Effects of variable canopy retention harvest on epixylic bryophytes in boreal black spruce – feathermoss forests[1]

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Abstract: Modification of forest attributes and structural components like downed wood (DW) during forest harvest can lead to local species loss. Epixylic bryophytes have been proposed as good indicators of such changes. Unharvested control, variable canopy retention, and single pass harvest represent a gradient in forest harvest impact and can be used to test the response of epixylic bryophytes to different levels of environmental change. The objective of this study was to see if variable canopy retention attenuates environmental change associated with harvesting, consequently maintaining an epixylic community more similar to unharvested stands than single pass harvesting. Environmental conditions and DW characteristics were sampled on 225 DW pieces distributed in 45 permanent plots. Results showed that treatment affected epixylic richness through its impact on canopy openness and DW diameter and decomposition class. Fewer species were found in more open habitats and more species were found on bigger and more decomposed DW. Most epixylic species were more commonly found on the forest floor than on the DW. In conclusion, variable canopy retention harvest offered microclimatic conditions and DW availability and quality more suitable for epixylic species than single pass harvest, which was less suitable for epixylic species.

Résumé : La modification des attributs forestiers et des composantes structurales tel les débris ligneux grossiers (DLG) peut entraîner la perte locale d'espèces associées. Les bryophytes épixyliques ont été suggérées comme de bons indicateurs de ces changements. Un témoin non perturbé, une coupe à rétention variable de canopée et une coupe totale constituent un gradient d'impact des activités forestières et sont utilisés pour observer la réponse des épixyliques aux niveaux de perturbation. L'objectif de cette étude est de voir si la rétention variable de canopée atténue les changements micro environnementaux et la destruction des DLG associée avec la récolte maintenant ainsi une riche communauté d'épixyliques. Les résultats montrent que le traitement influence la richesse des épixyliques à travers son effet sur l'ouverture de la canopée, le diamètre moyen et la classe de décomposition. Moins d'espèces sont retrouvées dans les habitats ouverts et plus d'espèces sont retrouvées sur les gros DLG bien décomposés. La plupart des épixyliques sont plus communément retrouvées au sol que sur les DLG. La coupe totale est le traitement le moins propice à la colonisation par les épixyliques alors que la rétention variable de canopée offre le microclimat et une disponibilité de DLG de qualité propice à la colonisation par les épixyliques.

Introduction

Forest harvest alters biodiversity by changing forest attributes and structural components like downed wood (DW) on which many organisms depend for food and shelter (Harmon et al. 1986). Modification of environmental conditions and moving or crushing of currently available DW can change habitat characteristics and lead to local loss of species associated with DW. Traditional harvesting techniques like single pass harvest (where all merchantable stems are removed at once) strongly impact environmental conditions and interrupt the cycle of DW input within a stand. It has been suggested that leaving standing living trees may offer a continuous input of DW as well as providing patches of shaded forest floor and consequently reduce the impact of harvest at the stand level (Harvey et al. 2002). Techniques like variable canopy retention harvest are expected (Fenton et al. 2008) to have less effect on microclimate and thus on forest floor species, as some trees are retained throughout the stand. These techniques emulate natural secondary disturbances such as windthrow and spruce budworm that bring pulses of DW into the stand (Harmon et al. 1986). As such, unharvested stands, variable retention, and single pass harvest represent a gradient in intensity of microclimatic and substrate change and it has been suggested that within a management context, variable harvesting may protect some DW-related species compared with single pass harvest.

Bryophytes (divisions Bryophyta, Marchantiophyta, and Anthocerotophyta) have been shown to be sensitive to forestry operations (Andersson and Hytteborn 1991) because most forest bryophyte species lack individual adaptations for water retention (Shaw and Goffinet 2000) and for protection

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Table 1. Values for stand characteristics at each site.

	Site		
Variable	Fenelon	Gaudet	Puiseaux
Harvesting year	2004	2003	2004
Harvesting season	Fall	Winter	Winter
Variable retention cut surface area (ha)	80	67	87
Mean basal area (site; $m^2 \cdot ha^{-1}$)	12.55	22.66	19.68
% harvested in variable retention (% stems >9 cm)	76	76	63

Note: All sites haves been harvested using multifunctional machinery.

from intense sunlight (Marschall and Proctor 2004). Consequently, forest bryophyte species are good indicators of microclimatic change. Epixylic species (epi: prefix taken from the Greek that means "on, upon, over, on top, against"; xylic: suffix taken from the Greek that refers to the xylene part of trees) preferentially grow on decaying wood, a substrate whose dynamic in time and space is directly affected by harvest, and as such, they are particularly interesting for evaluating changes in DW availability and quality.

