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Understory Vascular Plant Species Diversity in the Mixedwood Boreal Forest of Western Canada

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SFM Network Project: Understanding how Fire Behavior Characteristics Shape Tree Population Dynamics, Diversity and Forest Patterns

by

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EXECUTIVE SUMMARY

Abstract. One of the goals of ecosystem management has been to maintain plant species diversity. Consequently, in this fire influenced boreal forest ecosystem, the objectives were to determine: 1) the relative importance of time-since-fire, moisture and nutrients, and light availability (canopy coverage) in controlling understory plant species diversity, 2) the local diversity patterns resulting from the organization of species=tolerances and species overlap along the most important environmental gradient and 3) the landscape diversity patterns by weighting the environmental gradients by their relative importance. One hundred and twenty-one upland stands in the mixedwood boreal forest of Saskatchewan were sampled for herbaceous species richness, diversity and evenness in thirty 25 cm by 25 cm quadrats per stand. Stands ranged in age from 1-234 years since fire and showed no evidence of anthropogenic disturbance.

Results showed that understory species richness, diversity and evenness are primarily controlled by moisture and nutrient gradients and secondarily by a combination of light availability and time since the last disturbance. Communities of high species richness showed high overlap of narrow tolerances along the moisture and nutrient gradient. Moisture and nutrient gradients are determined by hillslope position and surficial geology. Moisture and nutrient gradients also organize canopy species. Therefore, at the local (hillslope) scale, species richness and diversity are highest in aspen stands, moderate in mixedwood and jack pine stands and lowest in black spruce stands. Within slope positions (i.e. canopy types), basal area (light availability) and age (time-since-fire) further determine species richness. At the landscape scale, species richness shows small scale variability, unlike the large scale pattern of time-since-fire. In short, the hillslope (and surficial geology), and not fire, is the fundamental unit of diversity.

Keywords: light disturbance, diversity, ecosystem management, evenness, fire, hillslope moisture-nutrient gradients, mixedwood boreal forest.

ACKNOWLEDGMENTS

INTRODUCTION

Plant species diversity is influenced by species distribution and abundance. A number of factors have been shown to affect plant species distribution and abundance. These include site conditions, i.e. moisture and nutrient gradients (Day Jr. and Monk 1974, Whittaker and Niering 1975, Marks and Harcombe 1981, Roberts and Christensen 1988, Host and Pregitzer 1992), canopy coverage, i.e. light availability (Kull and Zobel 1991, Uemura 1994) and time since the last distubance (Specht et al. 1958, McConnell and Smith 1970, Auclair and Goff 1971, Dix and Swan 1971, Holland 1971, Shafi and Yarranton 1973, Nicholson and Monk 1974, Mellinger and McNaughton 1975, Roberts and Christensen 1988, Schoonmaker and McKee 1988, De Grandpré et al. 1993, Halpern and Spies 1995). The boreal forest is considered a fire dominated ecosystem since fire is a primary large-scale disturbance. As such, fire is thought to play the principal role in determining plant diversity. Thus, one goal of ecosystem based forest management in the boreal forest is to preserve biodiversity patterns by emulating the Anatural@ (pre-European) fire regime (Hunter 1993, Attiwill 1994, Bender 1994, Weetman 1994). There is no doubt that disturbance influences diversity but the question is: how important is disturbance relative to site conditions (moisture and nutrient gradients) and to canopy coverage (light availability)?

Plant species diversity, because it is influenced by species distribution and abundance, is a reflection of community organization. The abundance and distribution of a species can be described by its tolerance curve. A tolerance curve reflects the ability of a species to survive and reproduce along one or more environmental gradients. Each gradient explains a different amount of the variation in species distribution and abundance. Local diversity patterns are determined by the combination of tolerance curves for each species in the community and their overlap along the environmental gradients. At the landscape scale, the combination of the relative importances of each environmental gradient determines the diversity patterns. Thus, our objectives were to determine: 1) the relative importance of moisture and nutrients, canopy coverage (light availability) and time-since-fire in controlling understory plant species diversity in the mixedwood boreal forest, 2) how the local diversity patterns result from the organization of species=tolerances and species overlap along the most important gradient and finally, 3) the landscape diversity patterns where the environmental resource gradients are weighted by their relative importance.

METHODS

Study Area

The 8000 km^2 study area is located in central Saskatchewan (Figure 1) within the Weyerhaeuser Forest Management Lease Area and Prince Albert National Park (53°34' N to 54°24' N and from 105°25' W to 107°52' W). The weather within the study area is characterized by long, cold winters and short, cool summers. The frost free period is generally less than 80 days and freezing can occur in any month. July and August are the warmest months with the average maximum temperature exceeding 20°C three days out of four. The average annual precipitation ranges from 400 to 500 mm, 70% of which occurs as rain.
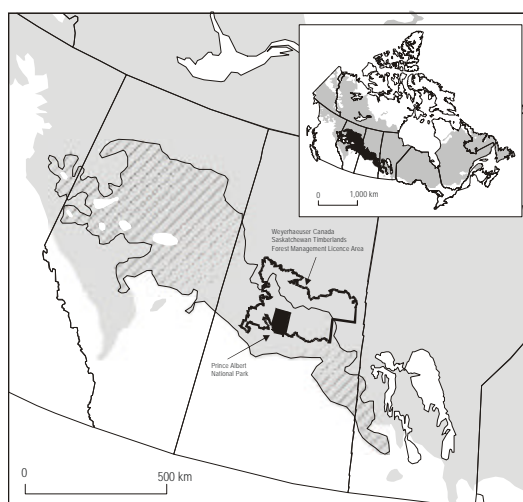

Fig. 1. Location of the study area: Prince Albert National Park and Weyerhaeuser=s Forest Management License Agreement. The light grey area represents the extent of the boreal forest in Canada and the dark grey area is the southern mixedwood boreal forest (cf. Rowe 1972).

