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Understory vegetation and site factors: implications for a managed Wisconsin landscape

K.D. Brosofske[a,*], J. Chen[a], T.R. Crow[b]

[a]School of Forestry and Wood Products, Michigan Technological University, Houghton, MI 49931, USA
[b]School of Natural Resources and Environment, The University of Michigan, 1024 Dana Building, Ann Arbor, MI 48109, USA

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Abstract

We investigated relationships between edaphic and environmental factors (soil, forest floor, topography, and canopy) and understory vegetation (composition, richness, and Shannon–Wiener diversity index, H') among 77 plots representing seven major patch types comprising a landscape in northern Wisconsin that has a long history of human management. Sampled patch types included: (1) mature hardwoods; (2) young hardwoods; (3) mature red pine; (4) mature Jack pine; (5) young mixed pine; (6) clearcuts; and (7) open pine barrens. Within each plot, percent cover of understory plant species was estimated, along with canopy cover (%), litter cover (%), coarse woody debris (%), duff depth (O_e and O_a horizons, cm), slope, aspect, and overstory data. Soil samples were taken and analyzed in the laboratory for pH, moisture, organic matter, nitrogen, and carbon. Multi-response permutation procedures (MRPP) and stepwise multiple linear regression were used to examine differences in variables among patch types and to quantitatively relate the environmental variables to species richness and H'. Differences in species richness were only found between clearcut and hardwood patch types. Of the site variables, canopy cover differed most among patch types. Relationships between diversity and site factors were weak overall, but improved somewhat when patches were separated by overstory characteristics (i.e., coniferous, deciduous, open canopy), with soil factors differing in their relative effects on vegetation according to overstory properties. This suggests that a higher-level control pertaining to the overstory type overrode the effects of local variables on understory plant diversity. Important site variables influencing vegetation were canopy cover, pH, and forest floor characteristics. DCA ordination separated patch types according to canopy cover, soil moisture, and duff depth gradients. Species composition showed greater differences among patch types than did quantitative measures of diversity; these differences occurred primarily between patch types that were less qualitatively similar in terms of overstory. Thus, managers should focus on composition rather than numeric diversity measures to maintain landscape-level plant diversity. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Chequamegon National Forest; Community ecology; Landscape ecology; Plant diversity; Soils; Vegetation–site relationships

1. Introduction

Interest in how various landscape components affect biotic and abiotic resources has grown over the past 2–3 decades, especially with the emergence of landscape ecology and the refinement of management paradigms. Current management guidelines on many public lands call for maintaining a variety of patch types, sizes, shapes, and successional stages in an effort to provide for multiple uses and to maximize biological diversity at the landscape level (Crow et al., 1994). The idea is that such structural diversity will

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[*] Corresponding author. Tel.: +1-906-487-3417; fax: +1-906-487-2915.
E-mail address: kdbrosof@mtu.edu (K.D. Brosofske).

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provide a variety of habitats for plants and animals, thus increasing the number of species present in the landscape. Empirical information concerning ecological differences among the various patches maintained in a landscape is therefore valuable for assessing the effectiveness of this approach. The goal of this study was to determine whether and how diversity and composition of understory plant communities differed among the interiors of major patch types created and/or maintained by the USDA Forest Service within the Chequamegon National Forest in northern Wisconsin. Further, we sought to identify variables important in controlling plant diversity and composition by examining relationships among vegetation, various local edaphic and environmental variables, and patch type.

Strong associations between local environment and plant community composition have often been documented where human disturbance is minimal (Wales, 1967; Pregitzer and Barnes, 1982; Pregitzer et al., 1983). In areas subjected to considerable human disturbance, these relationships may be obscured (Walker, 1975; Foster, 1988); disturbance may sometimes override the site influences, especially where differences in these factors are relatively small, resulting in weaker associations between the vegetation and site conditions. However, some studies have found relatively strong relationships even in disturbed areas (Hix, 1988). Further information concerning vegetation–site relationships in areas that have been subjected to repeated management by humans is needed to elucidate the important influences on vegetation at multiple scales within the managed area. Such information could be useful for land managers, especially given the increased emphasis on non-economic values of the landscape (e.g., biological diversity) in current management paradigms.

Our study attempts to clarify some of these relationships between vegetation and site factors in a landscape that has a long history of active management. We investigated plant diversity across a broad range of structural and disturbance conditions, with sampled patch types ranging from clearcuts to intact, mature northern hardwoods (relatively undisturbed), and across two age classes (mature and young) for hardwoods and pines. Frequency of, and time since, disturbance is known to influence plant species diversity (White, 1979; Pickett and White, 1985; Collins and Glenn, 1988; Keenan and Kimmins, 1993; Roberts and Gilliam, 1995). The intermediate-disturbance hypothesis, which suggests that intermediate frequency and intensity of disturbance results in greatest diversity at intermediate stages of succession, has considerable evidence to support it (Bazzaz, 1975; Naveh and Whittaker, 1979; Hibbs, 1983). However, several other patterns have also been advocated. Schoonmaker and McKee (1988) describe six different patterns that have been proposed to describe the relationship between succession and plant diversity, including: (1) an increase in diversity throughout succession; (2) a decrease through succession; (3) a unimodal pattern with diversity peaking at intermediate successional stages (see IDH above); (4) a decline and then an increase, with more than one possible peak in diversity; (5) peaks at early and late stages of succession; and (6) no relationship between succession and diversity. Obviously, this issue is far from resolved and needs extensive field data for further elucidation.