DW offers many significant services for epixylic species, including safe, available habitat with a stable, humid microclimate. DW provides safe habitat by offering safe sites or refugia for small bryophytes, particularly liverworts (division Marchantiophyta), as the elevated situation protects them from debris falling onto the forest floor such as broadleaf deciduous leaves (Söderström 1988*a*). Furthermore, this elevated position also allows them to extract themselves from the continuous mat of larger forest floor bryophyte species commonly present in boreal forests (Frego 1996), therefore avoiding competition from these larger species (Rydin 1997). Moreover, DW influences the local microclimate in closed or shaded forests, as they retain much humidity in their tissues, which creates a stable humid habitat for bryophyte establishment and growth (Muhle and LeBlanc 1975). However, in exposed situations, DW is dried out and its positive effect on local microclimate is significantly reduced. Finally, DW is a substrate that is dynamic in time and the benefits discussed above may diminish with increasing decomposition (Andersson and Hytteborn 1991), forcing epixylic species to continually disperse to new habitats, maintaining a colonist life strategy (During 1992).

The objective of this study was to see if variable canopy retention attenuates the microclimatic change and the DW destruction associated with harvest and consequently maintains an epixylic community more similar to unharvested stands than to stands that had been harvested by single pass harvesting. The hypotheses of this study were that (1) DW characteristics (i.e., number of pieces, relative abundance of decomposition, and size classes) will be correlated with the forest management gradient (unharvested control, variable canopy retention, and single pass harvest), (2) canopy openness and temperature on the surface of DW will be higher after forest harvest and correlated with the forest management gradient, and (3) these changes in coarse woody debris characteristics and environmental conditions will result in differences in the bryophyte community along the harvest gradient, with fewer epixylic species present after single pass harvest, an intermediate amount in the variable canopy retention harvest, and the highest number of species in the unharvested control. Individual species are also expected to respond in a similar way to this gradient. Species with wider habitat preferences were predicted to be less sensitive to harvesting techniques that modify environmental conditions than epixylic species with narrower habitat requirements.

Methods

Study sites

Field work for this study was conducted during the summer of 2009 in the Clay Belt region of Quebec. The forest type was black spruce (*Picea mariana* (Mill.) B.S.P.) – feather moss (*Pleurozium schreberi* (Brid.) Mitt.) forest of northwestern Quebec. (Grondin 1996) The annual mean temperature recorded at the closest weather station (La Sarre, Quebec), is 0.7 °C and the annual precipitation is 890 mm (Environment Canada 2011)

The studied sites are part of the Réseau d'expérimentation des coupes partielles en Abitibi (RECPA), an experimental network of permanent plots (400 m^2) scattered throughout Abitibi and Nord-du-Québec (see Fenton et al. 2008 for a detailed description of the RECPA network) for testing the feasibility of variable canopy retention harvest techniques to develop sustainable forest management. In each site, two harvest treatments were applied to stands: cut with levels of canopy retention (between 24% and 37% of canopy remaining after harvest) and single pass harvest, which removes all merchantable stems (9 cm diameter at breast height) from the stand but preserves advance regeneration and protects most of the soil. Each site of the RECPA network also includes an unharvested control, an unmanaged mature stand naturally regenerated after fire that has experienced no anthropogenic disturbance (Table 1) (for more information, see Fenton et al. 2008). The sites used in this study were harvested in 2003 and 2004, and therefore, the harvests were 5–6 years old when the inventory was carried out in 2009.

All sites were dominated by black spruce trees with a few trembling aspen (*Populus tremuloides* Michx.) and balsam fir (*Abies balsamea* (L.) Mill.) stems. The shrub layer, when present, was dominated by alder (*Alnus rugosa* (Du Roi) Spreng.). The low shrub layer was dominated mostly by *Vaccinium angustifolium* Ait., *Vaccinium oxycoccos* L., *Gaultheria hispidula* (L.)T. & G., *Ledum groenlandicum* Retzius, *Cornus canadensis* L., and *Rubus chamaemorus* L. The ground layer was overall dominated by bryophytes, with *P. schreberi*., *Dicranum polysetum* Swartz, *Hylocomium splendens* (Hedw.) B.S.G., and *Sphagnum* species (*Sphagnum fallax*, senso lato *Sphagnum fuscum* (Schimp.) Klinggr., *Sphagnum russowii* Warnst., and *Sphagnum capillifolium* (Ehrh.) Hedw.).

Five permanent plots were randomly selected in each treatment block (single pass harvest, variable retention, and unharvested control) in each of three sites (Fenelon, Gaudet, and Puiseaux) for a total of 45 permanent plots. A 23 m linear transect was established in each selected permanent plot to assess the number of pieces of DW present. All inventoried DW were black spruce and species identification was confirmed after a visual observation of the wood pieces. Diameter and decomposition class at the intercept were recorded for each piece of woody debris. Decomposition class varied from 1 (fresh material) to 5 (well decomposed) and was based on Hunter (1990). From the total of all DW inventoried, five pieces with a minimum diameter of 5 cm at the intercept (Andersson and Hytteborn 1991) were then selected in such a way that all decay classes were represented within the plot, when possible. No significant differences were found between the decay class distribution of the selected DW and the total DW pool (χ^2 test, $p = -0.9934$).

