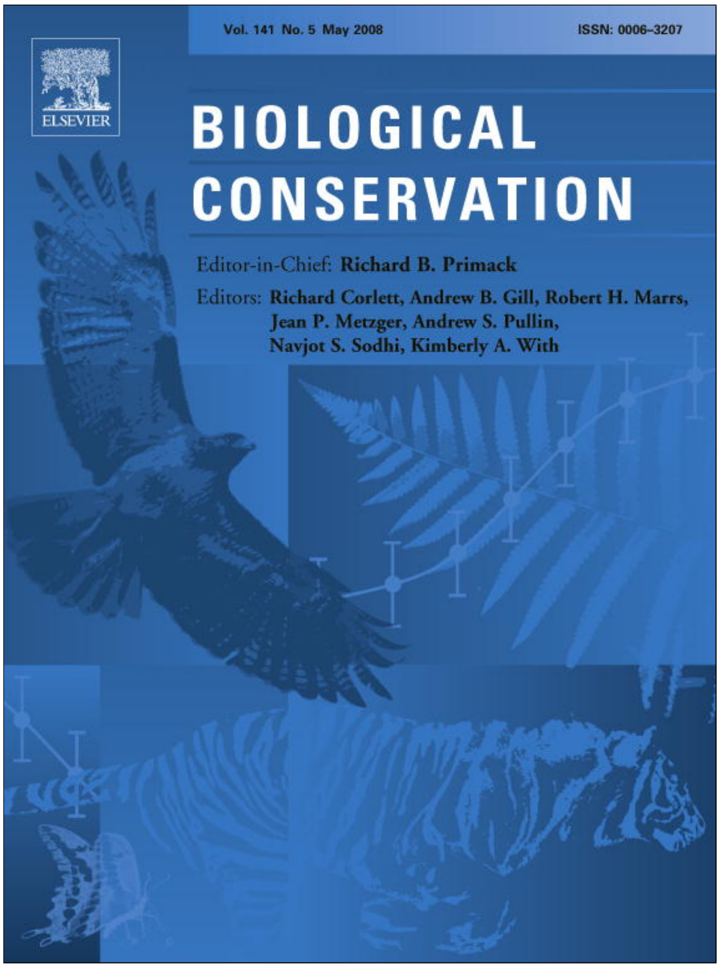
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Does time or habitat make old-growth forests species rich? Bryophyte richness in boreal *Picea mariana* forests

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ABSTRACT

The relative importance of time since disturbance and habitat variables in creating diversity in old-growth forests will influence conservation strategies. However, the independent roles of these factors are not well understood, as they are rarely examined independently. This study examines the respective roles of habitat variables and time (stand age) in determining bryophyte diversity in *Picea mariana* (Mill. (BSP)) forests. Bryophytes are frequently used as indicators of old-growth forest, but their true dependence on forest continuity is unknown. Bryophytes were classified into taxonomic–habitat guilds: true mosses (forest), forest liverworts, bog liverworts and sphagna (bog). Diversity increased with age and peaked at approximately 275 years since fire, driven by liverworts. Multiplicative habitat modeling indicated that time and habitat played different roles for the different taxonomic–habitat guilds. True mosses and forest liverworts were primarily influenced by habitat variables, while sphagna and bog liverworts were influenced by time and habitat variables. The models for sphagna were particularly strong, indicating that many important factors were included, while forest liverwort models were particularly weak. This unexplained variability may represent site specific random factors, such as secondary disturbances that create habitat in a fully occupied space. Overall, high richness was created by small species dependent on habitat variables and chance factors for establishment. Therefore, time since disturbance was not the primary factor limiting richness in these forests. These results suggest that in boreal North America, where forest fragmentation is limited and recent, conservation strategies that emphasize habitat variables rather than forest continuity may be effective for some bryophytes.

1. Introduction

Habitat diversity is one of the main driving forces of plant community richness in forests, as a local variety of habitat types result in the needs of a greater number of species being met (DeGrandpré and Bergeron, 1997; Pharo and Beattie, 2002; Beatty, 2003; Mills and MacDonald, 2005). As a result conservation efforts frequently focus on creating or maintaining appropriate habitat for species or communities deemed to be at risk (Humphrey, 2005; Bergeron et al., 2007; Vanha-Majamaa et al., 2007).

The lack of some plant species in secondary forests that resemble undisturbed forests (established after a stand replacing anthropogenic disturbance) in Europe and temperate North America (e.g. Meier et al., 1995; Hansson, 1997) has resulted in a focus on the role of propagule dispersal. Species deemed to be dispersal limited because of the small distances that propagules travel in a single generation have in

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some cases been found to be restricted to forest stands which have not been disturbed, or have experienced only minimal anthropogenic disturbance (Gustaffson and Hallingbäck, 1988; Meier et al., 1995; Ross-Davis and Frego, 2002). This implies that the longer residence time of habitat within these "old-growth" forests has permitted dispersal limited species to reach and colonize the habitat. Conservation strategies should in this case focus on preserving undisturbed "old-growth" forest stands and assuring forest continuity over part of the landscape.

Bryophytes are a group for which both time and habitat appear to be important in driving community richness (e.g. Ross-Davis and Frego, 2002 vs. Mills and MacDonald, 2005). As they are frequently epiphytes or epixylics dependent on coarse woody debris (Berg et al., 1994; Nordén et al., 2007) they have been used as indicators of old growth forests in temperate and boreal zones (Nordén and Appelqvist, 2001; Frego, 2007). However, the relative roles of time and habitat in creating and maintaining bryophyte diversity has not been adequately addressed and it has consequently been questioned whether bryophytes truly are good indicators of old growth forest (Nordén and Appelqvist, 2001; Öckinger et al., 2005; Frego, 2007).

The overall objective of this study is to determine the relative roles of time (as a proxy for dispersal limitation), and habitat availability in generating and maintaining bryophyte diversity in boreal black spruce (*Picea mariana* (Mill. (BSP))) forests. Specifically we addressed two questions: (1) Are there more bryophyte species present in old forests compared to young forests? (2) Is this higher diversity due to (a) more time for dispersal limited species to reach the forest stand; or (b) a greater structural (micro-habitat) diversity at the stand scale in older forests?

