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Bryophyte response to eastern hemlock decline caused by hemlock woolly adelgid infestation[1]

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Cleavitt, N. L. (8F Fernow Hall, Department of Natural Resources, Cornell University, Ithaca, NY 14853-3001), A. K. Eschtruth, J. J. Battles (University of California, Berkeley, Environmental Science, Policy, and Management, 137 Mulford Hall, Berkeley, CA 94720-3110), and T. J. Fahey (12 Fernow Hall, Department of Natural Resources, Cornell University, Ithaca, NY 14853-3001). Bryophyte responses to eastern hemlock decline following a hemlock woolly adelgid infestation. J. Torrey Bot. Soc. 135: 12-25. 2008.—The understory conditions of eastern hemlock stands in the Delaware Water Gap National Recreation Area have been altered by canopy decline caused by an exotic insect pest, the hemlock woolly adelgid. We consider the response of bryophytes to these changes, particularly increased availability of understory light and coarse woody debris (CWD). Pre-adelgid surveys and environmental measurements were taken at a network of 72 permanent plots in 1994 and 1995. Re-measurement of understory variables was conducted in 2003 and 2006. Bryophytes have responded to adelgid impacts through a sustained increase in plot-level richness, mainly achieved through a greater frequency of species occurring on CWD and to a lesser extent on bare soil in the plots. Greater gains in species richness took place in plots closer to the streams. Bryophyte responses to understory light availability and shrub density suggest that light availability may be more important for species maintenance than for species colonization. *Orthodicranum montanum* (Hedw.) Loeske had the greatest increase in frequency, occurring in two-thirds of all plots on one or more substrata by 2006. Several nitrophilous species had appeared by 2003 and 2006 including *Brachythecium rutabulum* (Hedw.) Schimp., which has now colonized almost one-third of the plots since the hemlock woolly adelgid invasion. Bryophytes are a significant component of the understory vegetation in eastern hemlock stands and this study is the first to document the dynamic nature of their response to hemlock woolly adelgid impacts.

Key words: bryophyte, coarse woody debris, eastern hemlock, forest, hemlock woolly adelgid.

Bryophyte ecology in eastern hemlock (*Tsuga canadensis* (L.) Carr.) dominated forests has received little attention beyond early descriptions of epiphyte communities (Cain and Sharp 1938, Phillips 1951, Culberson 1955, Slack 1976, Studlar 1982, Schmidt and Slack 1990). Understanding the ecology of the bryophyte community in these forests is currently of particular concern due to the widespread and dramatic hemlock decline caused by the invasion of an exotic insect pest, the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand). In addition, the cover of ground vegetation in intact hemlock forests is low with vascular plants and bryophytes contributing equally in diversity and abundance (Cleavitt and Fahey 1996, Battles et al. 2000). Thus to fully understand plant dynamics in these forest, the responses of the bryophyte community must be considered.

The understory environment of hemlock forests has been characterized by uniformly low light levels accompanied by little variation in light, temperature, and humidity conditions during the growing season (Rogers 1980,

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Frelich and Lorimer 1991, Battles et al. 2000). Many upland bryophyte species thrive under these conditions because of their physiological preference for constant humidity and moderate light levels (Proctor 1982, 2000). When forest understory conditions are altered by canopy disruption, leafy liverworts are often more sensitive than mosses to changes in environmental conditions (e.g., light levels, humidity) (e.g., Andersson & Hytteborn 1991, Åström et al. 2005, Fenton et al. 2003, Hylander et al. 2005, Nelson & Halpern 2005).

The understory conditions in many forests dominated by eastern hemlock are being radically altered through the impacts of HWA. Eastern hemlock has shown no resistance to HWA and decline is relatively rapid (Orwig and Foster 1998, Jenkins et al. 1999, McClure 2001, Eschtruth et al. 2006). Adelgid impacts on the understory environment have included increases in both understory light levels and availability of coarse woody debris (CWD) (Orwig and Foster 1998, Jenkins et al. 1999, Eschtruth et al. 2006). The initial responses of understory vascular plants to these changes were mainly to the increased light levels with expansion of fern cover and increased prevalence of birch seedlings (Orwig and Foster 1998, Jenkins et al. 1999, Eschtruth et al. 2006). In contrast, the pattern of bryophyte response to hemlock decline has not been previously considered.

Since the early 1990's, Delaware Water Gap National Recreation Area (DEWA) has coordinated a research and monitoring program focused on HWA and its implications for hemlock ecosystems in the Park. As part of these efforts we examined the response of the ground-level bryophytes to changes from HWA impacts in DEWA. Based on observed responses of bryophytes to disturbance in other forest ecosystems, we predicted the following responses to HWA disturbance: 1) a decline in bryophyte cover due to increased canopy opening; 2) an increase in bryophyte species richness owing to changes in substrata availability, especially from gains on CWD and bare soil; and 3) differential effects of canopy opening across taxa with a greater loss of liverwort species than moss species.