Total length, minimum and maximum diameter, percentage of the length directly in contact with the ground, and maximum distance from the ground were recorded along with the average cover of bryophytes and of epixylic species for each selected piece of DW. Epixylic species were distinguished from generalist or forest floor species according to the literature (e.g., Söderström 1988*b*; Andersson and Hytteborn 1991; Ley and Crowe 1999), as they are predicted to have a higher sensitivity to habitat changes associated with forest harvest (see Annex[2] for list of classified species). Generalist species were defined as species growing on a variety of habitats, while *Sphagnum*-associated species included sphagna and smaller species growing amidst the sphagna colony (e.g., *Calypogeia sphagnicola* (Arnell & J. Perss.) Warnst. & Loeske).

To complete the characterization of stand microclimate, temperatures were measured using ibuttons (Maxim Integrated Products, Sunnyvale, California). Eighteen ibuttons were installed beside the sampled DW in the open air using a metal rod holding them approximately 30 cm above the forest floor. They were left in place for 1 year and recorded temperature every 3 h. Bryophytes are more sensitive to high temperatures than to low temperatures (Dilks and Proctor 1979), as photosynthesis is dependent on plant hydration (Hopkins 2003). Consequently, mean temperatures were calculated using only temperatures recorded during summer days (from 6 a.m. to 9 p.m. from April to November).

Three belts of quadrats were installed on each piece of DW after general observation on all of the coarse woody debris length to capture intrapiece characteristic variability. Each belt was made up of quadrats in three systematically placed positions: the top of the DW (5 cm × 10 cm), the side of the DW (5 cm × 10 cm), and the ground directly next to the DW (10 cm × 10 cm). Larger quadrats were used on the forest floor because species growing on the forest floor are typically larger than those expected to be found on the DW. This precaution ensured that the same amount of surface was covered on the forest floor and on the total size of the quadrat on the DW. At each belt, canopy openness was measured at DW height using a densiometer, a concave mirror scored with a grid to allow estimation of the canopy cover. In this study, canopy openness is the inverse measure of the shade cover created by the conifer trees, shrub layer, and smaller plants and reflects the microvariation in light perceived at the bryophyte level. DW diameter (ranging from 5 to 21 cm) and decomposition class were evaluated for each belt. Percent cover bark, percent cover naked wood, and percent cover of bryophytes and lichens, as well as the cover of each individual bryophyte species, were evaluated in the quadrats on the top and the sides of the DW. Three levels of abundance were defined: rare (the species covered less than 5% of the quadrat), frequent (6%–50% covering), and abundant (more than 50% covering). Species impossible to identify in the field were collected and brought back to the laboratory for identification following the nomenclature of Ley and Crowe (1999) and Paton (1999) for liverwort species and Crum and Anderson (1981) for moss species. The frequency for common species was tabulated for each harvest type, and uncommon species were pooled for each species group (epixylic species, generalist species, and sphagna and associates). Only presence–absence data were used during analysis because most epixylic species were rare. Cover dominance for *Sphagnum* species was determined when they were classed as frequent or abundant in the quadrat.

Statistical analysis and model selection

R freeware (v. 2.12.2; R Development Core Team 2011) was used for the analyses. A significance threshold of $p \leq 0.05$ was set for all analyses. Normality and homogeneity of variance were tested prior to analysis and data were transformed as necessary. Data that were measured at the belt level (DW decomposition class, canopy openness, and bryophyte inventory) were amalgamated into one measure per DW. Mean canopy openness was calculated using the readings from the three belts. Modal decomposition class was given to the log when a decomposition class occurred more than one time on the three belts of the DW; otherwise, the decomposition class closest to the mean was given to the DW. Richness, which is the number of species, was calculated for the entire log, so a species occurring more than once on the three belts on a single log counted only for one in the total richness. Distinctions between samples taken on the DW and those taken on the forest floor beside it were made but the data were also aggregated in what we have called the "extended log".

Differences in DW characteristics and epixylic richness (see Table 2; Fig. 2) among forest harvest types and the relationships between epixylic species richness and others factors were tested using a linear mixed-effects model with REML in R using the function lme in the NLME library (linear and nonlinear mixed-effects models; Pinheiro et al. 2008). Linear mixed models are parametric models for longitudinal clustered or repeated data used to estimate relationships between continuous dependent variables and various predicator variables (West et al. 2007), and as such, the nested nature of the study design was taken into account in the statistics (nested in the random factors). Variability among sites and permanent plots was always very small in the preanalysis, and sites and permanent plots were subsequently treated as random effects to avoid sacrificial pseudo-replication errors seen when data from different experimental units are used as independ-

[2]Supplementary data are available with this article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/x2012-054.

Table 2. Mean values of plot characteristics for each treatment type.

	Treatment		
Variable	Unharvested control	Variable canopy retention	Single pass harvest
Number of logs	9.2±0.38a	10.34±0.49a	9.6±0.39a
Mean temperature (°C)	11.37±0.11a	12.51±0.11b	14.27±0.12c

Note: Values are means followed by standard error. Values followed by different letters are significantly different; $p <$ 0.05, $n = 212$.

Table 3. Mean values of DW characteristics for each treatment type.