The primary large scale disturbance is lightning caused crown fires. The fire cycle has changed at least twice in the last 200 years, and has varied from 15-75 years (Weir et al. 2000). Only 5% of the area is older than 200 years (Johnson et al. 1995). Insect outbreaks do not seem to have been a major source of large scale disturbance in the last hundred years.

The area has a gentle relief with elevation ranging from 450 m to 900 m a.s.l. The surficial geology of the study area is primarily undifferentiated glacial till and glaciofluvial substrates, with only a small proportion of the area covered by glaciolacustrine substrates. The surficial geology determines the shape of a hillslope and thus the rate of change of moisture and nutrients down a hillslope (Bridge and Johnson 2000).

The study area is part of the southern mixedwood boreal forest (Rowe 1972). It is

characterized by white spruce (*Picea glauca* (Moench) Voss.), black spruce (*Picea mariana* (Mill) B.S.P.), jack pine (*Pinus banksiana* Lamb.), balsam fir (*Abies balsamea* (L.) Mill.), tamarack (*Larix laricina* (Du Roi) K. Koch), trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh.). Bridge and Johnson (2000) depicted the general landscape patterns of vegetation composition based on surficial geology and hillslope position. On glaciofluvial hillslopes, jack pine are found in higher abundance on hilltops while black spruce are found in higher abundance further downslope. On glacial till hillslopes, trembling aspen are found in higher abundance on hilltops while mixedwood stands, i.e. trembling aspen, white spruce and balsam fir, are found further downslope.

Sampling Regime

Understory plant species diversity (H) was partitioned into species richness (S) and evenness (E) by H = ln(S) + ln(E) (Buzas and Hayek 1996). Note that tree and shrub species were included as understory plant species if they were <1 m in height.

One hundred and twenty-one upland stands were sampled. One hundred and one of these stands were from Bridge and Johnson (2000). The other 20 stands were younger than 15 years since last fire. Each stand was greater than 4 hectares in size, had vegetation rooted in the mineral soil with no evidence of standing water in the top 30 cm of the mineral soil, were visually homogeneous with respect to stand age, structure and species composition and had no evidence of significant anthropogenic disturbance. In each stand, vascular herbaceous species frequency was recorded in thirty 25cm by 25 cm quadrats. Species richness (S) was defined as the number of species summed over all 30 quadrats in each stand. Evenness (E) was estimated as exp(H)/S and diversity was defined as

$$H = \sum_{i}^{S} - (F_i \cdot \ln F_i)$$

where F_i is relative frequency of species i (Shannon 1948).

In this study, the moisture and nutrient gradient was measured as slope position. The study by Bridge and Johnson (2000) measured moisture and nutrients directly by collecting soil from the top 15 cm of mineral soil in three soil pits per stand for a total of 101 stands. The three soil samples per stand were combined and air dried. Detailed analysis of soil texture, pH, electrical conductivity, nitrate, ammonium, cation exchange capacity, % organic carbon, % organic matter, extractable phosphate, potassium, sulphate, calcium, magnesium, sodium were performed by the Plains Innovative Laboratory Services, Saskatoon, SK on samples from 40 stands, selected to represent the full gradient range. Soil water retention capacity at 33 kPa (field capacity) and 1500 kPa (permanent

wilting point) was determined for 88 samples using ceramic pressure plate analysis. The remaining 13 samples did not have enough soil for analysis. The vegetation and environmental data were used in a Redundancy Analysis to relate moisture and nutrients to vegetation composition. The moisture and nutrient gradients were in turn, significantly related to distance from the ridgeline (i.e. slope position) where both moisture and nutrients increased with distance from the ridgeline (Bridge and Johnson 2000). Surficial geology was determined from the land form, soil texture and colour, and a surficial geology map.

Light availability was measured as canopy basal area. It would have been preferable to measure light availability directly; however, due to the large number of stands, this was not realistic. On clear days, because of the rapid change in solar angle in the morning and late afternoon, sampling would have been restricted to 3 hours in the middle of the day. Also, since there is a large contribution of direct sunlight due to sunflecks, the data would have had to be temporally or spatially averaged. Light readings on overcast days would have been no more reliable because of the rapid change in cloud density. Therefore, although not ideal, canopy basal area was used as a surrogate measure of light availability within a canopy type since light availability decreases as canopy basal area increases (Cutini et al. 1998).

At the landscape scale, light availability is related to both the canopy species in high abundance and canopy basal area. For example, light transmittance through crowns of single spruce trees is **2** to 1/10 that of aspen trees of similar stem size (Constabel 1995). Canopy basal area (m^2/ha) was calculated by multiplying diameter at the base with canopy stem density. Canopy stem density (trees/ ha) was sampled using the point centred quarter method (Cottam and Curtis 1956).