Composition of the vegetative community as well as diversity must be examined in order to accurately assess differences among patch types and the possible effects of disturbance, including human-induced disturbance. For example, the introduction of non-native species into a landscape may be facilitated by extensive disturbance or the presence of roads, powerlines, or other anthropogenic corridors (McIntyre and Lavorel, 1994; Forman and Alexander, 1998). Without changing diversity, non-native species can alter the composition and possibly functional roles of the vegetative community, which could, consequently, influence ecosystem processes (Tilman et al., 1997). Thus, richness or diversity values alone, though interesting, are not as informative for practical purposes without compositional data.

In this study, we sought (1) to quantify and compare understory vegetation diversity (richness, Shannon–Wiener Index, and composition) among the sampled patch types, and (2) to determine whether and how these diversity measurements were related to site variables, such as soil, topographic, and structural characteristics, that may be affected by patch type. By so doing, we hoped to develop quantitative associations that would help elucidate the important processes driving diversity in this landscape, thereby providing feedback for adaptive management and strategy development.

2. Methods

2.1. Study area

This study was conducted in northern Wisconsin, USA, within the northernmost portion of the Washburn Ranger District, Chequamegon National Forest (46°30′–46°45′N, 91°02′–91°22′W). The area is characterized by Precambrian shield bedrock and late Wisconsin-age glaciated landscapes. Soils are deep, loamy, glacial outwash sands, classified as Psamments and Orthods. Topography is flat to gently rolling, with level terrace and pitted outwash landforms. Elevation ranges from 232 to 459 m. The growing season ranges from 120 to 140 days, and average annual precipitation is 762–813 mm (Albert, 1995).

2.2. Sampling and laboratory methods

During August 1997, we sampled 77 sites (i.e., patches) representing seven dominant patch types, as determined from Landsat TM images (Wolter et al., 1995) and defined on the basis of overstory vegetation or management regime. Sampled patch types included: (1) H, mature northern hardwoods; (2) YH, young hardwoods (10–15 years); (3) RP, mature red pine (*Pinus resinosa*); (4) JP, mature Jack pine (*Pinus banksiana*); (5) YP, young, mixed Jack/red pine (7–15 years), (6) CC, clearcut (~3–8 years old, previously red and/or Jack pine sites); and (7) PB, open canopy Jack pine barrens (see Table 1 for overstory composition). Sampled patches were initially located randomly based on Landsat TM images (Wolter et al., 1995). If the randomly chosen patch was intact and large enough to accommodate a plot at least 100 m from any physical edge at the time of sampling, it was sampled.

Within each sampled patch, a 0.05-ha circular plot was established to sample overstory trees. Diameters of all trees >6 cm DBH (diameter at breast height) were measured. A rectangular (5×20 m) subplot was established within the overstory plot to sample understory vegetation. Orientation of this subplot was randomly determined, but its center was located at the

Table 1
Summary of overstory composition for seven patch types of the Chequamegon National Forest, Wisconsin[a]

Species	H ($n=16$)[b]	YH ($n=10$)[c]	RP ($n=8$)[d]	JP ($n=8$)[e]	YP ($n=10$)[f]	CC ($n=15$)[g]	PB ($n=10$)[h]
Acer rubrum	4.60	0.33	0.15	0.60	0.17	0.01	–
Acer saccharum	1.87	0.02	–	–	–	–	–
Betula papyrifera	3.82	0.25	–	0.01	–	–	–
Ostrya virginiana	0.02	0.02	–	–	–	–	–
Pinus banksiana	–	–	0.15	13.91	2.69	–	0.07
Pinus resinosa	–	–	24.19	0.92	8.41	0.01	–
Pinus strobus	0.34	–	–	0.01	–	–	–
Populus grandidentata	5.54	2.68	1.55	–	0.02	–	–
Populus tremuloides	–	2.32	–	–	–	–	–
Prunus pensylvanica	–	–	–	–	0.01	–	–
Prunus serotina	–	–	–	0.01	0.09	0.01	–
Quercus ellipsoidalis	–	0.04	0.30	0.48	–	–	–
Quercus rubra	16.90	0.55	0.38	0.22	–	–	–
Snags	2.08	0.14	0.51	10.48	0.06	0.08	–
Total BA	35.17	6.35	27.23	26.64	11.45	0.11	0.07
Average canopy height (m)	21.4	8.5	21.9	20.5	5.8	3.8	4.6

[a] Values are average basal area (BA, $m^2\ ha^{-1}$).

[b] Mature hardwoods.

[c] Young hardwoods.

[d] Mature red pine.

[e] Mature Jack pine.

[f] Young mixed (Jack and red) pine.

[g] Clearcut.

[h] Jack pine barrens.

center of the circular plot. Within each subplot, percent cover was estimated for all understory plant species (bryophytes, herbs, shrubs, and tree species <6 cm DBH), bare ground, vegetative litter, and coarse woody debris. In addition, canopy coverage of the subplot was estimated using a moosehorn densiometer (100 evenly-spaced readings). Depth (cm) of the undecomposed forest floor litter and relatively decomposed duff (O_e and O_a horizons) were also measured, as were slope (%) and dominant aspect (°).