	Treatment		
Variable	Unharvested control	Variable canopy retention	Single pass harvest
Total length (cm)	872.47±44.72b	695.77±45.3a	669.7±43.25a
Minimum diameter (cm)	3.36±0.41a	6.27±0.48b	4.81±0.49c
Maximum diameter (cm)	13.87±0.54a	14.52±0.56a	12.85±0.64a
Mean diameter (cm)	9.11±0.26b	10.8±0.4a	9.28±0.42b
% contact with the ground	72.37±5.94a	60.73±3.96a	63.68±4.11a
Maximum distance to the ground (cm)	21.49±2.21a	20.12±2a	18.46±2.34a
Decomposition class	2.77±0.14a	2.93±0.12a	2.83±0.13a
Canopy openness	39.51±1.15a	56.64±2.7b	82.39±1.94c

Note: Values are means followed by standard error. Values followed by different letters are significantly different; $p < 0.05$, $n = 212$ DW except for canopy openness where $n = 146$.

ent replicates and pooled in the same analysis (Hurlbert 1984).

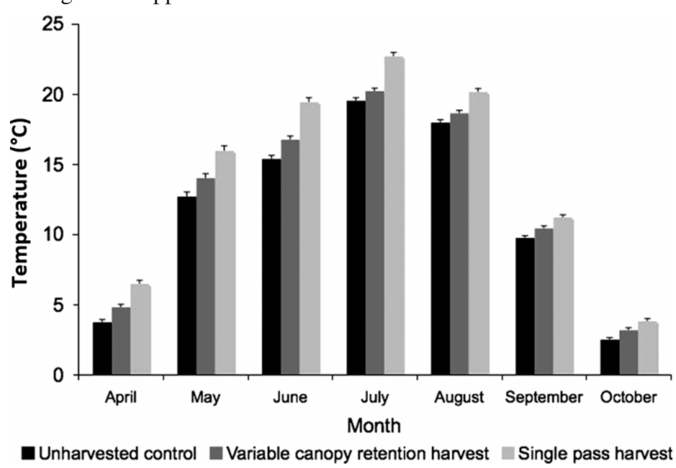
In addition, models to explain epixylic richness were evaluated via model selection. Model selection was completed using the Akaike information criterion (AICc), which compares the models taking into account both the weight of each factor in every model and the weight of each model (Akaike 1981). The model with the lowest AICc is the best model to determine how the included factors influence epixylic richness. AICwt indicates the level of support (i.e., weight of evidence) in favour of any given model being the most parsimonious among the candidate model set. Number of DW, percent contact with the ground, and maximum distance from the ground were not significant factors affecting epixylic richness and were therefore removed from the models. The fit of the models was assessed by correlating the fitted values and the data with a simple Pearson correlation.

Results

Forest management and coarse woody debris characteristics

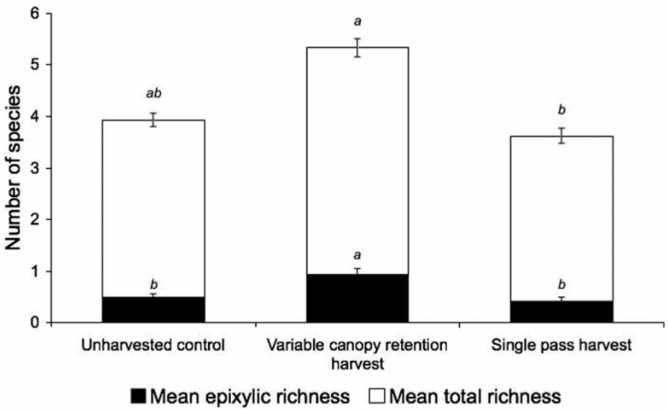
Following the analysis completed using linear mixed models for nested data, differences were observed among treatments for characteristics listed in Tables 2 and 3. Specifically, DW were significantly longer in the unharvested control than in the variable canopy retention ($p = 0.015$) or than in the single pass harvest ($p = 0.008$). Minimum diameter was smaller in the unharvested control than in the variable canopy retention ($p < 0.001$) or than in the single pass harvest ($p = 0.050$). Minimum diameter was also smaller in the single pass harvest than in the variable canopy retention ($p = 0.036$). However, no differences were observed among forest harvest types in maximum diameter, decomposition class, contact with the forest floor, distance from the ground, and number of pieces of DW.

Fig. 1. Mean and standard error of air temperature at DW height during the daytime in summer for unharvested control, variable canopy retention, and single pass harvest. Temperatures were recorded during the growing season of 2010 using Maxim's ibuttons programmed to record information every 3 h. Measurements were then averaged using only daytime measurements. Significant differences among series appear as a different letter.