Disturbance was measured as time since the last fire and was determined from a map created for a fire frequency study in Prince Albert National Park (Weir et al. 2000).

Analysis

Standard partial regression coefficients from a standard least squares multiple regression were used to determine the relative importance (Snedecor and Cochran 1971, Zar 1984) of stand characteristics (slope position, canopy basal area and time-since-fire) on species richness, diversity and evenness. Standard partial regression coefficients estimate the fraction of the variance in the dependent variable (i.e. species richness, diversity or evenness) attributable to its linear regression on the stand characteristic, corrected for scale. Scale correction is achieved by estimating the change in the dependent variable, as a fraction of the standard deviation in the dependent variable, produced by one standard deviation change in the stand characteristic (Snedecor and Cochran 1971).

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The patterns of species richness, diversity and evenness at the hillslope scale were determined using the Tukey-Kramer Honestly Significant Difference (HSD) test (p<0.05) by making multiple comparisons of mean species richness, diversity or evenness between all slope positions regardless of substrate.

Tolerance, tolerance-overlap, beta diversity and the percent of rare species per stand were used to determine how species richness was related to community organization. To calculate both tolerance and overlap, slope position had to be given a numeric value; therefore, the slope was divided into distances from the ridgeline. This was done using the Image Analysis software PCI^{TM} version 5.2 (PCI Inc., 1994), a Digital Elevation Model (DEM) and an algorithm developed by Warren (1999) that located the closest ridge based on a path of water flow calculated from local aspect. Intervals were divided based on two criteria: 1) that there be more than one stand in an interval and 2) that intervals be continuous and equal along the gradient. The glacial till hillslope is longer than the glaciofluvial slope (Bridge and Johnson 2000). Unfortunately, on glacial till, there were few stands sampled further downslope and thus those intervals did not meet the first criterion. As a result, both the glaciofluvial and glacial till substrates were divided into 5 distance classes from the ridgeline.

Tolerance (W_i) was measured as the variance in the relative frequency of species on the hillslope (cf. McNaughton and Wolf 1970):

$$W_i = [\frac{\sum_{j=1}^{5}(x_j \cdot j)^2 - [(\sum_{j=1}^{5}(x_j \cdot j)^2 / \sum_{j=1}^{5} x_j]}{\sum_{j=1}^{5} x_j}]^{1/2}$$

where W_i is the tolerance width for species i, x_j is the relative frequency of species i in slope position j where j is the slope position weighted from 1 to 5, 1 being the top slope and 5 being the toe slope. Therefore, mean tolerance width per stand ($\overline{W}$) is:

$$\overline{W} = \frac{\sum_{1}^{S} W_i}{S}$$

Overlap of species tolerances was calculated following Horn (1966):

$$R_o = \frac{\sum_{i=1}^{n_j}[(x_{ij} + x_{ij+1})\log(x_{ij} + x_{ij+1})] - \sum_{i=1}^{n_j}[x_{ij} \log x_{ij}] - \sum_{i=1}^{n_j}[x_{ij+1} \log x_{ij+1}]}{(X_j + X_{j+1})\log(X_j + X_{j+1}) - X_j \log(X_j - X_{j+1})\log(X_{j+1})}$$

where x_{ij} is the relative frequency of species i in slope position j, x_{ij+1} is the relative frequency of species i in the adjacent slope position $j+1$, n_j is the number of species found at slope position j, and

X_j is the sum of the relative frequencies of all species in slope position j:

$$X_j = \sum_{i=1}^{n} x_i$$

In addition, multiple comparisons were made of beta diversity between each pair of slope positions. Beta diversity is calculated as percent similarity (Renkonen 1938):

$$\% \, similarity = \sum_{i=1}^{n} [minimum(x_{ij}, x_{ij+1})]$$

Percent similarity is one of the best quantitative measures of similarity available (Wolda 1981) since it is not greatly affected by sample size or by species diversity.

Finally, to determine which slope positions supported more rare species, multiple comparisons were made between each pair of slope positions ($p<0.05$) of the number of species with a relative abundance of less than 5% (i.e. rare species).

A LANDSAT TM image (for cover type and percent coverage), a Digital Elevation Model (DEM) for hillslope position (i.e. moisture and nutrients) and a time-since-fire map were used to predict the patterns of species richness on the landscape using the image analysis software PCI^{TM} version 5.2 (PCI Inc. 1994). The LANDSAT TM image was taken on July 12, 1990 under cloud free conditions. Stands were located on the image with coordinates obtained from a differential global positioning system. The pixels were randomized and half of the pixels in each stand were used as training sites in a supervised classification and the other half were retained as test sites to calculate accuracy. The supervised classification requires the user to delineate classes. Based on herbaceous species richness from our field sampling, stands were grouped into four classes from species rich to species poor on each of the two substrates. Non-forested areas were divided into seven classes using a combination of aerial photographs and forestry cover maps. A maximum likelihood classifier (PCI Inc. 1994) was then used to classify each pixel into one of the eleven classes. The maximum likelihood classifier is preferred because it evaluates both the variance and correlation of the categories= spectral response patterns when classifying unknown pixels (PCI Inc. 1994). However, it assumes that the distribution of points in the training data is Gaussian. The overall accuracy of the classified map was assessed using the kappa coefficient of agreement (Hudson and Ramm 1987, Congalton 1991) which compares the similarity of two raster maps after the similarity due to chance has been removed. Since diversity was not greatly affected by evenness, only a map of species richness was constructed.