Materials and methods. STUDY SITES. The Delaware Water Gap National Recreation Area (DEWA) is an approximately 27,800 ha National Park on the Pennsylvania–New Jersey border. In 1993, resource managers in DEWA initiated intensive studies to document pre-HWA ecological conditions in two hemlock ravines, Adams Creek (AC) and Van Campens Brook (VC). Adams Creek and Van Campens Brook are tributaries to the Delaware River (41° 31′ N, 74° 49′ W) and they are 18.5 km straight-line distance apart. The ravine sides are steep and range from 3 to 80% slope with shallow, droughty, and acidic soils (Battles et al. 2000). At the start of the Park study in 1993 neither ravine was infested by HWA. Hemlock woolly adelgid was detected on trees in both ravines by 1995, but adelgid-induced canopy damage was not visible until 2000. Although HWA is present at both sites, AC is in a more advanced state of decline. In 2006 the percent of trees in severe decline or dead was 11% at VC up from 9% in 2003. At AC the percent of trees in severe decline or dead was 42% in 2006 increased from 34% in 2003 (Eschtruth et al. 2006, Eschtruth unpublished data).

The regional climate is humid continental with mean annual temperatures of 9.7°C and mean annual precipitation of 115.5 cm (NOAA 2002, Station 110). During the study interval, the region experienced a moderate dry period in the 1995 growing season and a mild dry period from 1999 to 2002 (NCDC 2005). Five years (1998, 2001, 2002, 2005, and 2006) were warmer than average (NOAA 2007).

The pre-adelgid flora of the ravines has been reported for both vascular plants and bryophytes (Cleavitt and Fahey 1996, Battles et al. 1997). In ravine-wide floristic surveys conducted in 1994 and 1995, AC had 175 species of vascular plants and 107 species of bryophytes and VC had 67 species of vascular plants and 60 bryophyte species. All voucher specimens are deposited at the Bailey Hortorium (BH), Cornell University. The flora of the ravine slopes, where study plots were located, was very similar for the two sites and included approximately 30 vascular plant species and 50 bryophyte species (Battles et al. 1997). Bryophyte taxonomy follows Schuster (1966–1992) for liverworts and Crosby et al. (1999) for mosses except the genus *Orthodicranum*, which follows Peterson (1979).

PERMANENT PLOTS. The intensive sites set-up by managers in the DEWA consisted of a network of points selected randomly using aerial photographs. At these random points in each hemlock ravine, monitoring transects were established at 10, 30, and 50 m upslope from the stream edge if the surrounding forest was dominated by hemlock (basal area > 50%). Our permanent understory vegetation plots were located at the mid-point of each transect. In addition, ravine edge plots were also established only if the edge of the hemlock-dominated forest was within 100 m perpendicular distance from the 50 m plot, when the ravine extended further than 100 m then no edge plot was established for that group of plots. For each plot, the base was set parallel to the streambed and centered on the permanent point. These permanent plots were marked with metal stakes to form the outline of 2 × 4 m sampling plot with a 0.5 × 1 m nested subplot in the downstream corner referred to as the bryophyte subplot. A total of 72 permanent points were established with their associated plots (20 plots each at 10, 30, and 50 m, and 12 edge plots).

PLOT SURVEYS. In 1994/95, 2003 and 2006, understory light availability was characterized using hemispherical canopy photos (Battles 1999, Eschtruth et al. 2006), substratum cover classes were visually estimated and plot vegetation was surveyed. All canopy photos were taken at 1 m above ground under diffuse light conditions using scientific grade photographic lenses (Nikkor 8 mm). Any shrubs or subcanopy tree branches close to the tripod were held back while taking the photograph thus the photographs are a representation of changes in the tree canopy coverage rather than changes in ground-level light conditions. We used the Gap Light Analyzer software to compute the fraction of total transmitted radiation reaching each photo point during the growing season (Canham 1988, Frazer et al. 1999). The above-canopy radiation model was based on long-term results from the nearest National Weather Service station (Scranton, PA; Knapp et al. 1980). Precision error associated with photographic analyses was less than 5% root mean squared error. Substratum cover classes (visual cumulative cover estimates of substrata available for plant establishment) included coarse woody debris (CWD), tree (live trunk and roots), rock, leaf litter, bare mineral soil, and bryophytes. Separate estimates were made for the upstream and downstream 2 × 2 m areas. The shrub and subcanopy tree layer were grouped together as woody vegetation ≥ 1 m tall, but not nearing the height of the canopy and were quantified by a 5 m radius plot centered at the plot center point with all stems tallied by species. Visual cover estimates were recorded for vascular plants less than 1 m in height in the 2 × 4 m plot. Because the bryophyte subplot is located in the downstream half of the plot, we use data for only the 2 × 2 m downstream half of the plot in this paper. Bryophyte subplot data were taken as species presence by substratum type and did not include cover estimates as very few species ever achieved 1% cover. Note that bryophyte cover estimates were made as part of substratum estimates at the 2 m^2 level. Because of difficulties in identification of bryophytes in permanent plots, it was sometimes necessary to collect specimens for verification of species identity with microscopic characteristics. A summary of the 1994–1995 baseline data is given in Battles et al. (1997, 2000). A more detailed analysis of the vascular plant response including the tree and shrub layers is presented by Eschtruth et al. (2006).