2. Methods

2.1. Study area

The Clay Belt of Quebec and Ontario (48° 46′N, 79° 13′W) is a major physiographic region created by the deposits left by Lakes Barlow and Ojibway after their maximum extension during the Wisconsonian glacial period (Vincent and Hardy, 1977). In its northern portion, it is dominated by black spruce (*P. mariana*)-feather moss (*Pleurozium schreberi*) forests (Grondin, 1996). This region is particularly prone to paludification (development of a treed bog from a forest on mineral soil over time; Foster, 1985; Fenton and Bergeron, 2006a) between fires due to its poorly drained clayey soil, mild topographic variation, and moderately cold humid climate [889.9 mm of precipitation annually; annual mean temperature 0.7 °C (Environment Canada, 2004)]. Forests intermingle with ombrotrophic bogs at the landscape scale, and anthropogenic disturbance (forest harvest) began in the 1970s in the southernmost extreme of this region, and in the 1990s in the north, where most of the sites are located. The dominant natural disturbance type is large fires that kill all above ground vegetation. Between 1850 and 1920 the fire cycle was ca. 135 years, and it has since increased to ca. 398 years (Bergeron et al., 2004), as a result the average age of the forests is in excess of 100 years.

2.2. Site selection and sampling

The chronosequence approach was used to address successional changes. The main weakness of this approach is the possibility that initial conditions were not identical for all stands. While this is a valid argument, the chronosequence used here has been extensively validated. This study is part of a larger project, investigating the causes and consequences of paludification on the Clay Belt of Québec and Ontario. As such the chronosequence has been validated via stem analysis (Lecomte et al., 2006), and in situ analysis of the forest floor (Lecomte et al., 2005). In addition site selection included a detailed analysis of slope and soil texture to establish that the sites established in similar edaphic conditions. Similarly, the establishment of the stands after a high severity fire was verified by determining that charcoal was uniquely found at the interface of the mineral and organic horizons in the soil. See Lecomte et al. (2005) for a more detailed description of site verification.

During the summer of 2003, 13 black spruce dominated sites ranging from 50 to 350 years since fire were sampled. Sites were chosen based on a stand initiation map of the area (Bergeron et al., 2004) and were selected in the field on the basis of proximity to road, and presence of a mild slope and clay dominated soil. They are spread over an area approximately 5000 km^2. Time since fire (TSF) was established by verification of stand initiation map dates by dating basal cross-sections of a few dominant trees (for more details see Lecomte et al., 2006). However, in the oldest stands (>200 years TSF) C^{14} dating of charcoal particles in a few of the sites suggest that the oldest trees were established a considerable period after stand replacing fire. While the C^{14} dates suggest that the stands are considerably older than first believed (300–1000 years) they did not alter the order or the groupings of the sites. For this reason dendrochronology dates were used as they are consistent across the sites.

Within each site, five plots of 100 m^2 were installed, with four nested quadrats of 25 m^2. The first 100 m^2 plot was established at least 50 m from the road, and subsequent plots were placed at least 10 m apart along a randomly chosen bearing. Within each 25 m^2 quadrat all bryophyte species were identified and their percent cover visually estimated. Special habitats, such as coarse woody debris, exposed mineral soil, and water holes at the bases of trees ("peat pits") were sampled with particular care. Samples of all non-easily identifiable species were retained and were identified in the lab, particularly troublesome liverwort species were verified by an expert (although the first author assumes responsibility for any errors). The samples are retained at the Université du Québec en Abitibi-Témiscamingue collection. Nomenclature follows Anderson (1990) for *Sphagnum* spp., Crum and Anderson (1981) for the mosses, and Schuster (1965–80) for the liverworts.

A series of habitat variables (both abiotic and biotic) affecting substrate availability and microclimate were measured in order to interpret the bryophyte pattern (Table 1). Substrate variables included: depth to mineral soil, canopy cover, % cover of coarse woody debris (>5 cm in diameter; CWD) by decay class [1 freshly fallen; 2 bark loosening; 3 bark falling, softening of wood; 4 very soft, shape collapsed (modified from