RESULTS

The Relative Importance of Moisture and Nutrients, Light Availability and Time-Since-Disturbance in Explaining Species Richness, Diversity and Evenness

The standardized multiple regression using slope position, canopy basal area and time-since-fire was significant (p<0.0001) and accounted for 52% of the variation in species richness (Table 1).

TABLE 1. Standardized least squares multiple regression of the effect of stand characteristics (slope position, canopy basal area and time-since-fire) on herbaceous **species richness**. Relative importance was assessed using standardized partial regression (beta) coefficients.

A) Analysis of variance					
Source	df	F	Prob>F	R^2	
Model	6	20.105	<0.0001	0.52	
Error	111				
Total	117				

B) Parameter estimates					
Variable	df	Parameter Estimate	t	Prob<F	Relative Importance (Beta Coefficient)
Intercept		16.96	16.09	<0.0001	0
Slope position:	3				**Total = 1.44**
Glaciofluvial top slope vs glacial till toe slope		0.388	0.43	0.6662	0.04
Glaciofluvial toe slope vs glacial till toe slope		-6.546	-6.26	<0.0001	0.59
Glacial till top slope vs glacial till toe slope		6.719	9.69	<0.0001	0.81
Canopy basal area	1	0.0005	1.59	0.115	
Time-since-fire	1	0.022	1.41	0.162	
Interaction of Canopy basal area and Time-since-fire	1	-1E-05	-3.3	<0.0013	**0.53**

Slope position showed a significant relationship with species richness. The low relative importance of glaciofluvial top slope versus glacial till toe slope indicates that species richness is similar between the two. The high relative importance of the remaining two slope position categories indicates that species richness is very different between these slope positions and that slope position has a strong effect on species richness. Canopy basal area and time-since-fire were not individually significant. However, the interaction between canopy basal area and time-since-fire did show a significant relationship with species richness. This relationship is described by a parabola (Figure 2) which indicates that at a constant richness there is a trade off between canopy basal area and time-since-fire (i.e. as time-since-fire increases basal area decreases). Note that the parameter estimates (Table 1) for canopy basal area and time-since-fire simply give the intercepts for the interaction and not relative importance since the relative importance of the interaction contains the same information.
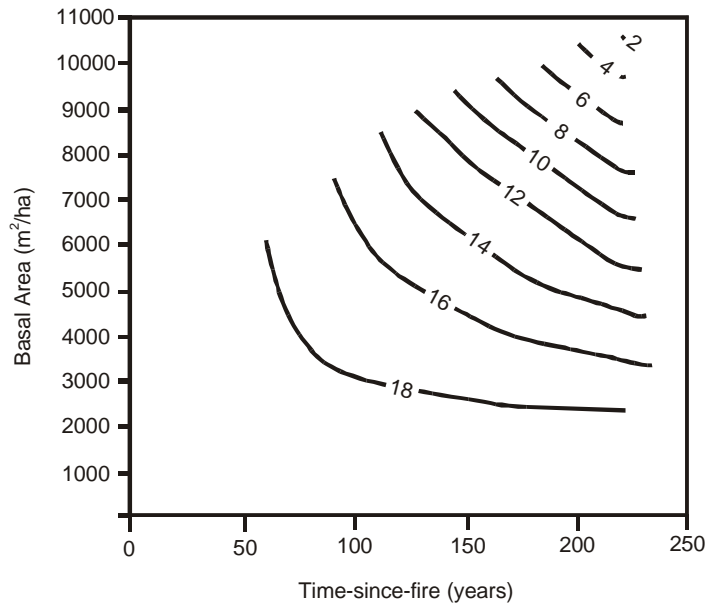
Fig. 2. A contour plot showing how species richness (number on contours) is related to the interaction between canopy basal area (m^2/ha) and time-since-fire (years) predicted from the standardized least squares multiple regression. The parabolic relationship indicates that there is a trade-off between canopy basal area and time-since-fire and that species richness decreases as stands age and as canopies become denser.

The standardized multiple regression for diversity (Table 2) and evenness (Table 3) showed the same trend in relative importance as species richness, where slope position had the highest relative importance and the interaction between canopy basal area and time-since-fire had the next highest relative importance. However, only 47% of the variation in diversity and only 16% in evenness is accounted for. Therefore, from the relationship $H = \ln(S) + \ln(E)$ (Buzas and Hayek 1996), diversity is largely determined by species richness.

TABLE 2. Standardized least squares multiple regression of the effect of stand characteristics (slope position, canopy basal area and time-since-fire) on herbaceous **species diversity**. Relative importance was assessed using standardized partial regression (beta) coefficients

A) Analysis of variance

Source	df	F	Prob>F	R^2
Model	6	16.26	<0.0001	0.47
Error	111			
Total	117			

B) Parameter estimates

Variable	df	Parameter Estimate	t	Prob<F	Relative Importance (Beta Coefficient)
Intercept		2.33	30.83	<0.0001	0
Slope position:	3				**Total = 1.49**
Glaciofluvial top slope vs glacial till toe slope		0.0346	0.53	0.5944	0.05
Glaciofluvial toe slope vs glacial till toe slope		-0.519	-6.87	<0.0001	0.68
Glacial till top slope vs glacial till toe slope		0.434	8.66	<0.0001	0.76
Canopy basal area	1	3E-05	1.25	0.2144	
Time-since-fire	1	0.0012	1.07	0.2877	
Interaction of Canopy basal area and Time-since-fire	1	-5.88E-07	-2.52	0.0131	**0.43**

TABLE 3. Standardized least squares multiple regression of the effect of stand characteristics (slope position, canopy basal area and time-since-fire) on herbaceous **species evenness**. Relative importance was assessed using standardized partial regression (beta) coefficients.