DATA ANALYSES. Changes through time in the plot-level environmental and vegetation characteristics were tested with an analysis of variance. Significant differences in individual characteristics were tested with Tukey's post-hoc comparisons. Given the absence of normally distributed errors, these tests were performed on the ranks of the data (equivalent to a non-parametric Kruskal-Wallis). Correlations between variables were explored with two-tailed Pearson-Product Moment Correlation. Statistically significant changes in species composition of the plots over time were assessed using multi-response permutation procedure (MRPP) with Sørensen's distance (McCune and Grace 2002). Groups were defined by sample year and analysis was done in PC-ORD (ver. 4; McCune & Medfford 1999).

The response of bryophytes in terms of plot richness, species gains and species losses were analyzed with generalized linear models (GENMOD in SAS ver. 9.1; SAS 2004). The response variables were fitted to a negative binomial distribution and the log link function was used to describe the relationship between the expected values and the linear predictors. For the bryophyte richness response, five categorical explanatory variables were entered into the model: plot, ravine, position in the ravine, year sampled, and identity of nearby canopy tree (hardwood or conifer); and six continuous variables: substrata cover, understory light availability, shrub density, herbaceous species richness, herb cover, and the number of species in each plot found on CWD. Plot was the exchangeable repeated variable to account for repeated measures in the design. During the model building process, several decisions were made regarding highly correlated variables. Light levels and year were highly correlated (df $= 216$, $r = 0.665$, $P < 0.001$) and light was chosen as the more biologically relevant variable for inclusion in the model. Similarly, estimates of substratum covers were not independent and leaf litter cover was chosen as the most integrative measure of overall change in substrata availability. The ''full model'' for comparison of reduction in log likelihood was the model with all main effects and all possible two-way interactions. A fully saturated model was not possible because of degrees of freedom restrictions. The ''best model'' maximized reduction of log likelihood while including all significant terms in the model (Hosmer and Lemeshow 1989).

The models explaining species gains and species losses were similar in structure to the model for bryophyte richness; however, explanatory variables were derived from the differences between variables for the sample periods. Categorical variables in the models were plot, year interval, ravine, and position in ravine. The continuous variables were original number of bryophyte species, change in light availability, change in shrub density, change in leaf litter cover, change in herbaceous species richness, and change in herbaceous cover. Plot was the exchangeable repeated variable to account for repeated measures in the design.

Changes in species frequency on the four substratum types (CWD, rock, soil, and tree) and species specific changes in frequency were examined by comparison of slopes for relationship between frequency and survey years. As a conservative multiple comparison test, slopes whose 95% confidence intervals did not overlap were considered significantly different at $\alpha = 0.05$. In addition, logistic regression was used to predict the presence/absence of species on the two most prevalent substratum types, CWD and bare soil. The explanatory variables entered into the logistic regression models were the same as for the bryophyte richness model, except that CWD cover was included in the CWD model and bryophyte cover was included in the soil model since these variables seemed to best express plot-level availability of these substrata. The ''full model'' contained all main effects and their two-way interactions. The final model was built by using an iterative process of adding and removing variables to select the optimal model based on a combination of variable significance, deviance reduction, and Wald statistics (Hosmer and Lemeshow 1989). These logistic regression models were run using SPSS (ver. 14; MathSoft 2005).

Results. CHANGES IN PLOT ENVIRONMENT AND GROUND VEGETATION. There were four distinct patterns of temporal change in the environment and vegetation characteristics of the permanent plots. These patterns fell into the following categories (relevant variables indicated in parentheses): (1) no change (shrub density and rock cover); (2) significant increase only in 2006 (cover of CWD, number of species on CWD and bryophyte cover); (3) significant increase by 2003 and remained the same for 2006 (leaf litter cover and herbaceous species richness); and (4) significant increase in 2003 with further increase in 2006 (light, bryophyte species richness and herbaceous cover) (Table 1). We found strong positive correlations between light levels and herbaceous cover and herbaceous richness. These correlations were present for both actual values and changes in values (Table 2). However, these relationships were not present in all time periods. Herbaceous species richness and cover were correlated for all three sample times (Table 2).

