cover types

Based on percent basal area of hardwood species, eastern hemlock and pine species, six forest cover types were identified

Table 1
Composition of forest cover types.

	Cover type							
	All	Hardwood	Hemlock	Hardwood–hemlock	Pine	Hardwood–pine	Mixed	Regenerating ^a
Total Plot #	386	142	49	86	11	45	41	12
BA (m ² /ha)	24.0 (0.6)	19.9 (0.7)	32.5 (1.8)	27.8 (1.0)	31.0 (3.4)	21.1 (1.4)	28.0 (1.4)	0
% BA of HW/P/HM ^b	69/11/20	97/2/1	38/2/60	73/1/26	14/84/2	67/33/0	54/30/16	0/0/0
Snag BA (m ² /ha)	1.0 (0.1)	0.9 (0.1)	1.5 (0.3)	0.8 (0.2)	1.7 (1.7)	0.7 (0.2)	1.6 (0.3)	0
% Basal area by species								
<i>Acer rubrum</i>	12.7	18.7	4.9	12.1	0	16.0	10.8	0
<i>Acer saccharum</i>	6.7	13.1	1.3	7.7	0	2.4	2.0	0
<i>Betula alleghaniensis</i>	1.8	1.6	2.0	2.5	<1.0	<1.0	2.0	0
<i>Betula lenta</i>	6.8	8.3	5.6	6.7	5.4	7.8	4.2	0
<i>Betula papyrifera</i>	1.7	2.3	2.0	1.8	0	<1.0	1.0	0
<i>Carya</i> spp. ^c	3.1	6.4	<1.0	1.8	<1.0	3.2	1.6	0
<i>Fraxinus americana</i>	4.6	9.9	<1.0	3.2	<1.0	3.2	2.0	0
<i>Pinus strobus</i>	11.0	<1.0	1.9	1.2	70.3	32.5	30.1	0
<i>Prunus serotina</i>	<1.0	1.6	<1.0	<1.0	1.4	1.2	<1.0	0
<i>Quercus alba</i>	5.2	5.0	5.2	3.5	<1.0	7.8	8.6	0
<i>Quercus rubra</i> ^d	24.7	29.3	14.3	31.9	4.1	22.6	20.1	0
<i>Tsuga canadensis</i>	19.9	1.7	60.4	26.3	2.0	0	16.0	0

Values in parenthesis following means indicate ± 1 standard error.

^a No basal area at time of survey.

^b Hardwood/Pine/Hemlock.

^c Includes *Carya glabra*, *C. ovata*, *C. cordiformis*.

^d Includes *Quercus rubra* with some *Q. velutina*.

and grouped: hardwood, hemlock, hardwood–hemlock, pine, hardwood–pine and mixed (Table 1). An additional group, regenerating, consists of plots with no basal area at time of survey. After plots were assigned to one of each of the groups, cluster analysis verified the consistency of groupings with only 4% of plots falling into mixed clusters.

Mean basal area ranged from 19.9 m²/ha (hardwood) to 32.5 m²/ha (eastern hemlock), with all plots combined averaging 24.0 m²/ha. Within the hardwood cover type, species of the red oak group had the highest percent basal area, followed by red maple, sugar maple, black birch, and white ash. The highest plot percentages of hemlock basal area in the hemlock cover type plots was 78%, while the highest percent pine basal area in the pine cover type plots was 98%. The mixed cover type group contained the most even distribution of all the three major basal area groups.

5.2. Understory species richness and within plot frequencies

5.2.1. Species richness estimates by forest cover types

Richness estimates show that the sampling intensity captured between 66% and 85% of the estimated richness for the cover types (Table 2). The regenerating cover type shows the lowest percent of estimated richness captured. The hardwood cover type shows the highest percent richness captured, other than all plots combined.

Table 2
Understory sampled richness and estimated richness for cover types.

Cover type	# of plots ^a	Sampled richness	Estimated richness ^b	Sampled percent of estimated ^c
All plots combined	386	144	169	85%
Hardwood	142	127	155	82%
Hemlock	49	53	72	74%
Hardwood–hemlock	86	82	110	75%
Pine	11	43	61	70%
Hardwood–pine	45	84	108	78%
Mixed	41	78	97	80%
Regenerating	12	49	74	66%

^a Individual plots are 50 m².

^b Estimation of total richness for cover types using first-order jackknife estimator.

^c Sampled richness/estimated richness.

The pine cover type shows the lowest estimated total richness, while the hardwood cover type shows the highest estimated richness, other than all plots combined.

5.2.2. Species richness relationships with forest cover types and topography

Understory species richness at the plot-level was significantly related to forest cover type, and slope position (Table 3). ANOVA *F*-values indicate that slope position has the greatest influence on species richness. Slope aspect was not a significant factor in determining understory richness. Within plot frequency of understory species was also significantly related to cover type and slope position, but not slope aspect (Table 3). ANOVA *F*-values indicate that cover type and slope position similarly influence within plot frequency.