Canopy openness varied significantly with the harvest gradient, with the unharvested control having a cover of 60%, variable canopy retention retaining 43% forest cover, and single pass harvest keeping only 17% canopy cover (Table 3). Temperature also varied with the gradient, with mean temperatures of 11.37, 12.51, and 14.27 °C for unharvested control, variable canopy retention, and single pass harvest, respectively (Table 2). Temperature was always warmer in the single pass harvest and always cooler in the unharvested control for every month of the growing season except for October ($p = 0.090$) (Fig. 1). Differences in temperature between single pass harvest and the two other treatments were more pronounced during June and July; July was the warmest month

Fig. 2. Mean and standard error of epixylic species richness compared with total richness on the extended DW (DW and adjacent forest floor) for unharvested control (n = 225), variable canopy retention harvest (n = 222), and single pass harvest (n = 189). Significant differences among series appear as a different letter.



with a mean temperature of 19.52, 20.21, and 22.71 °C for unharvested control, variable canopy retention, and single pass harvest, respectively.

Forest management and the bryophyte community

Compared with total measured species richness, measured epixylic species richness on the extended log was typically low (Fig. 2). About one third of the DW supported no epixylic species, 40% of the DW supported only one epixylic species, and less than 10% supported two epixylic species. Altogether, 87% (184 DW) of the investigated DW supported no, one, or two epixylic species. However, if overall bryophyte richness is examined, which also includes the generalist species and the *Sphagnum* species, DW supporting only no, one, or two species accounted for only 4% (nine DW) of the total 212 DW sampled. Most DW supported an overall richness between four and seven species (121 DW, 57% of the total DW investigated).

Initial models indicated that the number of DW pieces, DW length, contact with the forest floor, and maximum distance from the forest floor had no effect on species richness and these variables were therefore removed from the models. Similarly, analyses indicated that while epixylic richness and total richness on extended log differed among the different forest harvest types (Fig. 2), with higher richness in the variable canopy retention (p = 0.059), forest harvest had no direct effect on epixylic richness that was not mediated by its impact on other variables that were themselves affecting richness (Table 3).

Model selection (Table 4) indicated that three factors affected epixylic richness on extended log: canopy openness, mean DW diameter, and modal DW decomposition class. The variability in the data set was well described by the model with an R^2 of 0.68 between the data and the predicted values. Epixylic richness was negatively correlated (r = –0.31) with canopy openness (Fig. 3*a*), which was in turn significantly different among harvest types (Fig. 2). Less species were found in the single pass harvest, which was the treatment with the most open canopy. Similarly, epixylic richness was positively correlated with maximum DW diam-

Fig. 3. Epixylic richness as a function of three factors. Raw data appear as dots and model predictions as the solid line. Broken lines represent the 95% confidence of the predictions. (*a*) Canopy openness measured at DW height ranging from 0 (completely closed canopy) to 100 (no canopy); (*b*) mean diameter of DW (cm) (average of the three quadrats sampled on the DW); (*c*) decomposition class ranging from 1 (fresh material) to 5 (well decomposed).

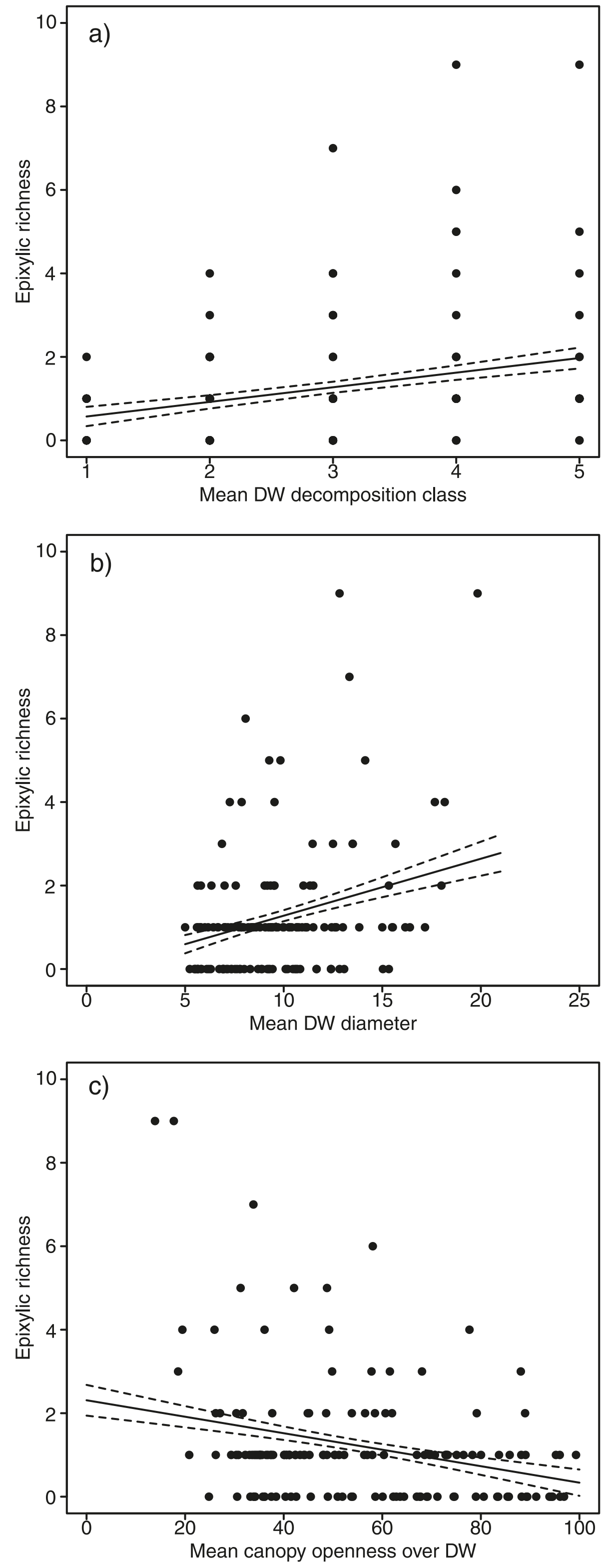


Table 4. Models tested for factors influencing epixylic richness, variables included, AICc, and AICwt.