Table 1 – Mean values of environmental variables for each time since fire group

Variable category	Variables	Time since fire				
		<100	150	200	275	>350
Paludification	Forest floor depth	19.25 ± 0.69a	31.75 ± 1.90b	45.48 ± 2.79c	62.37 ± 3.49d	90.00 ± 10.30e
	Water table depth	30.86 ± 0.94a	48.87 ± 1.42c	51.35 ± 0.81c	40.06 ± 1.67b	28.07 ± 1.62a
	Water table index	−12.76 ± 1.20a	−18.61 ± 2.10a	−0.99 ± 1.76b	16.07 ± 3.28c	65.21 ± 10.97d
CWD[A]	% CWD 1	1.40 ± 0.63	0.80 ± 0.46	0.20 ± 0.17	0.30 ± 0.25	0.00 ± 0.00
	% CWD 2	4.50 ± 0.84ab	6.00 ± 1.22ab	7.90 ± 1.43b	6.30 ± 1.35b	0.00 ± 0.00a
	% CWD 3	7.20 ± 0.75	7.30 ± 1.18	11.60 ± 1.10	13.80 ± 1.24	8.50 ± 1.10
	% CWD 4	3.70 ± 0.57a	0.80 ± 0.28ab	6.60 ± 0.74b	6.90 ± 0.71b	4.00 ± 0.93a
	% Mineral soil	1.70 ± 0.37a	1.20 ± 0.33a	2.00 ± 0.43a	4.30 ± 0.86b	3.00 ± 0.56ab
	% Leaves	10.90 ± 1.80b	1.40 ± 0.64a	2.10 ± 0.74a	2.90 ± 1.4a	0.00 ± 0.00a
	# Tip ups	1.50 ± 0.17ab	0.90 ± 0.17a	1.70 ± 0.12b	2.10 ± 0.15b	0.80 ± 0.25a
	# Snap offs	2.60 ± 0.26	2.60 ± 0.20	2.30 ± 0.17	2.20 ± 0.22	2.40 ± 0.27
	% Ericaceous	5.20 ± 1.24a	31.30 ± 3.42b	64.20 ± 2.68cd	59.90 ± 2.78c	76.00 ± 1.84d
Canopy	Dens. conif	59.00 ± 1.42c	45.00 ± 1.59b	40.20 ± 1.75b	29.90 ± 1.87a	25.20 ± 3.29a
	Dens. decid	0.65 ± 0.026	0.35 ± 0.22	0.035 ± 0.035	0.21 ± 0.13	0.00 ± 0.00
	Dens. open	40.37 ± 1.36a	54.69 ± 1.54b	59.77 ± 1.76b	69.88 ± 1.87c	74.83 ± 3.29c
	Tot basal area	0.11 ± 0.0048d	0.089 ± 0.0069c	0.060 ± 0.0041b	0.050 ± 0.0042b	0.018 ± 0.0038a
	Mean dbh[B]	14.19 ± 0.34c	12.59 ± 0.26b	13.81 ± 0.29bc	13.82 ± 0.49bc	9.49 ± 0.27a
	BA[C] b spruce[D]	0.095 ± 0.0044d	0.086 ± 0.0067c	0.058 ± 0.0041b	0.048 ± 0.0042b	0.018 ± 0.038a
	Lcr[E] b spruce	31.00 ± 1.20b	33.00 ± 2.10bc	37.00 ± 2.50bc	41.00 ± 3.20c	16.00 ± 4.30a
	BA balsam fir	0.0009 ± 0.0004b	0.00 ± 0.00a	0.0014 ± 0.0005b	0.0018 ± 0.0006b	0.00 ± 0.00a
	Lcr balsam fir	21.0 ± 9.8	0.00 ± 0.00	36.00 ± 6.5	58.33 ± 8.6	0.00 ± 0.00
	BA jack pine	0.013 ± 0.0028	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	Lcr jack pine	35.00 ± 1.9b	0 ± 0.0a	0 ± 0.0a	0 ± 0.0a	0 ± 0.0a
	BA aspen	0.0031 ± 0.0012b	0.0015 ± 0.0015b	0.0004 ± 0.0004a	0.00 ± 0.00a	0.00 ± 0.00a
	Lcr aspen	15.00 ± 4.0	20.00 ± 0.0	30.00 ± 0.0	0 ± 0.0	0 ± 0.0
	BA tamarack	0.00 ± 0.00	0.0008 ± 0.0005	0.00 ± 0.00	0.0002 ± 0.0002	0.0003 ± 0.0003
	Lcr tamarack	0 ± 0.0	50.00 ± 14.1	0 ± 0.0	60.00 ± 0.0	80.00 ± 0.0

Values are means followed by standard error. Values followed by different letters are significantly difference, $p < 0.05$; $a < b < c$, etc. See Section 2 for variable codes.

A CWD: coarse woody debris.
B DBH: diameter at breast height.
C BA: basal area.
D b spruce: black spruce.
E LCR: live crown ratio.

Söderström, 1987)]; % cover of deciduous leaves; % cover of peat pits (water holes developed in deep organic forest floors). Factors affecting the microclimate included stand variables such as density measured as basal area (m^2/ha) of trees greater than 8 cm in diameter (breast height) by species and in total, live crown ratio (lcr, percent of stem with living foliage, which influences light availability at the forest floor), # of tip ups, and # of stem breaks. The total % cover of ericaceous species was visually estimated. *Rhododendron groenlandicum* was the dominant ericaceous species, with *Kalmia angustifolia* and *Chamaedaphne calyculata*.

Steel rods 120 cm long were used to measure the depth of water table in the soil in each 25 m^2 quadrat in 7 of the 13 chronosequence sites. The rods are placed in the soil for several weeks and orange–brown rust forms at the interface of the oxygenated and non-oxygenated zones of the soil profile (Carnell and Anderson, 1986), which approximates the position of the water table. When the rods were removed 40 days later the distance from the soil surface to the zone of orange–brown rust was identified and measured. In order to account for the change in apparent soil surface position (due to increase in forest floor thickness with age) an index was created, where forest floor thickness was subtracted from orange/brown rust depth. Therefore, values less than 0 indicate that the water table was in mineral soil, while values greater than zero indicate that the water table was in the forest floor. For more details on the habitat variables see Fenton and Bergeron (2006a).

The variable "habitat richness" was included in initial analyses of the data, but was not found to be significant in any model, and was subsequently dropped.

2.3. *Analyses*

Sites were separated into five age groups: 100 TSF (85–95 TSF, 4 sites, 80 quadrats), 150 TSF (130–150 TSF, 2 sites, 40 quadrats), 200 TSF (180–220 TSF, 3 sites, 60 quadrats), 275 TSF (260–300 TSF, 3 sites, 60 quadrats) and >350 TSF (1 site, 20 quadrats). Strictly speaking the 20 quadrats per site are pseudoreplicates, however the intra plot and inter plot variability was shown to be very high in a previous study (Fenton and Bergeron, 2006a), justifying the use of quadrats as individual samples.

As bryophytes demonstrate a variety of life-strategies with different habitat requirements and reproductive systems (*sensu* During, 1992) the species list was divided into taxonomic/habitat guilds: mosses, sphagna, forest liverworts and bog liverworts. Mosses (bryopsida or "true mosses" Buck and Goffinet, 2000) in this dataset were primarily species occupying spatially and temporally discrete habitats most commonly found in forests (e.g. tree trunks, coarse woody debris (CWD)). These "pocket species" (sensu Økland et al., 2003) were numerically superior to the more abundant but species poor forest floor and feather mosses (*P. schreberi, Hylocomium splendens, Ptillium crista-castrensis, Dicranum polysetum, Dicranum ontariense*). As this latter group were so few and so ubiquitous, they were not split into a second taxonomic/habitat guild. Sphagna (sphagnopsida or peat mosses) were predominantly found in habitats associated with bogs (e.g. forest floor composed of a deep, wet organic layer). The liverworts (Hepatophyta), which were predominantly pocket species, were divided into "forest liverworts", which occurred in habitats primarily found in forests and "bog liverworts" which occurred in habitats primarily found in bogs. Classification of species into taxonomic/habitat guilds is available in Appendix A.