Slope position within forest cover types, it has a significant effect on understory species richness at the plot-level (Table 3). Mean species richness of some forest cover types (hardwood, hardwood pine, mixture) increased consistently from ridge sites down to valley sites (Table 4).

Understory species richness at the plot-level was greatest for the hardwood cover type followed by the regenerating, pine, and hardwood pine cover types (Table 5a). The lowest species richness was found at the hemlock and hardwood–hemlock cover types, with mixed being slightly higher.

Table 3

ANOVA results for understory species richness and within plot frequency values in relationship to cover types, slope position and slope aspect.

	DF	F	P
Richness			
Cover type	6	15.16	<0.0001
Slope position	2	69.51	<0.0001
Aspect	2	3.00	0.0590
Cover type × slope position	11	2.03	0.0028
Within plot frequency			
Cover type	6	5.56	<0.0001
Slope position	2	6.90	0.0011
% slope	3	3.30	0.0205
Aspect	3	0.89	0.4099
Cover type × slope position	11	1.12	0.0600

Table 4

Mean species richness by slope positions within cover types.

	Ridge	Midslope	Valley
HW	7.0 (1.1)b	11.8 (0.7)b	21.3 (1.2)a
HM	3.8 (0.9)a	3.9 (0.7)a	7.0 (1.5)a
HMHM	4.4 (0.8)a	7.1 (0.7)a	15.3 (4.5)a
P	8.0 (1.4)a	13.0 (2.5)a	9.7 (1.5)a
HWP	7.8 (1.6)ab	8.8 (0.9)b	16.8 (1.8)a
MIX	3.3 (1.4)b	6.8 (1.2)b	14.6 (2.8)a
REG	15.5 (1.5)a	8.9 (2.3)a	^a

Values are arithmetic means for 50 m² plots. Numbers in parenthesis are ±1 standard error. Means followed by the same letter are not significantly different at the $p < .05$ level using Tukey–Kramer adjusted multiple comparison test. Cover types: HW = hardwood, HM = hemlock, HMHM = hardwood–hemlock, P = pine, HWP = hardwood–pine, MIX = mixed, REG = regenerating.

^a No plots at valley position for regenerating cover type.

Plot-level species richness increases significantly from ridge sites down to valley sites (Table 5a). The increase is nearly three-fold from ridge to valley, with consistent increases at midslope sites.

Understory species at the regenerating, pine, hardwood, hardwood–pine and mixed cover types tend to have the greatest within plot frequencies (Table 5b). Hemlock and hardwood–

Table 5a

Plot-level ANOVA results for species richness.

	HW	HM	HWHM	P	HWP	MIX	REG
Cover type	13.6 (0.7)a	4.4 (0.6)c	6.9 (0.6)c	10.3 (1.2)abc	11.0 (0.9)ab	8.3 (1.2)bc	11.0 (1.9)abc
Slope position	Ridge 5.8 (0.6)c	Mid-slope 8.6 (0.4)b	Valley 17.4 (0.9)a				
Aspect	NE 11.3 (0.8)a	INT 9.4 (0.6)a	SW 9.1 (0.6)a				

Values are means for 50 m² plots. Numbers in parentheses are ±1 standard error. Means followed by the same letter are not significantly different at the $p < .05$ level using Tukey–Kramer adjusted multiple comparison test. Cover types: HW = hardwood, HM = hemlock, HWHM = hardwood–hemlock, P = pine, HWP = hardwood–pine, MIX = mixed, REG = regenerating.

Table 5b

Plot-level ANOVA results for within plot frequency.

	HW	HM	HWHM	P	HWP	MIX	REG
Cover type	2.0 (0.04)a	1.6 (0.13)c	1.7 (0.08)bc	2.4 (0.17)a	2.1 (0.14)ab	1.8 (0.13)abc	2.3 (0.13)abc
Slope position	Ridge 1.7 (0.09)b	Midslope 1.9 (0.05)b	Valley 2.2 (0.05)a				
Aspect	NE 1.9 (0.06)a	INT 1.8 (0.06)a	SW 1.9 (0.07)a				

Values are means for 50 m² plots. Numbers in parentheses are ±1 standard error. Means followed by the same letter are not significantly different at the $p < .05$ level using Tukey–Kramer adjusted multiple comparison test. Cover types: HW = hardwood, HM = hemlock, HWHM = hardwood–hemlock, P = pine, HWP = hardwood–pine, MIX = mixed, REG = regenerating.

hemlock have the lowest frequencies. There are slight but significant differences in within plot frequencies between slope positions, with valley sites having higher frequencies than both midslope and ridge sites.