A) Analysis of variance

Source	df	F	Prob>F	R^2
Model	6	3.37	0.0043	0.16
Error	111			
Total	117			

B) Parameter estimates

Variable	df	Parameter Estimate	t	Prob<F	Relative Importance (Beta Coefficient)
Intercept		0.688	36	<0.0001	0
Slope position:	3				**Total = 0.82**
Glaciofluvial top slope vs glacial till toe slope		-0.0387	-2.36	0.02	0.29
Glaciofluvial toe slope vs glacial till toe slope		0.0511	2.59	0.011	0.33
Glacial till top slope vs glacial till toe slope		-0.022	-1.75	0.083	0.2
Canopy basal area	1	-5E-06	-0.76	0.045	
Time-since-fire	1	0.00017	-0.62	0.539	
Interaction of Canopy basal area and Time-since-fire	1	6.3E-08	1.08	0.285	**0.23**

     Species richness and diversity (Table 4) were significantly different between all combinations of slope positions (p<0.05) with the exception of glaciofluvial top slopes and glacial till toe slopes (p>0.05). Therefore, within substrates, species richness and diversity decrease from top slopes to toe slopes. Evenness (Table 4) was only significantly different between glaciofluvial top and toe slopes

and between glacial till toe slopes and glaciofluvial top slopes ($p<0.05$). The results from the standardized multiple regression (Tables 1-3) and the multiple comparisons for slope position (Table 4) were consistent.

TABLE 4. Mean understory vascular plant species richness, diversity and evenness divided by slope position

Slope position	Richness	Diversity	Evenness
Glaciofluvial top slope	17.5	2.38	0.659
Glaciofluvial toe slope	10.07	1.8	0.752
Glacial till top slope	23.15	2.75	0.686
Glacial till toe slope	15.03	2.32	0.732

These comparisons can be summarized with respect to canopy species (Figure 3), since canopy species are organized according to slope position (Bridge and Johnson 2000). On glaciofluvial top slopes, jack pine stands are relatively species rich and diverse while toe slope black spruce stands have fewer species and are less diverse. On glacial till top slopes, aspen stands are species rich and diverse and toe slope mixedwood stands of aspen, white spruce and balsam fir are species poor and less diverse. However, jack pine stands and mixedwood stands have similar species richness and diversity even though jack pine stands are found on the top slopes of glaciofluvial substrates and mixedwood stands are found on toe slopes of glacial till. Evenness is only significantly different between jack pine and black spruce stands and between jack pine and mixedwood stands. However, remember that within slope position (i.e. canopy species), richness will differ because of basal area and age (Figure 2).
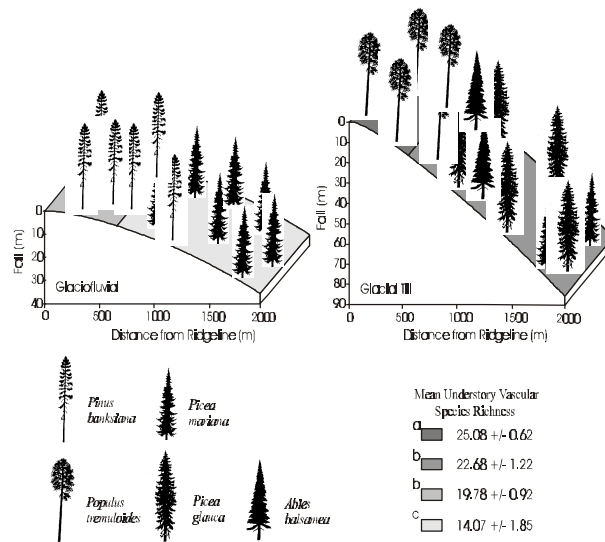
Fig. 3. General landscape patterns of vegetation composition where the shapes of the hillslopes depict the actual profile of most hillslopes in the southern mixedwood boreal forest (cf. Bridge and Johnson 2000). The tree symbols depict the general change in dominant canopy species down the hillslope, which is based on the relationship between stand positions on the moisture and nutrient gradients, and the stand distances from the ridgeline. Mean understory species richness is represented on the hillslopes using grey scales, where dark grey represents high species richness and light grey represents low species richness. Mean species richness values with the same letter are not significantly different (p<0.05) based on multiple comparisons and the Tukey-Kramer MSD test.

Species Richness in Relation to Community Organization

In our study area the community is organized such that high species richness is correlated to narrow tolerances and high overlap. Mean tolerance decreases with increasing species richness (Figure 4).
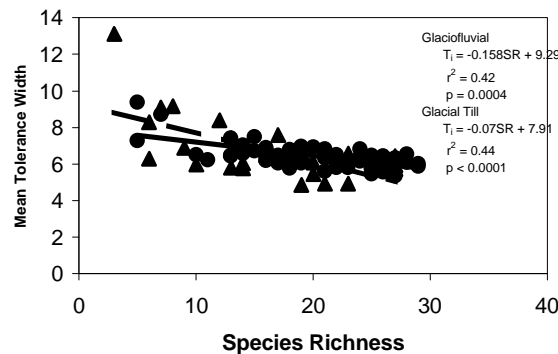

Fig. 4. The relationship between mean tolerance width and species richness of stands on glaciofluvial or glacial till substrate.