Species area curves and richness and evenness by taxonomic/habitat guild group were calculated with PC-Ord v.4 (MjM Software, 2000). Richness in this study is simply the number of species found, while evenness is calculated as $H'/\ln(\text{richness})$, where H' represents Shannon's diversity index. The mean values of richness and evenness per plot were compared among age groups with ANOVA followed by Bonferroni post-hoc tests, $p = 0.05$ (SPSS v. 12.0).

Non-parametric multiplicative regression [NPMR; Hyperniche v. 1.04 (McCune and Mefford, 2004)] was used to create habitat models of plot level species richness and evenness, in order to assess the relative roles of age and habitat in creating and maintaining species diversity. NPMR overcomes many of the problems associated with trying to describe species habitat models with statistical methods that are essentially linear and do not take into account complex interactions of habitat factors (McCune, 2006). Default settings were used for all factors. For each dependent factor (e.g. moss richness) the best model for a given number of habitat factors (independent factors) are suggested. Each model includes a measure of fit (XR^2) and a tolerance value for each habitat factor. Tolerance is the breadth of values that a habitat factor can vary without invoking a response in the dependent factor (e.g. size of the plateau). As with multiple regression a balance between increased precision and the inclusion of spurious factors is needed in selecting a model. Once a model was selected (generally when adding an additional factor did not increase the fit of the model by more than 0.01), the sensitivity of the habitat factors was evaluated. Sensitivity indicates the size of the response in the dependent factor for each incremental change in the habitat factor. For example if the sensitivity of moss richness to CWD 4 is 0.5, changing the value of CWD 4 from 1 to 2 result in a 0.5 increase in moss richness.

The role of age in the models was assessed in two ways. Initially the tolerance and sensitivity of the independent variable age was assessed in the best model for each dependent factor. Subsequently, to ensure that age, which was correlated with most of the habitat factors, did not mask the influence of any habitat variables, the models were re-run without the independent variable "age" in the dataset. The use of multiple overlapping data sets with NPMR and subsequent comparison permits complex interactions between different variables to be teased out, as was shown by Derr et al. (2007) and Ellis et al. (2007).

Once the models were complete, habitat factors were summarized into variable categories in order to determine which type of factor was the most important (Table 1). The categories were: paludification (forest floor thickness, water table position, water table index), CWD (CWD 1, CWD 2, CWD 3, CWD 4), % cover of mineral soil, % cover of leaves, # tip ups, # of break offs, % cover of ericaceous species, and canopy (amount of open, coniferous and deciduous canopy; total basal area; mean tree size; and the basal area and live crown ration of black spruce, jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*), and tamarack (*Larix laricina*)). The number of times habitat factors were included in all the models as a dominant factor (strongest factor or with a sensitivity over 0.5) was assessed as was the total number of inclusions. This number was then divided by the number of factors within a category (e.g. by 3 for paludification) to give the relative frequency of the variable category. Only the richness models are presented, as the evenness models illustrated the same trends.

As the NPMR technique is new and unfamiliar, stepwise linear regressions (SPSS v. 12.0) were performed on the dataset as well, to verify the Hyperniche procedure. As the results were generally similar, they are not presented in this article, but are available in Appendix B.

3. Results

3.1. *Change in richness and evenness across a time gradient*

The bryophyte communities found were surprisingly rich, and 87 species were identified in total: 36 mosses, 11 sphagna and 40 liverworts. Forty-eight species were found in the 100 TSF group, 29 species in the 150 TSF group, 59 and 62 species were found in the 200 and 275 TSF age groups, respectively, and 34 species in the >350 TSF group. Despite this richness, species area curves (Fig. 1) indicate that even with extensive sampling only the sphagna reached a plateau in richness. Therefore, further sampling would be expected to reveal additional species of mosses and liverworts. Illustrating the difficulty in exhaustively describing the community is the fact that most species were infrequent, with over 50% of species occurring less than six times in the entire data set (data not shown).

At the scale of 25 m^2 quadrats, total species richness generally increased with time since fire, from 9.04 and 7.63 species in the 100 TSF and 150 TSF groups to 11.25 and 10.79 species per quadrat in the 275 and >350 groups (Fig. 2). Within taxonomic groups, moss richness declined with TSF, while sphagna and liverwort richness increased with TSF.

Total species and moss evenness was highest in the 150 TSF, 275 TSF and 350 TSF age groups (Fig. 2) at 0.613 and