5.2.3. Species richness relationships with forest structure variables

Multiple regression analyses for all plots combined showed significant relationships between forest structure variables and species richness and within plot frequencies (Table 6). The analysis showed 42% of the variation in species richness was explained by the combination of percent cover of mountain laurel (– effect), percent basal area of eastern hemlock (– effect), and percent basal area of hardwood (+ effect). Twenty-two percent of the variation in within plot frequency was explained by percent cover of mountain laurel (– effect), % basal area of eastern hemlock (– effect) and % basal area of hardwood (+ effect).

Multiple regression analyses for the hardwood cover type also showed significant relationships between forest structure variables and understory species richness and within plot frequency (Table 6); with 52% of the variation in species richness explained by the combination of percent cover of mountain laurel (– effect), total basal area of oak spp., (– effect), total basal area of white ash (+ effect), and total basal area of red maple (+ effect). For within plot frequency percent cover of mountain laurel alone explained 27% of the variation and had a (–) effect (Table 6).

Variables that showed no significant effect at the $p < 0.05$ level were: percent total transmitted light, Beer's aspect, percent cover of Pennsylvania sedge, percent cover of hay-scented fern, percent basal area of pine, and other individual hardwood species listed in Table 1.

5.3. Compositional diversity of understory flora

5.3.1. Relationships between species composition, topography and forest structure

Independent Mantel tests identify variables that characterize both topographic and forest structure as having significant effects on species composition both for all plots combined and for the hardwood cover type (Table 7). Similarity in species composition for all plots combined was most associated with similarity in

Table 6

Stepwise multiple regression models for relationships between forest structure and understory species richness (*S*) and within plot frequency (*wpF*).

Model	r^2	<i>F</i>	<i>p</i>
ALL ^a			
$S = 12.544 - 0.106(\text{kala}) - 0.120(\% \text{tsca ba}) + 0.032(\% \text{hw ba})$	0.4184	6.28	0.0126
$wpF = 2.512 - 0.0008(\text{kala}) - 0.003(\% \text{tsca ba}) + 0.010(\% \text{hw ba})$	0.2209	5.81	0.0164
HW ^b			
$S = 16.381 - 0.107(\text{kala}) - 0.383(\text{qusp ba}) + 0.664(\text{fram ba}) + 0.31552(\text{acru ba})$	0.5205	7.59	0.0067
$wpF = 2.192 - 0.007(\text{kala})$	0.2686	51.41	<0.0001

Stepwise regression models incorporating variables that are significant at the $p < 0.05$ level. Variables included in models: kala = percent cover of mountain laurel (*Kalmia latifolia*), %tsca ba = % of total basal area in eastern hemlock (*Tsuga canadensis*), fram ba = total basal area in white ash (*Fraxinus americana*), qusp ba = total basal area in oak (*Quercus* sp.), %hw ba = % of total basal area in combined hardwood species, acru ba = total basal area in red maple (*Acer rubrum*).

^a Regressions run with all forest cover types pooled.

^b Regressions run only on hardwood cover type.

percent cover of mountain laurel and total basal area of eastern hemlock. Weaker associations between similarity in species composition and similarity in percent slope, slope position, and cover type were also apparent.

In general, species compositional associations for both topographic and forest structure variables were stronger within the hardwood cover type than for all plots combined (Table 7). Most obvious is the increased effect size of slope position within the hardwood cover type, with that variable showing a stronger relationship than both total basal area and percent cover of mountain laurel. Other variables that correspond with shifts in understory species composition include total basal area of oak spp., and total basal area of white ash (Table 7).

Variables that were tested but showed no significant effect on species composition were: percent total transmitted light, Beer's aspect, percent cover of Pennsylvania sedge, percent cover of hay-scented fern, percent basal area of pine, snag basal area, and individual hardwood species.

5.3.2. Understory species importance values for forest cover types

All forest cover types, except regenerating, are dominated by four clonally reproducing species typical of forest understory environments: wild sarsaparilla, Canada mayflower, star flower, and partridgeberry (Table 8). These species also have the highest importance values across all cover types combined. While all of

Table 7

Independent Mantel tests results for variables determined to have significant associations with species composition matrices.

Variable	r^a	p^b
All plots combined		
% cover KALA	0.130	0.0001
TSCA basal area	0.125	0.0001
Slope position	0.079	0.0002
Cover type	0.031	0.0020
Hardwood cover type		
Slope position	0.220	0.0001
% cover KALA	0.154	0.0001
FRAM basal area	0.118	0.0003
QUsp. basal area	0.079	0.0090

Variables: KALA = mountain laurel (*Kalmia latifolia*), TSCA = eastern hemlock (*Tsuga canadensis*), QUsp. = combined oak (*Quercus* sp.), FRAM = white ash (*Fraxinus americana*).