Soil samples (i.e., grab samples) were collected from the A, E, and B horizons, when present, from four randomly-placed pits dug within the circular plot. Samples from 65 of the 77 plots were taken within a 36 h period in September 1997. Soil samples were placed in coolers with ice for no more than 24 h for transportation to the laboratory, then were frozen until ready to be processed. Pre-processing included thawing in a refrigerator at 4°C, oven-drying at 60°C, and sieving to 2 mm or smaller particle size. We weighed samples before and after drying, allowing calculation of soil moisture content. Total organic matter content (%) was determined by weight loss of oven-dried soils after combustion at 375°C for 16 h. Soil pH (exchangeable acidity) was measured with a pH meter after extraction with calcium chloride. We also measured total carbon and nitrogen content (%) using a Nitrogen/Carbon Analyzer (NA-1500-NC Series 2) with Eager 200 Software (Fisons Instruments, Beverly, MA).

2.3. Data analysis

Soil data were averaged by site for the analysis. Before statistical analysis, all data were standardized by subtracting the mean and dividing by the standard deviation. Aspect was entered as an interactive variable with slope:

$$aspslp = \tan(slope) \times \cos(aspect - 45°),$$

where *slope* and *aspect* are in degrees (see, Ref. Stage, 1976). We used the multi-response permutation procedures (MRPP) in PC-ORD Version 3.0 (McCune and Mefford, 1997) to test for differences in species composition, richness, Shannon–Wiener diversity index (H', Shannon and Weaver, 1949), and environmental variables among patch types. When differences were found among groups, paired analyses were conducted to determine between which groups differences existed. To maintain an overall α of 0.05, we applied a Bonferroni correction (see, Ref. Harris, 1975) to the pairwise p-values (i.e., individual $p<0.05/n$ were considered significant, where n is the total number of comparisons).

The Mantel test in PC-ORD Version 3.0 (McCune and Mefford, 1997), which gives a measure of association between two distance matrices, was used with the Sorensen distance measure to indicate whether dissimilarity in local site conditions was an important driving factor for dissimilarity in vegetative community composition. Probability levels for the Mantel tests were calculated using 5000 Monte–Carlo randomizations. However, because this test can only compare two matrices at a time and it was undesirable to include all variables in the same matrix, independent tests were run for each variable, and a correction factor, as described above, was applied to the resultant p-values. Some variables that had particularly strong correlations and were qualitatively similar were combined within the same matrix. These included: litter depth and duff depth; and carbon and nitrogen content of each soil horizon.

Sampled plots were also ordinated based on understory species composition and abundance using detrended correspondence analysis (DCA, Hill and Gauch, 1980) within PC-ORD. Kendall's Tau was used to identify associations between ordination scores and environmental variables important for separating plots.

Finally, we performed stepwise multiple linear regressions in S-Plus Version 4.5 (MathSoft Inc., 1998) to identify environmental variables related to plant species richness and H' after establishing normality of the dependent variables through a Komolgorov–Smirnov goodness-of-fit test. Linear models were developed for all patch types combined, then for patch types separated into broad groups according to overstory composition and/or structure. We ran separate regressions for open canopy patch types (PB and CC), pine stands (RP, JP, and YP), and hardwoods (H and YH). Correlations between independent variables were analyzed using Spearman's rank correlation, and some variables were eliminated in order to minimize dependencies. Models developed by the stepwise procedure were further refined manually to maximize significance while minimizing autocorrelation in residuals.

3. Results

Across all sampled patches, 134 understory plant species were found. Thirty of these species were unique to only one of the patch types. Most notably, the mature hardwoods contained 10, the young hardwoods contained six, and the pine barrens contained nine unique species. The remaining five unique species were distributed among the red pine, Jack pine, young pine, and clearcut patch types (Table 2). Only six non-native (introduced) species were found among all sampled patches. These occurred primarily in the Jack pine, young pine, clearcut, and pine barrens patch types.

Table 2
Summary of vegetation and soil characteristics of patch types sampled in this study[a]

Variable	H[b]	Yh[c]	RP[d]	JP[e]	YP[f]	CC[g]	PB[h]
No. of plots: vegetation	16	10	8	8	10	15	10
No. of plots: soils	11	9	8	8	10	11	8
Canopy cover (%)	96.4	95.2	71.4	51.0	45.1	0.1	2.0
Total number of species	51	62	62	75	67	75	73
Mean species richness (R)	25.9	25.8	26.6	31.1	27.6	33.0	28.7
Mean H'	1.80	1.89	1.68	1.95	1.77	1.97	1.99
No. unique species	10	6	1	1	1	2	9
No. introduced species	1	0	0	4	3	4	3
Litter depth (cm)	1.2	1.7	1.4	1.7	1.7	1.7	1.1
Duff depth (cm)	2.2	2.5	2.2	2.1	1.1	0.9	1.2
Litter (%)	99.3	100.0	96.8	96.9	99.6	97.7	98.4
CWD (%)	10.5	14.7	12.3	25.8	5.6	31.5	6.5
Soil pH							
A	3.21	3.47	3.03	3.17	3.14	3.34	3.61
E	2.32	3.03	3.02	3.39	3.18	2.11	1.94
B	2.79	3.68	4.00	4.14	3.98	2.94	3.25
Soil moisture (%)							
A	13.93	22.04	7.44	8.16	8.23	5.60	5.50
E	4.17	5.09	4.25	3.84	3.79	2.66	1.11
B	5.78	7.82	5.22	5.83	5.00	4.03	3.18
Soil total N (%)							
A	0.25	0.38	0.11	0.18	0.17	0.13	0.18
E	0.03	0.04	0.05	0.04	0.05	0.02	0.02
B	0.03	0.04	0.03	0.03	0.04	0.02	0.03
Soil total C (%)							
A	5.55	7.99	3.05	4.73	3.82	3.29	3.52
E	0.65	0.71	1.08	0.90	1.09	0.52	0.31
B	0.55	0.86	0.65	0.62	0.79	0.49	0.58
Soil organic matter (%)							
A	10.14	15.26	6.26	9.98	7.39	6.17	9.18
E	1.73	1.87	2.43	2.38	2.75	1.45	0.96
B	1.99	2.77	2.35	2.38	2.48	1.64	2.20