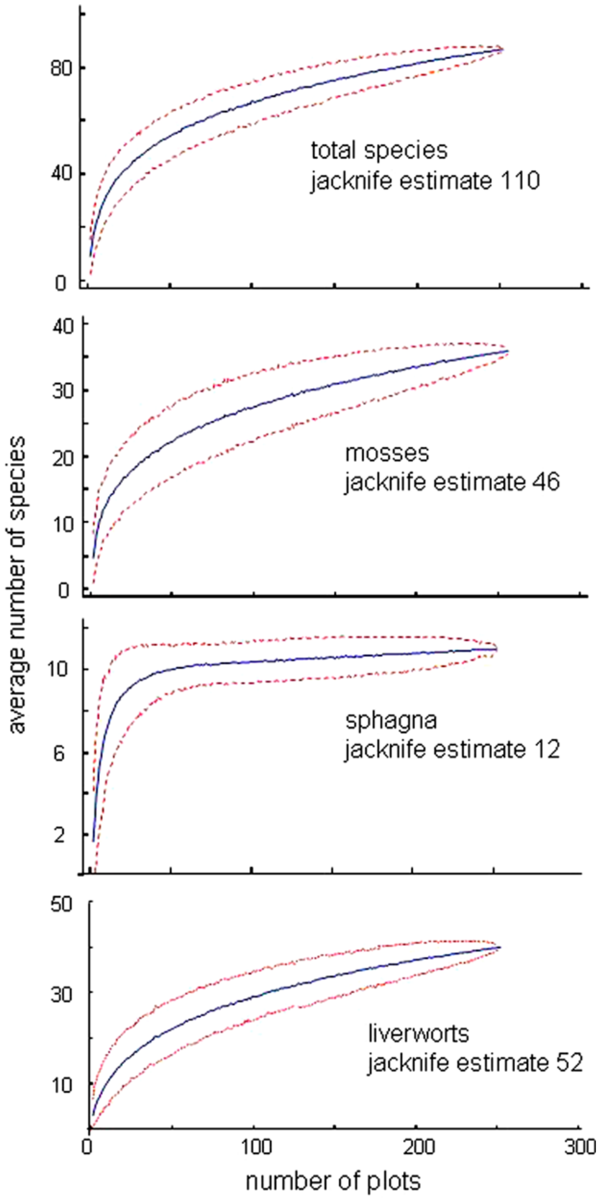

Fig. 1 – Species area curves (solid lines) with confidence intervals (dashed lines) for entire data set and taxonomic subgroups. First-order jackknife estimates are included for each curve. Jackknife estimates approximate the actual number of species if all species were found by sub-sampling the data set.

0.418, respectively. Sphagna evenness increased with times since fire to peak at 0.562, and liverwort evenness did not vary among the age groups.

3.2. *Mechanisms of diversity creation and maintenance*

3.2.1. *The role of time*

The models for richness and evenness for the entire dataset differed dramatically in strength, at 0.238 and 0.789XR^2, respectively (Table 2). Time, as represented by post-fire stand age, was an important factor in the model for evenness with a drop in XR^2 of over 20% when age was excluded as a potential factor (Table 2) and the tolerance for age was small and the sensitivity high. In contrast, there was very little change in the XR^2 when age was excluded from the richness model (Table 2) despite a relatively high sensitivity for age. This indicates that the variance explained by age is explained by habitat factors when age is excluded.

When the dataset is divided by taxonomic/habitat guilds sphagna had the strongest models (highest XR^2) while the liverworts had the weakest (Table 2). In the moss models, of intermediate strength, age was only an important factor in the evenness model, as the XR^2 dropped only 5% when age was excluded in the richness model. This is despite the high sensitivity of age in the moss richness model. As with the total dataset, the variance explained by age was absorbed by other variables when this variable was excluded. Age was a relatively important factor in the sphagna models, with decreases of 16% and 21% for the eveness and richness models, respectively, when age was excluded. However, tolerance for this factor was relatively large and of only a moderate sensitivity. For the liverwort models, age was only an important factor for the richness models, specifically the total liverwort model and the bog liverwort model. However, the results for the total liverwort model are contradictory as the XR^2 increased when age was excluded; this is despite a small tolerance and a high sensitivity for this factor. This suggests that habitat factors were able to explain the variance explained by age. Age was not selected as a factor in the forest liverwort richness model nor the total or forest liverwort evenness models. Bog liverwort richness was influenced by age, as indicated by the drop of 25% in the XR^2 when it was excluded from the model, however tolerance for age was relatively broad and sensitivity fairly low (0.40). Bog liverwort evenness was not modeled, as it is a qualitative variable, as all species were at "trace" levels.

3.2.2. *The role of habitat factors*

While age was an important factor in determining community diversity in some of the models, a considerable amount of variability was explained in models where age was excluded as a potential factor (Table 2). Age was the most frequent dominant factor (the most important factor as determined by sensitivity, and all factors with a sensitivity over 0.5) in the richness models when it was included (Fig. 3). Removing the age variable allows the portion of the habitat factor that is auto-correlated with age to be expressed, and represents the true impact of the habitat variable on the modeled variable. When age is not included, paludification variables become the most frequent dominant factors (100% of richness models; Fig. 3).

While dominant factors have a larger impact on the models, all variables included in the models were significant. When all of these factors are examined, paludification variables, the number of breakoffs, and % cover of mineral soil were all relatively common in the richness models where age is included (each present in 13% of models). In the richness models where age is not included % cover of mineral soil, paludification variables and % cover of ericaceous species were important (Fig. 3).

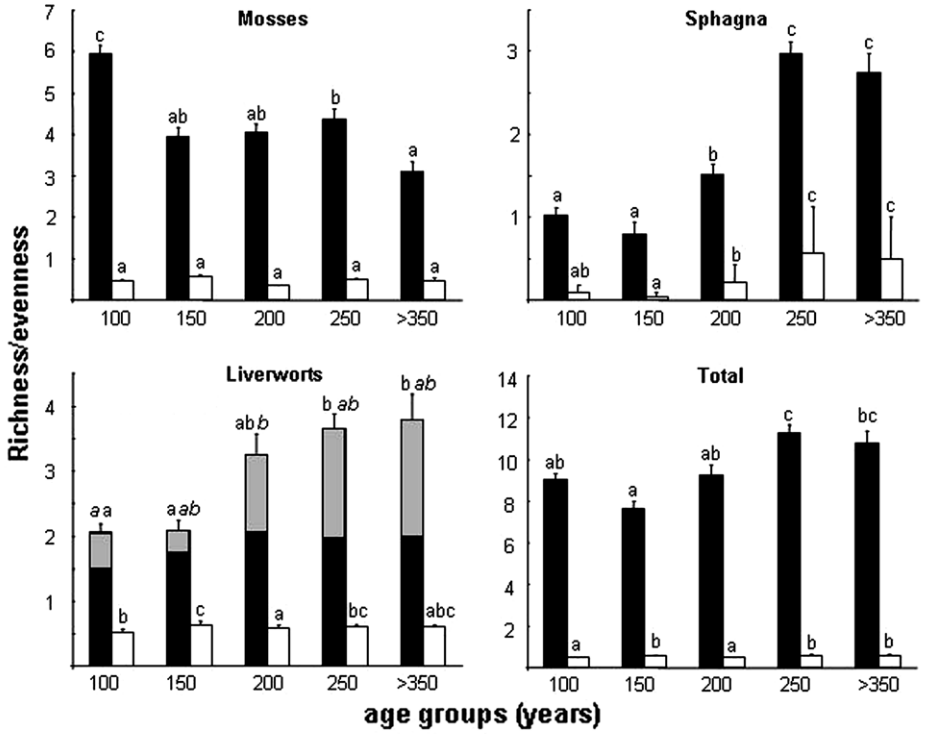

Fig. 2 – Richness (black) and evenness (white) of taxonomic groups among age groups. Forest liverworts are indicated in black, and bog liverworts in grey. Values are means and standard error. Letters indicate differences in richness or evenness as indicated by ANOVA, a < b < c. Differences among age groups in bog liverworts are in normal letters and forest liverworts are in italics.