^a Standardized mantel statistic.

^b Variables determined to be significant if $p < 0.05$.

these species, except partridgeberry, are important in regenerating cover type, they were replaced in dominance by species of the *Rosaceae*, *Asteraceae*, and *Vitaceae* families that are more typical of open light environments: whorled wood aster (*Aster acuminatus* Michx.) black raspberry (*Rubus occidentalis* L.), wreath goldenrod (*Solidago caesia* L.) sweet fern (*Comptonia peregrina* (L.) J.M. Coult) and Virginia strawberry (*Fragaria virginiana* Duchesne).

Apart from the four dominant understory species mentioned above, the hardwood cover type is dominated by a mix of both typical forest species and species of more open sites (Table 8). Forest species include Indian cucumber (*Medeola virginiana* L.), white wood aster (*Aster divaricatus* L.) jack-in-the-pulpit (*Arisaema triphyllum* L. Schott), sessile bellwort (*Uvularia sessilifolia* L.), and wild blue violet (*Viola sororia* Willd.), while open site species are represented by numerous *Rubus* spp., common yellow oxalis (*Oxalis stricta* L.) and dwarf cinquefoil (*Potentilla canadensis* L.). Two species groups that are also represented in the hardwood cover type are the woody vines, Virginia creeper (*Parthenocissus quinquefolia* (L.) Planch.) fox grape (*Vitis labrusca* L.) and poison ivy (*Toxicodendron radicans* (L.) Kuntze) and ferns, *Dryopteris* spp., Christmas fern (*Polystichum acrostichoides* (Michx.) Schott.) and New York fern (*Thelypteris noveboracensis* (L.) Nieuwl.).

The hemlock, and to a lesser extent, the hardwood–hemlock cover types are characterized by a very limited number of species considered common (Table 8). In addition to the four ubiquitous species, Indian pipe (*Monotropa uniflora* L.), along with Jack-in-the-pulpit, Allegheny blackberry (*Rubus allegheniensis* Porter.), New York fern and lowbush blueberry (*Vaccinium angustifolium* Aiton) were found to be common. These species were also found to be common at the hardwood–hemlock cover type, along with several forest species, white wood aster Indian cucumber, smooth Solomon's seal (*Polygonatum biflorum* (Walter) Elliot) sessile bellwort, and Christmas fern, and a second open site species in addition to Allegheny blackberry and fox grape. Similar to results for richness, the number of common species at the hardwood–hemlock cover type was intermediate between the hardwood and the hemlock cover types.

The pine and hardwood–pine cover types tend to have a mix of both open site and typical forest species that are considered common, and the numbers of these are greater than found at the hemlock and hardwood–hemlock cover types, respectively (Table 8). The only non-native invasive species considered common, Japanese barberry (*Berberis thunbergii* DC), was found only at the pine, hardwood–pine and hardwood cover types. Unlike the relationships between the hemlock, hardwood–hemlock, and hardwood cover types, the hardwood–pine cover type is more similar to the pine cover type in the number of common species, rather than intermediate with the hardwood cover type.

5.3.3. Floristic associations by slope position within hardwood cover type

Overstory basal area within the hardwood cover type was similar for ridge, midslope, and valley sites (Table 9). Percent cover of mountain laurel changed dramatically from ridge sites down to valley sites, decreasing from 43% cover at ridges to 4.3% in valleys. Plot-level richness at valley sites was three times higher than ridge sites, with midslope sites being intermediate between the two, while total richness at valley and midslope sites was similar but twice that of ridge sites. Twenty species occurred at $\geq 10\%$ of ridge plots, 37 species at midslope sites, and 56 species at valley sites.

Indicator species analysis identified numerous species that had strong associations with valley sites, the majority of which are considered relatively common upland species: Jack-in-the-pulpit, poison ivy, Christmas fern, American hogpeanut (*Amphicarpaea a bracteata* (L.) Fernald), Virginia creeper, northern dewberry (*Rubus*

Table 8
Importance values* for common^a understory species by forest cover type.