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From what we know of richness and slope position (Figure 3) we can now state further that mean tolerance decreases from top slopes to toe slopes on both glaciofluvial (p=0.0002) and glacial till (p<0.0001). Thus, when species richness was high, tolerances were narrow. Mean tolerance of species in glaciofluvial stands was about half of those found in glacial till stands and mean richness in glaciofluvial stands was about 70% of richness in glacial till stands. However, regardless of substrate, top slopes supported significantly more rare species than toe slopes (Table 5).

TABLE 5. The average number of species with a relative frequency of less than 5% (rare) within a stand and the standard deviation.

Slope Position	Average number of species with a relative frequency of less than 5%	Standard Deviation
Glaciofluvial top slope	9.22	5.22
Glaciofluvial toe slope	4.17	4.49
Glacial till top slope	13.94	4.33
Glacial till toe slope	7.35	5.1

Species richness was positively correlated to the overlap of species= tolerances (Figure 5). Overlap generally decreased from top slopes to toe slopes. Therefore, overlap was highest where species richness was high and lowest where species richness was poor. The decrease in overlap was more rapid in glaciofluvial stands than in glacial till stands.

Glaciofluvial
$R_o = -0.00058(Distance) + 0.91$
$r^2 = 0.89$
p = 0.0571
Glacial Till
$R_o = -0.00018(Distance) + 0.98$
$r^2 = 0.76$
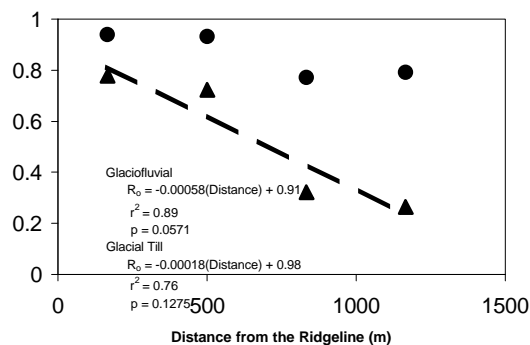p = 0.1275

Distance from the Ridgeline (m)

Fig. 5. The relationship between the overlap of tolerances along the glaciofluvial and glacial till hillslope where slope position was divided into intervals of distance from the ridgeline (see methods).

Beta diversity, the similarity in composition between different slope positions, ranged from 48% to 71% (Table 6). Glacial till top slopes and toe slopes had the highest beta diversity of 71%.

TABLE 6. Beta diversity (calculated as percent similarity) between each pair of slope positions.

Slope position	Glaciofluvial		Glacial till	
	top slope	toe slope	top slope	toe slope
Glaciofluvial top slope	1.00			
Glaciofluvial toe slope	0.59	1.00		
Glacial till top slope	0.54	0.48	1.00	
Glacial till toe slope	0.56	0.55	0.71	1.00

In summary, tolerances, overlap and percent of rare species decreased from top slopes to toe slopes. In addition, beta diversity was high (averaging 57%) across slope positions. Glacial till slopes have more overlap, narrow tolerances, more rare species, higher beta diversity and are richer than glaciofluvial slopes.

The Landscape Pattern of Species Richness

The supervised classification (Figure 6) using canopy species, hillslope position and the time-since-fire map was 76% accurate and had a kappa coefficient of 0.72. The majority of pixels were correctly classified (Table 7) with accuracies (reading diagonal in the table) ranging from 60.4% for glaciofluvial to 92.1% for low density aspen. The greatest misclassifications occurred between adjacent classes, e.g. glaciofluvial species rich and poor classes and glacial till species rich and poor classes (Table 7). This likely occurs because continuous variables have been divided into discrete classes.

TABLE 7. Error matrix: the percentage of pixels assigned to a category (using a maximum likelihood classifier (PCI Inc.)) relative to the actual category as verified by field data. The columns represent the field data while the rows indicate the classification generated from the LANDSAT TM image. Reading diagonal in the table gives the percentage of pixels correctly assigned to a category.

Category		Glaciofluvial		Glacial Till		Treed	Shrub	Deep	Shallow	Intermittent	Grassland	Low Density
	Null	Species Rich	Species Poor	Species Rich	Species Poor	Marsh	Marsh	Lakes	Lakes	Lakes		Aspen
Glaciofluvial Species Rich	1.6	60.4	15.2	5.1	7	3.5	4.7	0	0	0	0	2.5
Glaciofluvial Species Poor	2.7	3.4	82.4	3.4	7.4	0	0.7	0	0	0	0	0
Glacial Till Species Rich	8.5	5.4	7.1	63.5	11.5	1.1	1.1	0	0	0	0	1.8
Glacial Till Species Poor	7.7	4.3	9.6	13.6	63.3	1.3	0.2	0	0	0	0	0
Treed Marsh	5.4	4.4	4.9	1.5	1.7	77.5	4	0	0	0	0	0.6
Shrub Marsh	10.4	5.3	0.1	0.4	0	8.6	67.3	0	0	0.4	0.8	6.7
Deep Lakes	11.8	0	0	0	0	0	0	84.5	1.7	2.1	0	0
Shallow Lakes	4.7	0	0	0	0	0	0.1	26.7	66.1	2.4	0	0
Intermittent Lakes	13.6	0	0	0	0	0	0.1	1.8	0	84.5	0	0
Grassland	13.5	0	0	0	0	0	4.3	0	0	0	82.2	0
Low Density Aspen	1.6	0.8	0	0	0	0.6	4.8	0	0	0	0.1	92.1

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Fig. 6. The upland understory plant species richness for Prince Albert National Park based on a supervised classification using the canopy species, hillslope position, substrate and a time-since-fire map.