Table 2 – XR^2 for models for different sub-groupings of the data for the different diversity indicators, with and without age as a factor

Indicator	Richness				Evenness			
	Age	No age	% Change	Tolerance (sensitivity)	Age	No age	% Change	Tolerance (sensitivity)
All species	0.238	0.227	−5	29.00 (0.72)	0.789	0.610	−23	5.80 (0.89)
Mosses	0.306	0.292	−5	2.90 (5.62)	0.205	0.162	−21	34.80 (0.64)
Sphagna	0.484	0.384	−21	29.00 (0.61)	0.478	0.401	−16	29.00 (0.53)
Liverworts – total	0.224	0.285	+27	2.90 (7.37)	0.110	–	–	–
Liverworts – forest	0.206	–	–	–	0.072	–	–	–
Liverworts – bog	0.288	0.218	−25	29.00 (0.40)	–	–	–	–

The % change in the XR^2 when age is not included is also indicated, as is the tolerance and sensitivity to the variable age. Models where age was included as a potential factor, but where it was not selected are included in the "age" column for consistency. Consequently there are no values for % change, tolerance or sensitivity. Bog liverwort evenness was not modeled, as it is a qualitative variable, as all species were at "trace" levels.

4. Discussion

4.1. *Diversity across the chronosequence*

Eighty-seven species were found across the age gradient, with quadrat and stand level richness and evenness peaking in the 275 TSF and richness decreased slightly in the >350 TSF group. The coincidence of peak evenness and richness in the 275 TSF age group suggests that these forests have a community that is composed of smaller bryophyte colonies of a greater variety of species and that there is a higher turnover within and between stands than in the other age groups. This increase in richness is a pattern that is different than what has been suggested for old-growth boreal forests in western Québec, as previous studies have not found an increase in richness with age (Boudreault et al., 2002; Harper et al., 2003). Liverworts were primarily responsible for this increase, and their increased diversity may not have been captured in the past as they are infrequently thoroughly sampled due to their cryptic nature and difficulties in their identification (Albins-

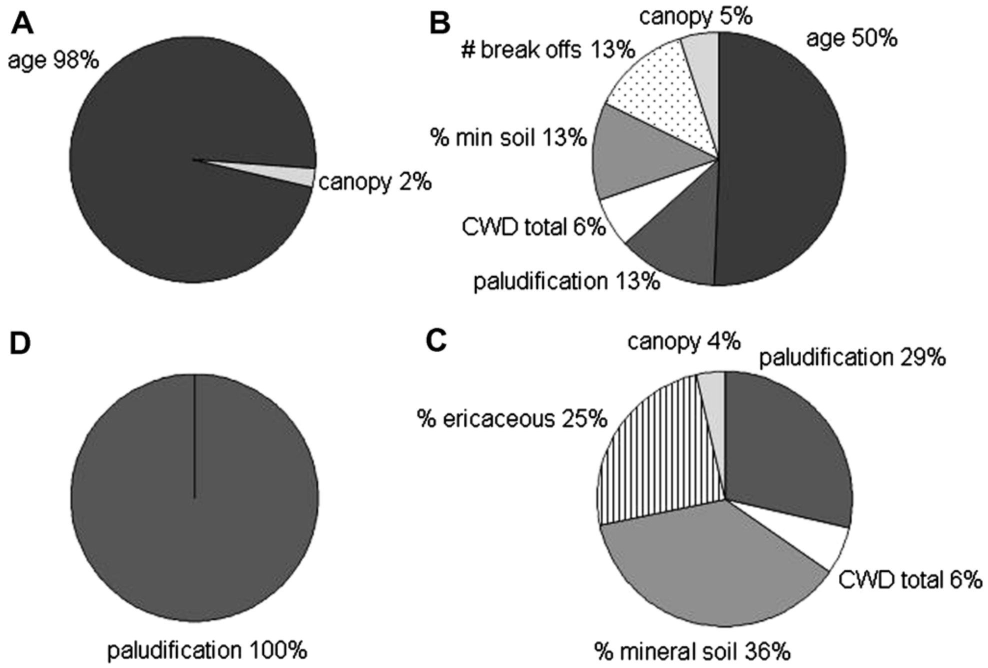

Fig. 3 – Relative proportions of habitat factors in richness models. (A) Dominant factors (see text for definition) when age is included, (B) all factors when age is included, (C) dominant factors when age is excluded, and (D) all factors when age is excluded.

son, 1997). The species area curve for the liverworts suggests that even greater regional diversity could be identified if sampling were to be extended. The forested peatlands of the Clay Belt appear to be areas of relative species richness in the relatively depauperate boreal landscape, as are the swamp forests of Scandinavia (Økland et al., 2003).

4.2. *Mechanisms of diversity creation and maintenance*

Two groups of models can be identified, those that were strongly influenced by habitat variables, and those that were strongly influenced by age and habitat variables.

4.2.1. *The role of habitat*

Habitat clearly played a dominant role in creating the richness patterns observed in the bryophyte community, particularly for the mosses and forest liverworts, as in these models age was a minor factor. For these taxonomic/habitat groups the increase in richness to the 275 TSF group is dependent on changes in habitat availability rather than ever longer forest continuity. These results are similar to those found in several other plant and fungal communities where habitat diversity (frequently referred to as "microhabitats") and availability drove community diversity (Ohlson et al., 1997; Pharo and Beattie, 2002; Økland et al., 2003; Rolstad et al., 2004). However, these previous studies did not specifically separated habitat and time as variables, as was done in this study (c.f. Ohlson et al., 1997; Pipp et al., 2001).