Species	Family	Cover type ^b								
		Habit ^c	REG	HW	HM	P	HWHM	HWP	Mix	All
<i>Amphicarpaea bracteata</i>	Fabaceae	HV	–	12	–	–	–	–	–	–
<i>Aralia nudicaulis</i>	Araliaceae	PDH	43	52	21	80	32	48	43	43
<i>Arisaema triphyllum</i>	Araceae	PDH	16	34	11	–	15	12	11	20
<i>Aster acuminata</i>	Asteraceae	PDH	11	–	–	–	–	–	–	–
<i>Aster divaricatus</i>	Asteraceae	PDH	21	29	–	15	15	11	12	18
<i>Berberis thunbergii</i> ^d	Berberidaceae	DSB	–	16	–	13	–	12	–	11
<i>Dryopteris</i> spp.	Dryopteridaceae	FN	–	13	–	17	–	–	–	–
<i>Gallium</i> spp.	Rubiaceae	PDH	21	15	–	11	–	11	–	–
<i>Gaultheria procumbens</i>	Ericaceae	PEH	15	–	–	10	–	21	27	13
<i>Lysimachia quadrifolia</i>	Primulaceae	PDH	10	–	–	–	–	–	–	–
<i>Maianthemum canadense</i>	Liliaceae	PDH	23	64	32	98	44	65	52	54
<i>Medeola virginiana</i>	Liliaceae	PDH	–	17	–	20	12	–	–	–
<i>Mitchella repens</i>	Rubiaceae	PEH	–	38	20	61	35	38	34	34
<i>Monotropa uniflora</i>	Monotropaceae	PSH	–	–	10	–	16	22	–	12
<i>Oxalis europaea</i>	Oxalidaceae	PDH	21	10	–	–	–	–	–	–
<i>Parthenocissus</i>										
<i>Quinquefolia</i>	Vitaceae	WV	–	22	–	15	–	19	11	13
<i>Polygonatum biflorum</i>	Liliaceae	PH	–	18	–	17	12	13	–	13
<i>Polystichum</i>										
<i>Acrostichoides</i>	Dryopteridaceae	EFN	–	26	–	–	13	–	11	14
<i>Potentilla canadensis</i>	Rosaceae	PDH	32	22	–	16	–	26	–	15
<i>Rhus radicans</i>	Anacardiaceae	WV	11	24	–	34	–	30	19	17
<i>Rubus alleghaniensis</i>	Rosaceae	DSB	95	35	14	39	11	34	15	27
<i>Rubus flagellaris</i>	Rosaceae	WV	43	39	–	51	10	46	29	29
<i>Rubus idaeus</i>	Rosaceae	DSB	20	–	–	16	–	–	–	–
<i>Rubus occidentalis</i>	Rosaceae	DSB	32	–	–	–	–	–	–	–
<i>Smilacina racemosa</i>	Liliaceae	PDH	–	13	–	–	–	13	–	–
<i>Solidago caesia</i>	Asteraceae	PDH	18	–	–	–	–	–	–	–
<i>Solidago rugosa</i>	Asteraceae	PDH	35	12	–	–	–	–	–	–
<i>Thelypteris</i>										
<i>Noveboracensis</i>	Thelypteridaceae	FN	16	32	15	14	18	22	14	23
<i>Trientalis borealis</i>	Primulaceae	PDH	56	53	55	91	60	68	62	59
<i>Uvularia sessilifolia</i>	Liliaceae	PDH	–	35	–	–	14	27	17	22
<i>Vaccinium angustifolium</i>	Ericaceae	DSB	33	27	11	14	21	38	24	24
<i>Vaccinium corymbosum</i>	Ericaceae	DSB	–	10	–	11	–	–	12	–
<i>Viola sagittata</i>	Violaceae	PDH	31	–	–	11	–	–	–	–
<i>Viola sororia</i>	Violaceae	PDH	20	24	–	–	13	–	–	14
<i>Vitis labrusca</i>	Vitaceae	WV	39	24	–	–	10	29	–	17

Species importance values are calculated as: (((# of plots in which species occurs/total # of plots) + (# of quadrants in which species occurs/total # of quadrants))/2) × 100. *As cover types do not contain equal numbers of plots, importance values should only be read as relative within cover types (vertically) rather than across cover types (horizontally).

^a Species are considered common if importance value is ≥ 10.

^b Cover types: REG (regenerating); HW (hardwood); HM (hemlock); P (pine); HWHM (hardwood/hemlock); HWP (hardwood/pine); Mix (mixed); All (all plots combined).

^c Habit: HV (herbaceous vine); PDH (perennial deciduous herb); DSB (deciduous shrub); AH (annual herb); PEH (perennial evergreen herb); PSH (perennial saprophytic herb); WV (woody vine); FN (fern); EFN (evergreen fern).

^d Exotic invasive.

flagellari Willd.), sessile bellwort, smooth Solomon's seal, Japanese barberry and *Galium* spp. (Table 9). The majority of the species at the lower end of the indicator scale are wetland species that are strongly associated with hydric soil conditions: spice bush (*Lindera benzoin*, (L.) Blume), cinnamon fern (*Osmunda cinnamomea* L.) skunk cabbage (*Symplocarpus foetidus* (L.) Salisb ex Nutt.) meadowsweet (*Spiraea latifolia* L.), eastern marsh fern (*Thelypteris palustris* Schott.), groundsel (*Senecio aureus* L.), heartleaf foamflower (*Tiarella cordifolia* L.) white avens (*Geum canadense* Jacq.) halberdleaf tearthumb (*Polygonum arifolium* L.) and king-of-the-meadow (*Thalictrum pubescens* Pursh). Moderate associations were comprised of a mixture of both upland and wetland species.