Model name	Explanatory variable(s)	AICc	AICwt
Mod 5	Decomposition class, diameter, and canopy openness	513.26	0.95
Mod 4	Treatment and canopy openness	520.79	0.02
Mod 9	Decomposition class and diameter	522.00	0.01
Mod 10	Diameter and canopy openness	523.50	0.01
Mod 11	Decomposition class and canopy openness	523.58	0.01
Mod 8	Canopy openness	531.25	0
Mod 2	Treatment and decomposition class	532.73	0
Mod 6	Decomposition class	533.01	0
Mod 7	Diameter	533.70	0
Mod 3	Treatment and diameter	535.34	0

Fig. 4. Comparison of the number of DW supporting or not epixylic species versus DW supporting or not any bryophyte species (epixylic species, generalist species, and sphagna and associates) (n = 212 DW).

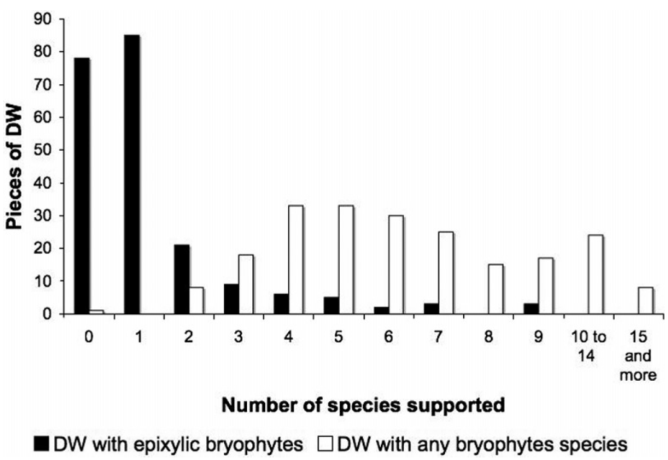
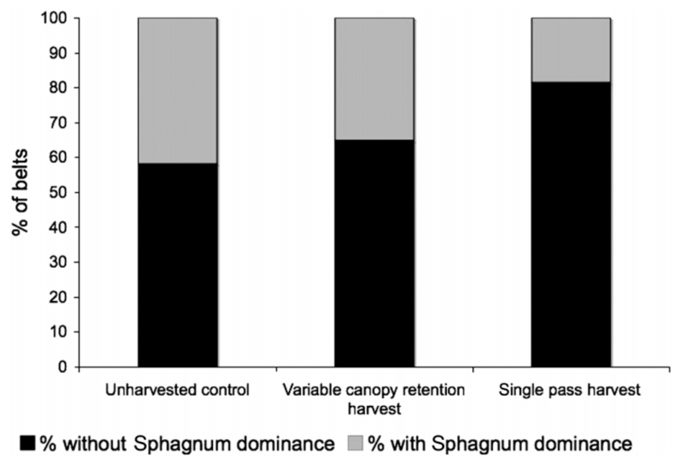


Fig. 5. Proportion of investigated quadrats dominated or not dominated by *Sphagnum* species for unharvested control (n = 225), variable canopy retention (n = 222), and single pass harvest (n = 189).



eter (r = 0.36) and decomposition class (r = 0.32) (Figs. 3*b* and 3*c*). Larger and more decomposed DW held richer epixylic communities. Epixylic species were always less commonly found on the WD than other bryophyte species (Fig. 4).

Individual species also responded to the forest management gradient. The distribution of the most common species among the treatments and relative to their position on the DW is shown in Table 5, separating epixylic species from generalist species and *Sphagnum* species. Surprisingly, nearly all species, including epixylics, were more commonly found on the forest floor than on the DW in all treatments. However, some differences are observed between the patterns of epixylic species and generalist and *Sphagnum* associated species. Not only was the epixylic bryophyte community richer in variable canopy retention harvest than in the other two treatments, but individual epixylic species were generally more frequent in the variable canopy retention. As such, epixylic species did not follow the harvest gradient. Furthermore, as mentioned above, only three species were found more often on DW than on the forest floor: *Anastrophyllum hellerianum* (Nees) Schust., an epixylic liverwort, in the single pass harvest and *Dicranum fuscescens* Turn., an epixylic moss, and *Ptilidium pulcherrimum* (G. Web.) Hampe, an epiphytic liverwort that usually grows on living trees, in the unharvested control. *Jamesoniella autumnalis* (Decandolle) Steph. was more frequent on the forest floor in the unharvested control and in the variable canopy retention but was found equally on the DW and on the forest floor in the single pass harvest. Interestingly, *Plagiothecium laetum*Schimp. in B.S.G. was never found on any DW in any treatment but was found on the forest floor in every treatment, being more present in the variable canopy retention, intermediate in the single pass harvest, and less present in the unharvested control. Other infrequent epixylic species (see complete species list in the Annex) showed the same pattern of distribution, with a higher frequency in the variable canopy retention and on the forest floor than in the other treatments or on the DW.