[a] Values are averages based on patch type.

[b] Mature hardwoods.

[c] Young hardwoods.

[d] Mature red pine.

[e] Mature Jack pine.

[f] Young mixed (Jack and red) pine.

[g] Clearcut.

[h] Jack pine barrens.

Mean understory plant species richness differed among patch types (overall $p<0.05$), but paired comparisons using the Bonferroni correction indicated that the differences in richness (individual $p<0.0024$) lay only between the clearcut (average richness=33 species) and hardwood (mature and young, average richness ~26 species each) patch types (Fig. 1). No other differences in richness, and no differences in H', were found among patch types.

Of the site variables (Fig. 1), canopy cover was most variable among patch types, with only five pairings found to be similar ($p>0.0024$). Litter depth (cm) and *aspslp* (the combined aspect-slope variable, see Section 2) did not differ among patch types. However, duff depth (cm) showed a gradient, with greatest duff depths in the hardwoods (young and mature, mean=2.5 cm in YH), then the mature pines, young pine, and pine barrens, and lowest in the clearcuts (mean=0.9 cm). Coarse woody debris cover (CWD) was lowest in the young pine stands (mean=5.6%), though this was only different from the Jack pine (mean=25.8%) and clearcut (31.5%) sites ($p<0.0024$). Litter cover (%) was higher in the young hardwoods than in the Jack pine and pine barrens, but it was relatively high (>90%) across all patch types.

No differences were found among patch types in soil properties of the E and B horizons, though differences ($p<0.0024$) were found in the A soil horizon for all soil properties measured (Fig. 1). The red pine had the lowest pH in the A soil horizon (mean=3.0), which differed from the young hardwoods (mean=3.5) and pine barrens (mean=3.6). The young hardwoods had the highest soil moisture (mean=22.0%), organic matter content (mean=15.3%), total carbon (mean=8.0%), and total nitrogen (mean=0.4%) of the patch types, although this usually did not differ from the older hardwoods.

Results from the multi-response permutation procedures (MRPP) indicated that compositional

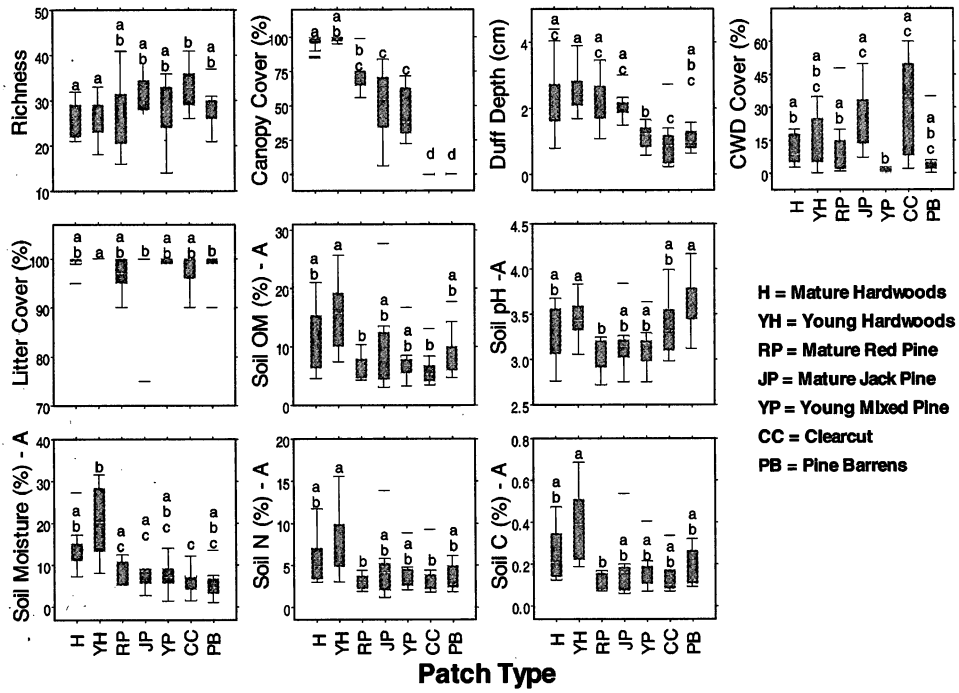

Fig. 1. Statistical summary of selected plant diversity and environmental variables measured in this study. Boxes represent the mean ±2 standard deviations. Also shown are the median, maximum and minimum values, and outliers. Patch types are indicated by abbreviations (see legend). Letters above the boxes indicate significant differences (i.e., patch types with the same letter were not significantly different; overall $p<0.05$, individual $p<0.0024$ using Bonferroni correction).