Indicator species analysis identified no species that were strongly associated with the midslope position (Table 9). American red raspberry (*Rubus idaeus* L.) was found to have moderate associations with ridge sites, while round-lobed hepatica (*Hepatica nobilis* Schreb. var. *obtusa* (Pursh) Steyererm.), had weak associations with ridge sites. There were no species identified to have an exclusive association with any of the slope positions within the hardwood cover type.

6. Discussion

6.1. Forest cover types and understory diversity

Results indicate that there are clear differences in understory species richness between most forest cover types. A decreasing pattern of richness follows the general trend of: hardwood > regenerating, hardwood–pine, and pine > mixed > hardwood–hemlock > hemlock. The hardwood cover type generally has the higher numbers of both early successional species typical of the regenerating sites and forest associated species. This could be the result of the greater heterogeneity of light conditions, especially at the beginning and end of growing season in comparison to coniferous stands, and the fact that hemlock dominated stands tend to be older in age. In addition the deciduous nature of the hardwood stands can cater to evergreen or ephemeral herbs which can utilize light during winter and early spring (White, 1979; Peet and Christensen, 1980).

It should be expected that regenerating stands would have the high species richness due to increased resource availability and

Table 9

Forest structure, species diversity and indicator species analysis results for hardwood cover type by slope position.

	Ridge		Midslope		Valley	
# of plots	22		81		39	
Overstory basal area (m ² /ha) ^a	22.0 (1.9)		19.5 (1.0)		19.6 (1.4)	
% cover KALA (m. laurel) ^b	43.1 (8.9)		28.4 (4.1)		4.3 (2.5)	
Plot richness ^c	7.0 (1.1)		11.8 (0.7)		21.3 (1.2)	
Total richness	50		102		97	
Indicator species analysis	Species	IV ^d	Species	IV	Species	IV
	<i>Rubus idaeus</i>	16.1	none		<i>Rhus radicans</i>	59.9
	<i>Hepatica nobilis var obtusa</i>	8.0			<i>Arisaema triphyllum</i>	56.2
					<i>Polystichum acrostichoides</i>	48.9
					<i>Amphicarpa bracteata</i>	46.4
					<i>Lindera benzoin</i>	45.0
					<i>Galium spp.</i>	44.4
					<i>Parthenocissus quinquefolia</i>	41.1
					<i>Rubus flagellaris</i>	36.2
					<i>Berberis thunbergii</i>	36.2
					<i>Uvularia sessilifolia</i>	35.5
					<i>Polygonatum biflorum</i>	35.2
					<i>Thelypteris noveboracensis</i>	34.8
					<i>Aster divaricatus</i>	29.0
					<i>Onoclea sensibilis</i>	25.4
					<i>Osmunda cinnamomea</i>	24.3
					<i>Smilacina racemosa</i>	22.7
					<i>Geranium maculatum</i>	21.9
					<i>Circaea quadrisulcata</i>	19.4
					<i>Adiantum pedatum</i>	18.3
					<i>Impatiens capensis</i>	17.4
					<i>Ilex verticellata</i>	17.3
					<i>Vaccinium corymbosum</i>	16.9
					<i>Thelypteris palustris</i>	16.5
					<i>Smilax herbacea</i>	14.4
					<i>Anemone quinquefolia</i>	13.8
					<i>Ranunculus pensylvanicus</i>	12.8
					<i>Spiraea alba</i>	12.8
					<i>Senecio aureus</i>	12.4
					<i>Dryopteris spp.</i>	10.8
					<i>Tiarella cordifolia</i>	10.3
					<i>Symplocarpus foetidus</i>	9.9
					<i>Thalictrum pubescens</i>	9.9

^{a, b, c} Values are arithmetic means for 50 m² plots, with numbers in parentheses indicating ± 1 standard error.^d Indicator values for species testing significant at $p < 0.05$ level using Dufrene and Legendre (1997) method.

growing space (White, 1979; Peet and Christensen, 1980; Oliver and Larson, 1996). High species richness also can be attributed to the combination of early successional species that colonize the site and the retention of forest associated species that are retained after a disturbance, as demonstrated by this study.

Plot richness results point to the inclusion of eastern hemlock basal area as having a muting effect on species richness. This negative relationship has been demonstrated by other studies for eastern hemlock stands, and is usually attributed to lower light intensities, reduced throughfall precipitation, and modified soil properties including low pH, high C/N ratios, and Al and Fe concentrations (Anderson, 1963; Beatty, 1984; Miles, 1985; Whitney and Foster, 1988). Pine stands may demonstrate some of the same tendencies, but the effects of pine on species richness is less well documented. One study shows contrary results with Jack pine (*Pinus banksiana* L.) and red pine stands in Wisconsin having higher understory species richness compared to pure hardwood stands (Brosofske et al., 2001).