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DISCUSSION

The mixedwood boreal forest (cf. Rowe 1972) of western Canada is relatively poor in vascular plant species. In the 121 stands sampled, 122 vascular species were recorded, 6 of which were trees. Further, the similarity between stands (beta diversity) was high. All pairs of stands shared at least 48% of their vascular species. Richness was the primary determinant of diversity, evenness being relatively constant.

The environmental variables of moisture and nutrients (i.e. slope position) are relatively more important in predicting herbaceous plant species richness, diversity and evenness compared to light availability and time-since-fire. Moisture and nutrient gradients are related to topographic position on the hillslope and surficial geology (Bridge and Johnson 2000). Therefore, the hillslope is the fundamental unit of species richness and diversity. Hillslopes are not assembled on the landscape randomly but are structured according to ridgelines and stream channels. Therefore, moisture and nutrient gradients are prevalent across the landscape due to the repeatability of hillslopes (Bridge and Johnson 2000). As soil water diverges on top slopes and converges on toe slopes (Anderson and Burt 1977, Harr 1977, Sinai et al. 1981, O=Loughlin 1981, 1986, Wood et al. 1988), it carries with it nutrients that are leached from top slopes to accumulate in toe slopes (Trudgill 1988, Litaor 1992, Tsuboyama et al. 1994). Therefore, top slopes of similar surficial material are relatively dry and nutrient poor while toe slopes are wet and nutrient rich (Malo et al. 1974, Harr 1977, Anderson and Burt 1977, Johnson 1981, O=Loughlin 1981, Sinai et al. 1981, Ciha 1994, Bridge and Johnson 2000).

Communities are organized along the moisture and nutrient (hillslope) gradient such that species rich communities show high overlap of narrow tolerances. The narrow tolerances result in a greater subdivision of the gradient and this allows for not only more species (high species richness) but also more species with lower abundances (more rare species). Species with narrow tolerances also have lower relative abundances (McNaughton and Wolf 1970, Johnson 1977) and lower biomass (Parrish and Bazzaz 1976). A possible reason for this is that species with wide tolerances and high abundance interact with individuals of the same species so that divergence of the individual=s tolerance occurs and thus the species= tolerances increase (Johnson 1977). Narrow tolerance species interact with individuals of different species. This interaction does not cause the divergence of tolerances to the same extent. Consequently, tolerances remain narrow and species diversity remains high.

The overlap of tolerances in communities is organized such that overlap decreases as species richness decreases. The high overlap is due to the high beta diversity between communities. Compared with glacial till stands, glaciofluvial stands have narrower mean tolerance widths and lower

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overlap and thus 20% lower beta diversity. Further, glaciofluvial overlap is low because mean tolerance width is narrower on glaciofluvial top slopes than on glacial till top slopes.

It is not too surprising that the interaction between light availability (canopy basal area) and time-since-fire is more important in determining species richness, diversity and evenness than either of these variables separately. Many studies in the boreal forest have suggested that light availability and time interact to produce understory vegetation patterns (e.g. De Grandpré et al. 1993, Lieffers 1994, De Grandpré and Bergeron 1997). As richness (Figure 2) remains constant, the trade-off is between high basal area (low light availability) and a short time-since-fire or low basal area and a long time-since-fire. Thus, there are two means of maintaining the same level of richness. The levels of richness (Figure 2) also show the effect of slope position (moisture and nutrient gradients) with high richness on top slopes and the low richness on toe slopes. However, again remember that within a slope position (i.e. canopy species), richness is also determined by basal area (light availability) and age (time-since-fire).

The pattern of understory plant species richness is related to the pattern of canopy trees where trembling aspen stands have high species richness and high diversity, jack pine and mixedwood stands have intermediate species richness and diversity and black spruce stands have low species richness and diversity. This is because both the canopy trees (Bridge and Johnson 2000) and the understory herbaceous richness are organized primarily by moisture and nutrient gradients which are determined at the hillslope scale. The similarity in richness and diversity between jack pine and mixedwood stands is likely due to a combination of both moisture gradients and light availability. Both moisture and nutrients increase downslope due to the surficial geology, however the magnitudes of moisture and nutrients differ. On glaciofluvial substrate, under jack pine stands, moisture and nutrients are low while downslope black spruce stands are characterized by high moisture and nutrients. On glacial till, moisture is low and nutrients are intermediate in aspen stands while further downslope in mixedwood stands moisture is intermediate and nutrients are high (Bridge and Johnson 2000). Therefore, both jack pine and mixedwood stands dominate the intermediate portion of the moisture gradient (Bridge and Johnson 2000). Also, light availability in mixedwood and jack pine stands is similar since light availability is greatest in aspen stands, lower in white spruce stands (Lieffers and Stadt 1994) and intermediate in pine stands. In a mixedwood stand of aspen and white spruce, light availability should also be intermediate.