While the pattern of greater frequency on the forest floor compared with DW continued for the generalist species, the pattern among forest harvest types is more variable. Some species such as *P. schreberi*, *Ptilidium ciliare* (Linnaeus) Nees, and *D. polysetum* were found in similar proportion on the DW and the forest floor in every treatment. *Cephalozia lunulifolia* (Dum.) Dum. was more frequent in the unharvested control and the variable canopy retention harvest than in the single pass harvest. *Cephalozia pleniceps* (Austin) Lindb. was the only generalist species more present in the unharvested control than in the variable canopy retention and in the single pass harvest and it was only growing on the forest floor, never on the DW.

Sphagnum species were more present in the unharvested control and in the variable canopy retention. *Sphagnum cap-*

Table 5. Species frequency on extended DW by treatment (unharvested control, variable canopy retention harvest, and single pass harvest) and by position relative to the DW (on the DW and on the forest floor) detailed by species for the most frequent species.

	Unharvested control		Variable canopy retention harvest		Single pass harvest	
	On DW	On forest floor	On DW	On forest floor	On DW	On forest floor
Epixylic species						
Anastrophyllum hellerianum°	0	1	4	8	1	0
Blepharostoma trichophyllum°	0	1	4	13	1	2
*Dicranum fuscescens**	5	3	12	16	2	14
Jamesoniella autumnalis°	0	6	6	13	2	2
*Plagiothecium laetum**	0	2	0	6	0	4
Ptilidium pulcherrimum°	38	26	25	32	14	17
*Tetraphis pellucida**	0	3	1	7	0	2
infrequent epixylic (13 species)	2	8	8	26	2	6
Generalist species						
*Aulacomnium palustris**	1	7	4	17	0	2
Barbilophozia barbata°	0	3	1	12	0	8
Brachythecium starchii *	0	1	1	10	0	3
Cephalozia lunulifolia°	2	16	5	15	0	6
Cephalozia pleniceps°	0	6	0	2	0	2
Cephaloziella rubella°	0	0	2	6	1	2
*Dicranum polysetum**	1	21	6	22	0	19
*Hylocomium splendens**	3	8	2	14	0	7
Lophozia ventricosa°	0	6	0	7	1	8
*Pleurozium schreberi**	48	73	49	73	32	63
Ptilidium ciliare°	29	52	23	43	17	50
*Pohlia nutans**	1	9	3	19	0	12
*Polytrichum commune**	0	1	3	6	1	5
*Ptilium crista-castrensis**	8	20	12	32	1	14
infrequent generalists (19 species)	2	12	7	24	0	15
Sphagnum and associates						
*Dicranum undulatum**	1	5	0	4	0	0
Sphagnum angustifolia	2	4	1	6	0	2
Sphagnum fuscum	10	21	1	2	3	4
Sphagnum capillifolium	17	34	18	32	7	25
Sphagnum russowii	3	8	3	5	2	6
Sphagnum fallax (sensus lato)	12	23	8	24	5	10
Sphagnum magellanicum	6	15	7	18	4	6
Sphagnum rubellum	18	36	9	27	4	16
Sphagnum wulfianum	0	0	1	12	0	2
Infrequent shagna and associates (7 species)	0	1	1	11	1	6

Note: °Liverworts, *mosses.

illifolium and *S. russowii* were found in similar proportions on the DW and on the forest floor in all treatments. *Sphagnum undulatum* Warnst. was never found in the single pass harvest, while *Sphagnum wulfianum* Girg. and infrequent *Sphagnum* associated species were never found in the unharvested control. *Sphagnum* species clearly dominate the forest floor in the control and in the variable retention but not in the single pass harvest (Fig. 5).

Discussion

Many attributes of DW influence the quality of habitat that it provides to epixylic species. Water content, texture, abundance, decomposition class, and position relative to the forest floor affect the utilization of DW by epixylic species (Söderström 1988*a*). Ohlson et al. (1997) have previously shown that DW abundance influences bryophyte diversity; however, in this study, harvesting technique did not seem to affect DW abundance and DW abundance did not appear to significantly affect epixylic richness. Contact with forest floor and distance from forest floor were expected to affect epixylic distribution, as these factors influence DW water content and therefore habitat humidity (Muhle and LeBlanc 1975). However, humidity may not be a limiting factor on the Clay Belt with its low potential evapotranspiration (Fenton et al. 2008).