Trends for within plot frequencies of understory species by forest cover types show less clearly defined trends, perhaps because of the lack of robustness of this method for quantifying species abundances. However there are some consistencies with the richness patterns, with hardwood, pine, and regenerating cover types at the higher end of the scale and hemlock stands at the lower end. It is interesting to note that pure pine stands tend to have high average within plot frequency. We speculate that for

several low-lying or creeping species (Canada mayflower, partridgeberry and northern dewberry) their higher importance values in pine stands may be from the lower smothering and shading effect of the needle litter in comparison to the leaf litter produced in hardwood stands.

The results of the compositional diversity analysis point to an understory flora that is dominated by common species that occur across the range of forest cover types. Primary of these are the clonal, forest associated species wild sarsaparilla, Canada mayflower, star flower and partridgeberry. Only the regenerating cover type contained species with high importance values that occurred in no other cover type. These species belonged mainly to the families Rosaceae and Asteraceae, as well as jewelweed (*Impatiens capensis* Meerb.), brackenfern (*Pteridium aquilinum* (L.) Kuhn.) and sweet fern, and are all species that cannot tolerate the low-light conditions provided by a forest canopy.

One species of special note is Japanese barberry, an exotic invasive species from Asia (Magee and Ahles, 1999). The species has been shown to be linked to past land-use history (Lundgren et al., 2004; Searcy et al., 2006), and thus may be more commonly associated with old-field white pine sites. However, our survey shows Japanese barberry has become more important in the pure hardwood cover type (that were likely formerly old-field pine stands), and has been documented as a common component in eastern deciduous forests (Ehrenfeld, 1997).

6.2. Forest structure and understory diversity

Regression analyses suggest that increasing percentages of eastern hemlock basal area within a stand has a strong negative effect on understory species richness and within plot frequencies. However, the percent cover of mountain laurel also has a strong negative influence on understory species richness and within plot frequency across all cover types. Mountain laurel, along with other evergreen, ericaceous shrubs, has been shown to inhibit woody seedling regeneration and depress floristic diversity when present (Monk et al., 1985; Clinton and Boring, 1994; Ducey et al., 1996). While allelopathy is sometimes considered to play an important role in this relationship, we speculate deep shade also leads to low levels of floristic diversity under this species (Beier et al., 2005; Eppard et al., 2005).

For the hardwood cover type, relationships between certain other overstory tree species, mainly red maple and white ash, are also apparent. Species richness is positively correlated with the percent of white ash in the overstory. This is likely an indirect relationship resulting from the fact that white ash prefers sites with high nutrient and moisture levels (Burns and Honkala, 1990), factors that would also benefit many understory species. The same relationship is also apparent with red maple, a species that is most common at lower slope positions. Unlike numerous other studies that demonstrate the importance of light to understory species diversity (Collins et al., 1985; Scheller and Mladenoff, 2002; Newman and Broersma, 2003; North et al., 1996), the amount of light present at each plot, as quantified through canopy hemispherical photos, was not found to significantly affect species richness or composition. This may be due to the fact that photos were taken very close to the forest floor, where understory vegetation may have acted as a filter and homogenized light levels, rather than reflecting the heterogeneous levels most often demonstrated by forest canopies (Bartemucci et al., 2006).

6.3. Topography and understory diversity

Slope position has been demonstrated to be an indicator of understory diversity patterns (Pregitzer and Barnes, 1982; Meilleur et al., 1992), and is also suggested to play an important role in species richness in this study. The three slope positions tested show significant decreasing trends in richness: ridge < midslope < valley for hardwood or hardwood pine cover types. A somewhat similar, although less pronounced, gradient is also apparent for within plot frequency. We speculate that species richness and within plot frequency are both increasing from ridge down to valley along a productivity gradient that includes higher concentrations of N at lower slope positions (Ashton et al., 1998; Han et al., 2004). In fact, Small and McCarthy (2005) found that N concentrations were highest at lower slope positions in an Ohio oak forest, and that C/N ratios were highly correlated with herbaceous plant composition. High species richness and frequency could be the result of valley sites containing plots which are in or proximate to wetlands, as indicated by the numerous wetland obligate species present. The percent cover of mountain laurel was found to be highest at ridge sites, followed by midslope sites, which had higher percent cover than valley sites. This inverse relationship with species richness may also be a factor contributing to patterns of diversity along slope positions. Indicator species analysis shows that there are no species significantly associated with midslope sites, while numerous species are associated with valley positions and a few species at ridge positions. This may indicate that species showing site affinities at this forest are reacting mainly to the ends of of an environmental/topographic gradient (ridge versus valley; dry versus moist; infertile versus fertile).