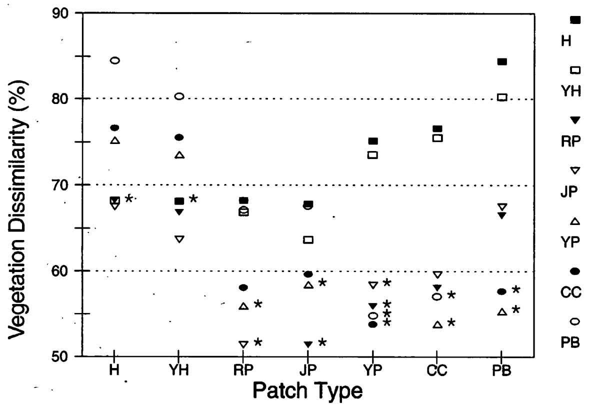

Fig. 2. Percent dissimilarity between pairs of patch types as measured by the Sorensen index. Asterisks indicate no significant differences (individual $p<0.0024$), as determined using MRPP in PC-ORD Version 3.0 (McCune and Mefford, 1997). H, mature hardwoods; YH, young hardwoods; RP, mature red pine; JP, mature Jack pine; YP, young pine; CC, clearcut; and PB, pine barrens.

differences in vegetation occurred primarily among patch types with differing overstory characteristics (Fig. 2). The mature and young hardwoods were similar in species composition, but differed in composition from all other patch types ($p<0.0024$). Likewise, the pine sites (RP, JP, and YP) were all similar compositionally, although the young pines were also similar to the clearcuts and pine barrens, whereas the red pine and Jack pine sites were different from all other patch types (mean dissimilarities 56–68%). Species compositions of the clearcuts and pine barrens, both open-canopy patch types, were similar to each other but different from all other patch types (mean dissimilarities 67–84%) except the young pine. Average Sorensen dissimilarity values for composition indicated that the mature and young hardwoods were more than 70% dissimilar to the young pine, clearcut, and pine barrens sites (Fig. 2). Interestingly, however, the average dissimilarity between the mature pines and young hardwoods was slightly lower than that between the mature and young hardwoods, even though the mature and young hardwoods were statistically determined to be compositionally similar to each other but different from the pines. Mantel tests showed that dissimilarity in vegetation composition among sites was positively associated with dissimilarity in soil moisture, carbon, and nitrogen (Table 3). Contrary to expectations, Mantel tests did not show a significant association between canopy cover and vegetation.

Table 3
Significant associations between species composition and site factor matrices as determined by independent Mantel tests

Variable	R[a]	p[b]
Soil moisture (A Horizon)	0.354	0.0002
Soil moisture (E Horizon)	0.236	0.0010
C, N (A Horizon)	0.188	0.0022

[a] Standardized Mantel statistic.

[b] Significance was determined using a Bonferroni correction to maintain an overall α of 0.05 (i.e., significant if individual $p<0.0024$). p-Values were calculated using 5000 Monte–Carlo randomizations.

Ordination of the patches showed a clear gradient from open canopy patches on the left (lower scores) to

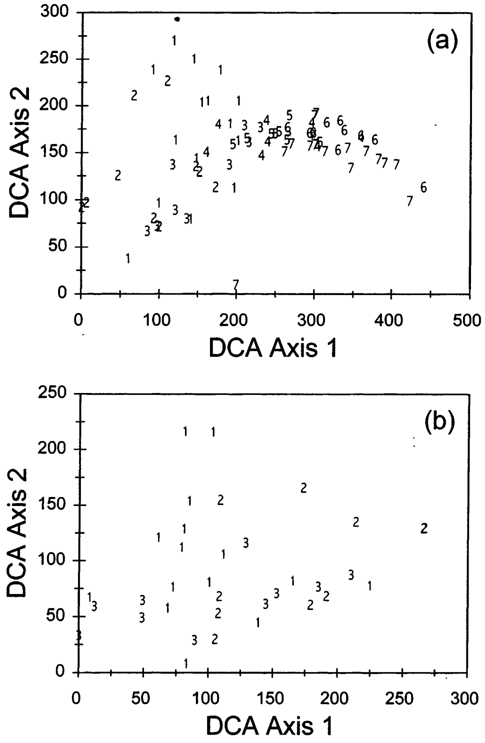

Fig. 3. First two DCA ordination axes obtained from PC-ORD Version 3.0 (McCune and Mefford, 1997) based on vegetation composition of (a) all sampled patches (eigenvalues are 0.5600 for Axis 1, 0.2269 for Axis 2), and (b) only CC, PB, and YH patch types from the left side of (a) (eigenvalues are 0.3462 for Axis 1, 0.2137 for Axis 2). Patch types are indicated by numbers (1, clearcut; 2, pine barrens; 3, young mixed pine; 4, mature Jack pine; 5, mature red pine; 6, young hardwoods; and 7, mature hardwoods).

closed canopy patches on the right (higher scores) (Fig. 3). Canopy cover was correlated with the first DCA axis (τ=0.64) (Table 4), as was soil moisture of the A horizon (τ=0.50). Duff depth and soil nitrogen, carbon, and organic matter in the A horizon were also weakly correlated with the first DCA axis. No strong correlations were found with the second or higher order DCA axes, although the patches with low Axis 1 scores showed considerable variation along Axis 2. We performed an additional ordination using only the patch types occurring primarily on the left side of Axis 1 (i.e., CC, PB, and YP) to attempt explanation of this variation. Axis 1 of this second ordination was somewhat correlated with pH and topographic characteristics (the aspect–slope variable), while Axis 2 was slightly negatively related to cover of coarse woody debris (Table 4).