Perhaps one of the most interesting results of this study is the ability to map species richness at the landscape scale. A LANDSAT TM image for cover type and amount, the DEM for hillslope position (i.e. moisture and nutrients) and the time-since-fire map were used to produce a supervised classification of richness (the most important determinant of diversity). Misclassification occurred

between slope positions of similar surficial geology. The richness map reveals that the pattern of richness shows small scale variability. This is due to the importance of hillslope position in determining both moisture and nutrient gradients and canopy species and coverage. Comparison of the richness map to the time-since-fire map (Figure 7) shows that under the present fire frequency regime, the larger scale pattern of forest age caused by fire is not clearly reflected in the richness map. In short, the hillslope appears to be a more fundamental unit of species richness than fire.

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Fig. 7. A digitized map of time since the last fire in Prince Albert National Park (Weir et al. 2000). The map colours range from light grey for the youngest stands through to dark grey for the oldest stands. The lakes are coloured white.

APPLICATIONS

Over the last 25 years, forest management has changed from a goal of simply regenerating the target tree species to sustainable ecosystem-based forest management (Perry 1998). Concern has centred on the conservation of biodiversity (Walton 1997, Boyle 1998). Conservationists suggest that managers should maximize the number of species preserved (Walton 1997), often with little understanding of ecological processes (Pickett et al. 1992). In fact, one goal of ecosystem-based forest management is to preserve biodiversity by emulating the ›natural‹ (pre-European) disturbance regime (Hunter 1993, Attiwell 1994, Bender 1994, Weetman 1994). This goal implies that natural disturbance play a significant, if not principal, role in determining diversity and that the variation in disturbance in the past (natural) is preferable to the current (European) disturbance variation. Thus, emulation, usually through forestry practices, is intended to remain within this preferred natural disturbance variation. Further, ecosystem management often implies that current and past forestry practices are outside of this natural disturbance variation and that diversity has changed as a consequence.

The boreal forest is considered a fire dominated ecosystem because fire is the primary large scale disturbance. This implies that fire is the principal determinant of diversity. However, as we have seen in this study, the vascular plant diversity in the mixedwood boreal forest is primarily determined by the moisture and nutrient gradient. This gradient is determined by the hillslope hydrology and surficial geology. Thus the primary pattern of vascular plant diversity is determined by both the hillslope shapes and the hillslope assembly between ridgelines and streams. The hillslope-basin structure ensures that species occupy a constant proportion of the basin regardless of basin size (Bridge 1996). This characteristic is due to the allometric relationship between drainage basin area and length. Large basins are thus disproportionately longer and narrower than smaller basins and therefore, hillslope length tends to remain constant (Hack 1957, Gray 1961, Shreve 1974, Newsson 1978). Thus, hillslope and surficial geology are the principal determinants of the variation in vascular plant diversity across the landscape.

Time-since-fire does affect diversity through its interaction with canopy coverage. Figure 2 shows clearly how these three variables organize vascular plant diversity. In the mixedwood boreal forest, the fire frequency has changed at least twice in the last 200 years (Weir et al. 2000). These changes have been attributed to large scale climatic changes because of their common timing over large parts of the boreal forest (Johnson 1992, Bergeron and Archambault 1993, Johnson et al. 1998). Changes in fire frequency were found to be unrelated to vegetation type, slope or terrain. The variation in the fire cycle (1/fire frequency) has been between 15 years and 75 years. Studies in other parts of the boreal forest have found variation in the fire cycle of the same magnitude but not

necessarily the same values (the fire cycle tends to be longer further north and in the wetter (eastern) parts of the boreal forest) (Johnson 1992, Bergeron and Archambault 1993). In fact, the data on fire frequency suggests that the ›natural‹ situation is frequent changes in fire frequency within a range between approximately 15 and 150 years. Therefore, there is no one preferred historic fire frequency that should necessarily be emulated (Johnson et al. 1998).

What does the variation in fire frequency in the past tell us about variation in diversity in the mixedwood boreal forest? Our findings indicate that shorter fire cycles will increase diversity and longer fire cycles will decrease diversity. However, the variation was never large enough to significantly change the diversity. This assumes that changes in climate were not large enough (or perhaps long enough) to cause major changes in the moisture and nutrient gradient. This assumption, however, should be accepted with considerable care given our level of understanding. Current forestry practises follow a rotation schedule of 70 years (Weyerhaeuser Canada 1999) in keeping with the current approximate 75 year fire cycle. Also cutting is being done to more closely follow the distribution of ages found in the fire frequency distribution before European intervention.

Our results suggest that fire frequency is not the principal determinant of diversity. Instead, the hillslope (and surficial geology) is the fundamental unit of diversity together with its interaction with light and fire (Figure 2). Furthermore, there is no one preferred historic fire frequency that should necessarily be emulated. The Anatural@ average fire cycle has ranged from 15 to 150 years. It is clear that site preparation such as disking and chaining after clear felling will lead to changes in vascular plant composition and sometimes diversity (Chipman 2000). This seems to be a consequence of these site preparation techniques not mimicking litter and duff consumption patterns in fire (Miyanishi et al. 1999). We still have a great deal to learn about fire behavior and its effects to be able to emulate fire in our forestry management (Johnson and Miyanishi in press).

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