Ashton et al. (1998) found that soil seed bank diversity at this forest was highest at midslope sites. This discrepancy with our study may be due to several factors. Firstly, higher numbers of species on midslope sites may exhibit abilities to store seeds in soil in comparison to valley sites. Second, the one species that has significantly higher densities at valley sites and occurs at valley sites in this study common blue violet (*Viola sororia* Willd.), is a relatively long-lived perennial that puts very little reproductive effort (4%) into seed production and can spread clonally (Bierzychudek, 1982). Lastly, low seed bank diversity at valley sites could also be because buried seeds may remain viable longer at midslope sites where soil moisture is lower and seeds are less likely to rot before germination.

Slope aspect was not shown to have a significant influence on either understory species richness or within plot frequency. This relationship has been shown to have both positive effects (Olivero and Hix, 1998; Small and McCarthy, 2005) and negative effects (Huebner et al., 1995) on understory floristic patterns. The non-significant results of this study may be due to the heterogeneous micro topography and limited elevation gradient at the forest, and a sampling design that was not originally intended to test for the influence of topography.

6.4. Combination of forest cover type and topography in relation to understory diversity

The combination of forest cover type with slope position has a significant influence on both understory species richness and composition. Most interesting is the compositional diversity relationship that is found when slope position is analyzed for the hardwood cover type only. In this case, slope position changes from having a minor influence on species composition for all cover types combined, to having the greatest influence of all variables tested for the hardwood cover type.

It is well known that vegetation patterns are the result of multiple biotic and abiotic site factors acting to expand or constrict the realized niche of species present on the landscape. For the combination of cover type and slope position, these results would indicate that forest overstory composition may have a higher order effect on understory species composition and richness than slope position (Brosofske et al., 2001). For our study, it may be the presence and abundance of eastern hemlock that mediates the effects of slope position on understory richness and composition. There may also be a temporal component to this process, as Gilliam et al. (1995) found that overstory composition plays a more important role in determining understory species diversity in later-seral stages of stand development.

7. Conclusions and management implications

If forest managers are to work within the framework of sustainable forestry guidelines, they need techniques that will allow them to identify and manage floristic diversity while producing timber resources. These techniques should be readily applicable in the field by taking advantage of typical inventory data, and should be general enough to work across the variety of landscapes and stand types that occur in a region. Results from this research identify forest cover type and topographic position as two features that can be used to assess floristic diversity patterns and incorporated into management decisions for southern New England managed forests.

Due to a long history of human disturbance, employing indicator species to identify sites of high conservation or diversity value is not as useful in southern New England as it may be in less disturbed areas such as the Pacific Northwest, USA or northern New England. Site sensitive species may have been extirpated from

the system or species may be relics from past stands rather than indicators of current conditions (Lindenmayer, 1999). This study identified no species which were exclusively associated with a particular stand type, other than common early successional species at regenerating sites. However, using forest cover type to assess levels of floristic richness is a simple and useful tool that may allow forest managers to evaluate and predict the outcome of silviculture prescriptions.

In addition, managers can work with topographic gradients in efforts to include understory floristics in their management prescriptions. The most apparent trend is the increasing richness from ridge to valley in hardwood stands. In addition, species associated with slope position occur mainly at the ends of the elevation range, either at ridge sites or valley sites. It may be important to design treatments that follow topographic contours. The data from this study also suggest that one species in particular, white ash, may be positively associated with both understory species richness and composition and is therefore a good indicator of understory plant diversity.

Last, the inclusion of eastern hemlock or to a lesser extent eastern white pine, within a stand will decrease richness, and may not benefit any specialist species dependent on those cover types. However, this study did not include late successional reserves, and from personal observations, one species, checkered rattlesnake plantain (*Goodyera tessellata* Lodd.), is only found at pure pine stands at the Yale Myers Forest. However, managers still need to understand the benefits that coniferous forest cover provides, especially as thermal cover for winter resident wildlife species. Due to mortality from the hemlock woolly adelgid (*Adelges tsugae*), it may be tempting to predict that as the abundance of eastern hemlock stands decline and are replaced by hardwood stands (Orwig and Foster, 1998), understory floristic diversity will increase. However, it may be more likely that in many areas, mountain laurel will usurp the newly available growing space instead, with the same negative influence on understory diversity as eastern hemlock.

In summary, managing for a mosaic of cover types and stand conditions may be one of the simplest ways to increase the probability of a high level of floristic diversity across the landscape, but this may also have its limitations in a highly disturbed forest system. Results of this study indicate that highest level of understory plant richness can be maintained in southern New England mixed-deciduous forests by (1) prescriptions that favor at least some degree of partial canopy protection of pure hardwood stands on valley sites, and (2) regeneration treatments that maintain a succession of stands in early stages of stand initiation.

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