These species groups for which age was not a significant factor in the richness models are dominated by pocket species that generally occupy spatially and temporally discrete micro-habitats (e.g. CWD, bare peat or mineral soil) within the matrix of a fully occupied ground layer (Frego, 1996; Økland et al., 2003). As these species are frequently among those believed to be dispersal limited (Kimmerer, 1991; Laaka-Lindberg et al., 2006) it is interesting that age was not an important factor in these models. Pocket habitats, which were frequently significant habitat factors included in the richness models when age was excluded, were generally created by secondary disturbance (but in the youngest stands in our study they are probably residual products of the last stand replacing fire) and are unpredictably available within the forest stand. This is due not only to the stochastic nature of their creation but also to their rapid colonization (Økland et al., 2003) and gradual decomposition. Availability of habitat may instead be the dominant factor in determining species richness and consequently time plays a minor role as dispersal is not the limiting factor. The importance of pocket habitats, as opposed to age, in influencing species richness has been found in other studies (Ohlson et al., 1997; Rambo, 2001; Økland et al., 2003) and their abundance as well as the processes that create them and the community dynamics of the species that inhabit them merit further study.

4.2.2. *The role of forest age*

Two richness models were influenced by age, those of sphagna and of bog liverworts, suggesting that richness of these species are limited by dispersal. Despite the circumpolar distribution of most of the sphagna species found in this study, and evidence of sexual reproduction occurring on small spatial scales (Cronberg, 1996), successful establishment of sphagna colonies by spores has long been considered rare to nearly impossible (e.g. Coates and Duckett, 1986). Furthermore spore trapping in these sites indicated that there were significantly fewer spores in sites with fewer sphagna colonies (Fenton and Bergeron, 2006b). This would explain the potential dispersal limitation found in this group.

Alternatively, there is a distinct shift in *Sphagnum* community composition as these forests age (Fenton and Bergeron, 2006a) and later successional sphagna species may be more dispersal limited than early successional species. While sphagna are generally classified as competitors (Slack, 1990) in Grime's plant strategies (1979), Økland (1990) suggested that while some species are typical competitors, other species show characteristics typical of stress tolerators or ruderals. Species classified as different strategies may be expected to be dispersal limited to different degrees [e.g. Söderström and Herben's (1997) modeling of During's (1992) bryophyte life-forms]. Competitors that form large colonies and are resident in one space for considerable periods of time produce fewer spores than ruderals, which move from patchy habitat to patchy habitat. The early successional species in these forests were classified as stress tolerators while late successional species in the paludified forest are classified as competitors by Økland (1990). This later group may therefore be particularly dispersal limited.

The relatively important role played by age in the bog liverwort richness model is in contrast to the other liverwort models (total and forest). Hepatics have been seen as a group to be potentially dispersal limited (Söderström and Jonsson, 1989), however mode of reproduction appears to be an important factor in determining to what degree this is true. Laaka-Lindberg et al. (2006) found that hepatic species that produce abundant spores were not dispersal limited at the scale of 20 m, while species that infrequently produce spores were dispersal limited at that scale. Perhaps bog liverwort species found in this study reproduced more commonly by asexual propagules than by spores compared to forest liverwort species.

The evenness models were all influenced by age, although the relationship was strongest in the total data set model. This relationship is more straightforward as the passage of time allows species to establish in the feathermoss carpet and to grow, gradually occupying more space. Furthermore, the strength of the total model supports the logical conclusion that colony growth is more easily predicted by habitat and time than is species establishment.

4.2.3. *The site specific random events*

Site specific historical random establishment events ultimately determine species presence in some communities (McCune and Allen, 1984; Kimmerer and Driscoll, 2000; Økland et al., 2003), particularly where a large regional species pool is present (Duncan et al., 1998). There will be a greater variation in which species colonizes an available habitat in a specific site when many species are present on the landscape then when there are few species present (Hurtt and Pacala, 1995). An accumulation of these random site specific events may result in differences in richness that are independent of age and site factors, as suggested by McCune and Allen (1984) and Økland et al. (2003). In this study, this phenomenon may explain some of the large difference in explanatory power (XR^2) among models. As there is no reason to believe that the weaker models contain a greater amount of systematic error, the low XR^2 of the moss and liverwort models may indicate that they are more influenced by site specific random events than the sphagna and bog liverwort models with a high XR^2. As the forest liverwort models were the weakest, this suggests that site specific random events had the greatest impact on forest liverwort species. The high number of species found, and the suggestion that the regional species pool may be much larger (species area curve), fit the model of Hurtt and Pacala (1995).

In contrast to these models, the sphagna richness models with the highest XR^2 of any richness model, indicates that the included habitat and time factors explained a considerable portion of the variation. This suggests that site specific random events were less important for this taxonomic/habitat guild, which are generally considered to be competitors in an equilibrium environment (Slack, 1990). More surprising is the fact that the bog liverwort model was stronger than either the total liverwort model or the forest liverwort model. However, Økland (1990) and Albinsson (1997) both suggest that some species of bog liverworts are in fact in competition with the sphagna that they overgrow, and they would therefore be more influenced by the equilibiral factors included in the model.

4.3. *The role of landscape and disturbance regime*

Several landscape scale factors in boreal North America differ significantly from what is found in Europe and temperate North America. This study took place in a relatively unaltered landscape where the distance between colonies is dictated by the natural disturbance regime. In addition, the North American boreal forest is a fire dominated landscape where large stand replacing disturbances are the norm, even in this portion of the boreal forest with a relatively long fire cycle (Bergeron et al., 2004). This fact, and the pan-boreal distribution of many bryophytes species suggests that long distance dispersal does occur in these species, at least periodically. However, the fire severity within large scale forest fires of the boreal forest is uneven, and many isolated pockets of forest are "skipped" (Kafka et al., 2001; Greene et al., 2002). These pockets of unburnt forest may represent refugia for the pocket species, significantly reducing dispersal distances, and therefore eliminating any visible signal of dispersal limitation.