Regression results demonstrated a relationship between plant species richness and H' and some of the local site variables (Table 5). Starting with all the site variables except soil moisture, organic matter, and nitrogen (due to extremely strong correlations with canopy and soil carbon) in the model for richness, stepwise regression eliminated all but canopy cover, which alone explained 22% of the variation in species richness (p=0.0003). The model for H', which identified canopy cover and pH of the B-horizon, was not significant (p=0.0703). Somewhat better models (r^2=0.20–0.59) were obtained from separate regressions for open-canopy patch types (PB and CC), pine stands (RP, JP, and YP), and hardwoods (H and YH) (Table 5). Richness in the hardwoods was more associated with environmental variables than in all other groups, and richness was better related than H' to environmental variables in all except the pine stands. Canopy cover and soil pH were the variables occurring most often in the final models, although structural features such as cover of coarse woody debris and litter were important in the open-canopy sites. The relatively low predictive power overall suggests that some factor we did not measure was influencing species diversity at our sites.

Table 4
Kendall's tau correlations (τ) between the first two DCA ordination axes and site variables

Site variable	Original ordination[a]		Second ordination[a]	
	Axis 1	Axis 2	Axis 1	Axis 2
Canopy cover (%)	0.640	−0.161	0.094	0.072
Litter cover (%)	0.275	0.030	0.280	0.067
Litter depth (cm)	0.078	0.067	0.029	−0.019
Coarse woody debris (%)	0.067	0.067	0.107	−0.303
Duff depth (cm)	0.375	−0.057	0.000	0.153
Aspslp	0.153	−0.137	0.360	0.197
pH (A)	0.010	−0.019	−0.314	−0.057
pH (E)	−0.233	−0.016	−0.177	0.119
pH (B)	0.243	0.038	0.124	0.190
Soil moisture (A)	0.497	−0.019	0.105	−0.057
Soil moisture (E)	0.249	−0.081	0.163	0.106
Soil moisture (B)	0.302	−0.049	0.177	−0.043
Organic matter (A)	0.325	0.033	−0.219	−0.133
Organic matter (E)	−0.136	−0.012	−0.105	−0.171
Organic matter (B)	0.259	0.077	−0.067	−0.210
Carbon (A)	0.331	0.090	−0.124	−0.076
Carbon (E)	−0.153	−0.062	−0.190	−0.124
Carbon (B)	0.174	0.070	−0.171	−0.219
Nitrogen (A)	0.317	0.060	−0.171	−0.048
Nitrogen (E)	−0.082	−0.035	−0.238	−0.152
Nitrogen (B)	0.121	0.103	−0.276	−0.248

[a] The original ordination included all the sampled patches; however, higher variation along Axis 2 for patches with low Axis 1 scores was unexplainable from the correlations. A second ordination was performed using only these patch types (i.e., CC, PB, and YP).

Table 5
Final stepwise regression models depicting the relationship between site factors and indices of plant diversity (understory species richness and the Shannon–Wiener diversity index (H'))

Group[a]	Model	r^2	F	p
ALL	Richness=0.083−0.449(canopy)	0.22	14.81	0.0003
ALL	H'=1.855−0.084(canopy)+0.055(pH B)	0.10	2.79	0.0703
HDWDS	Richness=26.08−2.276(canopy)+1.177(pH B)+2.139(C B)	0.59	7.56	0.0023
HDWDS	H'=1.816–0.094(canopy)+0.142(pH B)	0.39	5.41	0.0152
PINE	Richness=29.93−2.15(duff)−2.16(aspslp[b])+1.50(pH A)	0.37	3.50	0.0369
PINE	H'=1.851−0.194(canopy)−0.138(pH E)	0.49	9.01	0.0018
OPEN	Richness=30.400+1.955(CWD[c])+1.190(pH E)	0.29	3.40	0.0574
OPEN	H'=1.945+0.964(litter)	0.20	4.31	0.0533

[a] The *group* column specifies which patch types were used in formulating the model: ALL, all patch types; HDWDS, hardwoods only (H, YH); PINE, pine only (RP, JP, YP); OPEN, open-canopy only (CC, PB). Independent variables were standardized and selected for inclusion in the initial model based on a correlation analysis (see text), in order to reduce dependencies among the variables in the final models.

[b] *aspslp*=tan (*slope*)×cos (*aspect* — 45°) (see, Ref. Stage, 1976).

[c] Coarse woody debris.