The three factors affecting epixylic richness through their variation among treatments will be discussed individually. Differences seen in DW diameter between variable retention and the others treatments may be due to the origin of the DW. In the unharvested control, DW in place came from entire downed trees that retained their apex with a small diameter. In contrast, in the single pass harvest, DW came from cutting trees of various sizes and shapes, while in variable canopy retention harvest, DW came from debris left onsite after harvest and from a significant number of large trees that fell after the harvest (N.J. Fenton, personal communication). These larger diameter logs could have affected epixylic richness in two ways. Larger DW decomposes slower, therefore resting longer on the forest floor and consequently increasing availability for epixylic bryophyte colonization as demonstrated by Andersson and Hytteborn (1991). Söderström (1987, 1989) has previously shown that dispersal is the most important factor limiting epixylic species distribution, a factor particularly relevant for epixylic species where the dynamic substrate must remain on the forest floor long enough for spores to reach the new available habitat. In addition, larger DW lifts the epixylic community higher above the forest floor. This elevated situation allows epixylics to grow protected from fast-growing forest floor bryophytes (e.g., some *Sphagnum* species and *P. schreberi*) that can bury DW via lateral growth (Hagemann et al. 2010; Fenton et al. 2005). Ultimately, overgrowing (Dynesius et al. 2010), a phenomenon that involves DW sinking into the organic layer, and burying by forest floor bryophytes strongly impact resting time on the forest floor and therefore colonization time for epixylic bryophytes.

Rambo (2001) demonstrated that DW in an advanced stage of decay held a richer bryophyte community, particularly for epixylic species. Decomposition class distribution did not differ among treatments (data not shown) and DW in all stages of decay was available in all treatments; however, variable retention and unharvested control stands seemed to offer the highest habitat quality regardless of DW decomposition stage. Five uncommon species (including two epixylic species) were only found in unharvested plots and eight uncommon species were only found in variable retention plots. These differences in bryophyte colonization rate are probably due to microclimatic conditions that allowed for normal decomposition, in addition to the matrix of closed and open canopy that may be more suitable for a richer community of bryophytes, as theses plants can find the conditions of high humidity and low solar radiation that they need. In contrast, in the single pass harvest where DW was burnt and dried by solar radiation, and so the DW of the same decomposition class was of lower habitat quality because of other environmental characteristics, the epixylic colonization rate was lower, with only three uncommon species that were restricted to the single pass harvest plots of which only one was an epixylic moss.

Canopy openness and mean temperature are two factors modified by harvesting techniques. The intense canopy openness in single pass harvest blocks does not produce a suitable environment for theses poikilohydric organisms. Higher temperatures in this treatment are directly caused by canopy removal. As the sites were harvested only 5–6 years before the study took place, species richness was expected to be low and restricted to species adapted to high solar radiation, but surprisingly, we documented the presence of some epixylic species. Single pass harvest leaves some small trees in place and part of the site undisturbed and these undisturbed sites represent pockets of habitat that had retained some of the characteristics making them suitable for epixylic survival and can act as refuge for part of the bryophyte community while waiting for better conditions, such as more extensive canopy closure. Variable canopy retention offers a pattern of alternating machinery trails where all trees were harvested and leave strips where some to all trees remained, creating a variety of ecological niches that allow colonization by many different species of bryophytes requiring different habitats (Rambo and Muir 1998; Cole et al. 2008), as would be predicted by the intermediate disturbance hypothesis (Connell 1978). Moreover, even if species richness was expected to be low in single pass harvest, sampling of this treatment gives us information on the effect of drastic changes in environmental conditions for survival of the epixylic and the others species

Generalist and epixylic species were more frequent on the forest floor than on DW. The large amount of epixylic species found on the forest floor may be a reflection of the makeup of the forest floor. The forest floor was often composed of fine woody debris (small twigs, bark pieces, sawdust, and other woody material). These piles of fine woody debris may act, as a whole, as a larger woody debris and retain enough humidity for bryophyte implantation. As suggested by La Roi and Stringer (1976), many epixylics are not restricted to DW but show affinity for a few substrates. A more detailed analysis of the microtopography of the forest floor on which obligate epixylic species were found could provide more explanations by revealing pockets of suitable habitat.

Implications for conservation

Variable canopy retention, with its matrix of open and closed habitat, provides a suitable environment for epixylic bryophyte species, supporting a richer community than found in either the unharvested control or the single pass harvest. Diameter and decomposition class of the downed logs were the two other environmental factors affecting richness. As suggested by Anger et al. (2005), large logs must remain onsite to provide habitat durable in time. This suggests that to maintain bryophyte diversity in the long term on sites harvested with variable canopy retention, large logs must be retained during harvest, giving time for epixylic species to disperse and colonize the substrate. Similar results have been found for a number of species groups and forest types (McCullough 1948; Gustafsson and Hallingbäck 1988; Crites and Dale 1998; Humphrey et al. 2002; Franc and Götmark 2008); however, some studies have shown that small woody debris can play an important role in biodiversity conservation (Söderström 1993). Harvesting treatments that have a smaller impact on environmental conditions by emulating secondary natural disturbances, such as variable canopy retention harvest, can be seen as a means to keep habitat for epixylic species and therefore attain species and habitat conservation goals.

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