In contrast, in Europe and temperate North America much of the landscape has been altered (Gerhardt and Foster, 2002), and dispersal distances have been anthropogenically increased. Furthermore the natural disturbance regime historically operated at a smaller scale, with species dispersing over small distances (Kuuluvainen, 2002). Consequently species diversity may be doubly limited by dispersal, explaining the results of many studies indicating the important role of forest continuity in this biome (Hermy et al., 1999; Gerhardt and Foster, 2002; Hermy and Verheyen, 2007). The results of Paltto et al. (2006) support this hypothesis as they illustrated the importance of the naturalness of the surrounding landscape on the diversity present within a selected stand.

4.3.1. *Implications for conservation*

To a high degree the richness of paludifying black spruce forests on the Clay Belt was driven by infrequent pocket species: mosses and liverworts. These groups were primarily influenced by habitat availability and potentially by stochastic establishment factors, rather than forest continuity. This result adds to the growing evidence that forest continuity is less important for bryophytes than has been previously believed, and they should be used with caution as indicators of old-growth forest (Ohlson et al., 1997; Nordén and Appelqvist, 2001). The importance of habitat availability in driving bryophyte richness suggests that in boreal North America, where forest fragmentation is limited and recent, conservation strategies that emphasize maintenance of habitat or habitat creation at the landscape scale rather than forest continuity may be effective for this group. While no dispersal limitation was found for the mosses or forest liverworts, it is important to note that this is within a natural landscape. Anthropogenically increasing dispersal distances, for example by clear cutting large swathes of forest without leaving retention patches similar to natural fire skips, would be expected to create dispersal limitation within these groups, as has been observed in Europe and temperate North America. In addition, the potentially important role of site specific random events also creates a challenge for landscape managers, as the interaction between establishment habitat and propagule availability becomes important, and outcomes are not definite. Consequently, natural stand dynamics and dispersal distances need to be preserved on the landscape to ensure the continued presence not only of the dispersal limited groups (bog liverworts and sphagna) but also of the mosses and forest liverworts.

The importance of dividing species lists by habitat guilds was also illustrated by this study, as the explanatory power of the richness models increased substantially when individual groups were examined, compared to the dataset as a whole. Furthermore, the different groups were shown to be dependant on time and habitat to different degrees, which ultimately suggests that different conservation strategies should be adapted for different groups. A similar approach by Baldwin and Bradfield (2007) also indicated different strategies are appropriate for different bryophyte groups. While a lack of life history or strategy information may sometimes make the use of habitat guilds more difficult than pure taxonomic divisions, our understanding of forest processes can only be improved by this analytical strategy.

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Appendix A. Species list by habitat–taxonomic group

Mosses: *Aulacomnium palustre, Brachythecium campestre, Brachythecium salebrosum, Brachythecium starkei, Brotherella recurvans, Callicladium haldanianum, Calligeron stramineum, Campylium hispidulum, Ceratodon purpureus, Dicranella heteromalla, Dicranum flagellare, Dicranum fuscescens, Dicranum montanum, Dicranum ontariense, Dicranum polysetum, Dicranum scoparium, Dicranum undulatum, Drepanocladus revolvens, Drepanocladus uncinatus, Eurhynchium pulchellum, Herzogiella turfacea, Hylocomium splendens, Hypnum imponens, Hypnum pallescens, Mnium spinulosum, Oncophorus virens, Oncophorus wahlenbergii, Plagiothecium cavifolium, Plagiothecium laetum, Platygyrium repens, Pleurozium schreberi, Pohlia nutans, Polytrichum commune, Polytrichum juniperinum, Polytrichum strictum, Ptilium crista-castrensis, Tetraphis pellucida, Tomenthypnum nitens var. falcifolium, Ptillidium ciliare* (a liverwort, but included in the mosses because of its forest floor habitat).

Forest liverworts: *Anastrophyllum hellerianum, Anastrophyllum michauxii, Bazzania denudate, Blepharostoma trichophyllum, Cephalozia catenulate, Jamesionella autumnallis, Lophocolea heterophylla, Lophozia guttulata, Nowellia curvifolium, Ptillidium pulcherrimum.*

Bog liverworts: *Barbilophozia barbata, Barbilophozia kunzeana, Calypogeia integristipula, Calypogeia muellariana, Calypogeia neesiana, Calypogeia sphagnicola, Cephalozia connivens, Cephalozia pleniceps, Cephaloziella divaricata, Cephaloziella rubella, Cladiopella fluitans, Lepidozia repens, Lophozia laxa, Lophozia ventricosa, Mylia anomola, Scapania hyperborean, Scapania irrigua, Scapania mucronata.*

Species classified as both forest and bog liverworts: *Cephalozia bicuspidate, Cephalozia lunulifolia, Geocalyx graveolens, Jungermannia leiantha, Lophozia incisa, Lophozia longidens, Odontoschism denudatum, Riccardia latifrons, Trimotaria exsecta, Trimotaria exsectiformis.*

Sphagna: *Sphagnum angustifolium, Sphagnum capillifolium, Sphagnum fuscum, Sphagnum girgensohnii, Sphagnum magellanicum, Sphagnum rubellum, Sphagnum russowii, Sphagnum subtile, Sphagnum warnstorfii, Sphagnum wulfianum.*

Appendix B

Regressions of total species richness and taxonomic group against habitat values for 5 × 5 quadrats

Variable	Total richness	Moss richness	Sphagna richness	Liverwort richness
R^2	0.237	0.269	0.398	0.179
F (p)	10.79 (<0.001)	22.72 (<0.001)	54.60 (<0.001)	8.99 (<0.001)
Age	0.333		0.590	0.339
Water table depth	−0.263	−0.432		
Water table index		−0.272	0.0431 (0.499)	
Forest floor depth	0.083 (0.310)			0.097 (0.240)
BA black spruce		0.145		0.096 (0.178)
BA aspen		0.118		
Lcr balsam fir				0.101 (0.083)
Dens. open	−0.152			
Dens. decid.	0.104 (0.069)			
% Ericaceous				
% Mineral				
% Leaves				
% CWD[a] 1			0.81 (0.105)	
% CWD[a] 3	0.165			0.062 (0.316)
% CWD[a] 4				
# Of tip ups	0.162			

Variables included in each regression are listed with their standardized coefficients; p values that were greater than 0.05 are shown in parentheses.

a Coarse woody debris.

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