4. Discussion

Many studies have examined the impacts of various ecosystem processes and other factors on plant species diversity. Impacts of successional stage, disturbance, site and/or vegetative productivity, edaphic and topographic factors, and light availability have been documented (see, Refs. Zobel et al., 1976; Lapin and Barnes, 1995; Brunet et al., 1996; Elliott et al., 1997). However, much of our understanding of vegetation–site relationships comes from studies performed within ecosystems that are relatively undisturbed by humans or from investigations of effects of particular management strategies at small scales. With increasing recognition of the impacts of humans at the landscape level, including land-use change and alterations in the structure of the landscape, it is important to identify the primary driving forces of diversity not only in undisturbed ecosystems, but also across entire landscapes that have been actively and intensively managed for many years, in order to understand the cumulative effects of human activities across the landscape. Recent investigations emphasizing the role species diversity plays in the functioning of ecosystems (Tilman and Downing, 1994; Risser, 1995) provide an added impetus to identify the important influences on diversity when humans alter and control the structure of the landscape.

4.1. Environmental and edaphic factors

Plant distribution is well known to be related to local environmental and edaphic factors. For example, species diversity commonly declines with increased shading (Keenan and Kimmins, 1993), a relationship that holds in the current study. In addition, soil characteristics such as moisture, nutrients, and pH have been strongly correlated with vegetation (Wales, 1967; Pregitzer and Barnes, 1982; Pregitzer et al., 1983). In our study, the influence of soil characteristics and other local factors on species richness and H' became stronger after patch types were separated into groups according to overstory composition and structure. Among patch types, canopy cover alone explained 22% of the variation in species richness, but that leaves a large proportion of variation unaccounted for. Within groups of patch types, however, other site variables, particularly pH and structural characteristics, became more influential and were able to explain up to 59% of the variation in richness and H' (Table 3). This suggests a higher-level control (i.e., overstory characteristics) on understory vegetation that may override the controlling influence of local factors.

Nutrient availability at small scales has generally been shown to be negatively correlated with plant diversity (Rosenzweig, 1995). Differences in species richness, nitrogen, moisture, and organic matter between the clearcuts and hardwoods in our study suggested a similar pattern (Fig. 1), although this was not evident in the regression results. Increased local extinction caused by competitive displacement resulting from shading effects has been one of the primary explanations for the reduction in richness associated with increased plant or site productivity (Newman, 1973; Goldberg and Miller, 1990; Tilman, 1993). Indeed, light availability in our study (measured by percent canopy cover) was a primary variable influencing species richness and H' (always a negative association). Shading, resulting in increased local extinction, may therefore have been the driving force of diversity in these sites. Tilman (1993) emphasized the importance of local colonization as well as extinction in determining the diversity of a site. He hypothesized that a reduction in germination sites caused by greater litter depth in productive grasslands reduced colonization rates. Although litter depth was not different among our patch types, duff depth was negatively related to richness in the pines, perhaps suggesting that colonization ability was an important factor driving diversity in these (pine) patches.

While the discussion above has been devoted primarily to species diversity as measured by richness and H', local environmental and edaphic characteristics also determine, in part, the composition of the plant community. Although richness and H' varied little among our patch types, compositional differences were evident and were somewhat related to differences in site variables. For example, though they generally had lower richness than other patch types, the hardwoods (H and/or YH) contained a number of species not found in other patch types, primarily woody species and bryophytes. Because bryophytes generally require moist conditions, it is not surprising that they were found chiefly in the hardwoods, which had higher moisture levels in the surface soil horizon. Woody species are also usually more prevalent in the understory of closed-canopy stands (Naveh and Whittaker, 1979). The species found only in open patch types tended to be either grasses or disturbance-adapted species such as *Epilobium angustifolium*. Interestingly, the pine patch types contained relatively few unique species. Thus, the hardwoods and open patch types may have contributed more to (i.e., increased the range of) the overall species diversity and composition of the landscape than did the pines, which tended to be intermediate between the hardwoods and open sites in terms of almost all variables measured. This finding could have implications for conservation biology or management of this landscape, as the intermediate pine sites could potentially act as refugia or corridors for species of more extreme habitats.

4.2. Disturbance and succession

The relationship between successional stage and plant diversity has been a popular focus of study throughout the past several decades, but there is yet to emerge a concensus as to the pattern of the relationship (Schoonmaker and McKee, 1988). The intermediate-disturbance hypothesis, which contends that diversity will be highest at intermediate stages of succession (and intensities of disturbance) (Connell, 1978), has much evidence to support it (Bazzaz, 1975; Naveh and Whittaker, 1979; Hibbs, 1983). However, our young patches of hardwoods (YH) and pines (YP) did not differ in species richness, H', or composition from mature patches and, indeed, the YH were less rich than the recently-disturbed clearcuts. Likewise, one might expect from this hypothesis that thinned stands such as the mature red pine (RP) sites in our study might be more diverse than clearcuts or mature hardwoods. We found no differences.

Other studies have indicated that plant species diversity is highest in clearcuts in the stages before canopy closure (Schoonmaker and McKee, 1988). Hansen et al. (1991) postulate that this may be caused by the distinct structure, especially the amount of dead wood, characteristic of these areas. Other explanations of higher richness in clearcuts have included the increased availability of light and regeneration sites resulting from removal of overstory vegetation and soil disturbance (Denslow, 1985), as well as greater microhabitat variability. In our study, clearcut patch types were found to be richer than young or mature hardwoods, but they were not different from pine barrens, young pine, or mature pine patch types. Increased light availability and higher cover of coarse woody debris both seem to be plausible mechanisms related to the higher clearcut diversity in our study. Canopy cover differed more than any other variable among patch types, especially between the hardwoods and clearcuts. The hardwood patch types were heavily shaded, in contrast to even the mature pines, which had relatively more open canopies due to thinning (RP patches) or senescence and disease (JP patches). In addition, coarse woody debris was determined to be significantly associated with species richness in the clearcuts, which typically contained a great deal of logging slash. Because these were pine clearcuts, the vegetative legacy might also have been influential in increasing their similarity to the pine sites and dissimilarity to the hardwoods.

Disturbance in general has also been found to be related to the presence of non-native plant species (McIntyre and Lavorel, 1994), a matter of concern for today's land managers. Because they are often better colonizers and competitors on disturbed sites, non-native species can displace or eradicate native species, resulting in a fundamental change in species composition. Only six non-native species were found among all the patches we sampled, and these were primarily in the Jack and young, mixed pines and the open canopy patches. It has been suggested that both higher levels of disturbance and greater numbers of landscape corridors, such as roads, may facilitate the dispersal and establishment of exotic species (McIntyre and Lavorel, 1994; Forman and Alexander, 1998). The relatively low total number of non-native species in the present study might result from the fact that our sampling plots were located well away from edges and roads. Therefore, interior site conditions prevailed, and disturbance or proximity to roads may not have been great enough to allow significant establishment of exotic species.

4.3. Management

Management practices can have significant impacts on the soil properties of a site (Keenan and Kimmins, 1993). These effects can include soil compaction (Dickerson, 1976), alterations in decomposition rate (Covington, 1981), nutrient concentrations (Tritton et al., 1987), and other factors, although Rubio et al. (1999) found no effects of management on soil properties when comparing coppice and high forest stands in central Spain. In our study, differences in soil factors among patch types were found only in the surface soil horizon, possibly indicating some effect of management history. Management practices are likely to affect the surface soil horizons more significantly than deeper soil horizons, resulting in some influence on the vegetation. Because soil and other site characteristics that are typically affected by management practices (i.e., canopy cover, duff depth, etc.) were related to understory vegetation, it is reasonable to deduce that management practices may affect the understory vegetation indirectly, through their effects on the local site factors. However, direct effects on understory vegetation can also occur, particularly with site preparation activities and prescribed fire.

Fire has been suggested to increase plant species diversity in areas that have been historically subjected to frequent fire disturbance (Christensen, 1985; Denslow, 1985; Collins and Glenn, 1988). However, richness of our pine barrens sites, which are currently maintained by prescribed fire, was no different from that of other sites, which are influenced primarily by harvesting practices. In another study of the same landscape, however, Brosofske et al. (unpublished data) found that species richness of the pine barrens at the landscape level (i.e., along a 3000 m transect through the pine barrens) was almost twice that of three other unburned landscapes. This may have implications for the scale of the study. At a local scale differences were not found, while relatively higher diversity in the pine barrens was obvious when viewed at the landscape level. This, along with the finding that local environmental and edaphic influences on plant diversity were likely masked by a higher-level control, possibly canopy cover or disturbance characteristics, emphasizes the importance of examining multiple scales to obtain a more complete picture of plant diversity.

A long history of intensive management could alter the landscape enough through the years to weaken typical relationships between vegetation and soil properties, thereby effecting some homogenization of the vegetation (Whitney, 1991). Repeated changes in the structure of the landscape or alteration of the historic disturbance regime could facilitate dispersal and establishment of species originally somewhat restricted due to structural barriers to dispersal. This is particularly possible in this study area because the soils and topography are relatively similar throughout (i.e., differences exist on a finer scale than in many other areas). Although our data indicated that variation in richness and H' among patch types was low and less related to differences in site factors than diversity measures within patch types, the patch types were somewhat different compositionally. Therefore, some homogenization may have taken place in our study area, but local controlling factors continue to influence composition to some degree.

5. Conclusions

The results presented in this paper have shown little difference in quantitative diversity measures among major patch types of the study area. Canopy cover was the dominant site variable influencing diversity. Other local edaphic and environmental differences did exist, but were less extensive and influenced richness and Shannon–Wiener diversity primarily within groupings of patch types determined by overstory characteristics (e.g., pH), suggesting a higher-level controlling factor that overrode the local relationships. Stand age did not affect diversity measures, except that pine clearcuts contained higher richness than young or mature hardwoods. Young and mature patches of hardwoods and pines did not differ in measures of diversity.

Differences in composition among patch types were more distinct than differences in richness and H', which suggests this may be a better measure of influences of environment or management on vegetation. The sampled patch types occupied a relatively continuous gradient compositionally, with overlap between the young pine and open-canopy patches. The mature red and Jack pine patch types were also quite similar compositionally, suggesting that the species differentiation within pines (i.e., red vs. Jack) may not be important for maintaining understory plant composition. In addition, managers should not assume that specific site conditions will have consistent effects on understory species diversity in all patch types. Recognition of the variable influences of environmental factors under different canopy types will improve the ability to predict the effects of human-related disturbances on understory vegetation.

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