RICHNESS RESPONSE OF BRYOPHYTES. Three of the 72 plots did not contain bryophytes at any sample time in the 12 year span of the study. These three plots were all plots 50 m from the streams with high shrub densities and low CWD cover. For the remaining 69 plots that contained bryophytes, within plot composition changed significantly among the sample years (MRPP chance-corrected within group agreement $= 0.02$ ($P < 0.001$)) with plots becoming more similar to one another over time (distance values by year: 1995 (0.807); 2003 (0.752); 2006 (0.632)).

Table 1. Summary of values by year sampled for bryophyte species richness and measured continuous variables for the permanent plots. Values are given in the format of mean (SD) median. Values that are significantly different across years at $\alpha = 0.05$ are indicated by an asterisk with different letter superscripts for each post-hoc subset.

Variable	Units	1994/5	2003	2006
Bryophyte species*	spp. per 0.5 m^2	1.88 (1.66) 2^{a}	3.06 (2.19) 3^{b}	5.10 (2.77) 5^{c}
Bryophyte species on CWD*	spp. per 0.5 m^2	0.83 (1.39) 0^{a}	1.39 (1.79) 1^{a}	2.76 (2.07) 3^{b}
Shrub density	stems per ha	939 (546) 828	937 (634) 764	978 (812) 764
Bryophyte cover*	% of 2 m^2	1.44 (3.46) 0^{a}	2.85 (8.38) 0^{a}	3.03 (7.38) 1.5^{b}
Rock cover	% of 2 m^2	1.79 (5.50) 0	1.52 (3.94) 0	1.48 (3.93) 0
Leaf litter cover*	% of 2 m^2	91.8 (10.7) 96^{a}	89.8 (12.9) 94^{b}	85.9 (12.8) 90^{b}
CWD cover*	% of 2 m^2	3.56 (6.43) 1^{a}	4.54 (8.66) 2^{a}	6.46 (9.24) 3.5^{b}
Light*	% Transmitted 1 m above ground	5.18 (2.97) 4.38^{a}	11.2 (5.69) 10^{b}	15.8 (6.59) 14.1^{c}
Herbaceous species*	spp. per 2 m^2	4.32 (2.78) 4^{a}	5.75 (3.71) 5^{b}	5.65 (3.67) 5^{b}
Herb cover*	% of 2 m^2	2.67 (4.09) 1.25^{a}	9.33 (17.7) 2^{b}	15.6 (23.9) 4.75^{c}

Bryophyte richness in the plots increased at all positions in the ravine over time with a greater increase occurring in the 10 m and 30 m plots (Fig. 1a). Bryophyte richness in the plots was best explained by the number of species occurring on CWD in the plot, position of the plot in the ravine, shrub density, and interactions between light availability and leaf litter cover and between light availability and herbaceous species richness (Table 3). Variables that were not included in the model were ravine, identity of nearby canopy tree (hardwood or conifer) and herbaceous species cover. Bryophyte richness was highest in plots at 10 m and 30 m from the stream. These plots also had the highest richness on CWD and low shrub density. The positive relationship between light and bryophyte species richness was strongest in plots with highest cover of leaf litter and in plots with intermediate richness of herbaceous species.

The overall richness response can be viewed in terms of losses and gains of species in the plots (Fig. 1b). Naturally, with a net increase in bryophyte species richness, there were more gains than losses. From regression analyses, gains in species were best explained by year interval (df = 1; $X^2 = 13.09$; $P = 0.0003$) and an interaction between position of the plot in the ravine and change in herbaceous species richness (df = 1; $X^2 = 10.50$; $P = 0.0148$). This interaction related to a change from negative to positive relationship between herbaceous plant and bryophyte gains. In 10 and 30 m plots, plots with gains in the number of bryophyte species had a decrease in herbaceous species richness. In the 50 m and edge plots, plots with gains in the number of bryophyte species also had gains in the

Table 2. Pearson two-tailed correlation coefficients with comparison of change in variables above the diagonal and comparison of actual values below the diagonal. Correlations that were significant in all time periods (two time intervals for change and three years for actual values) are bolded. CWD richness is only relevant for the actual value comparisons. For actual values df = 216, and for change in values df = 144. * indicates a correlation is significant at the 0.05 level and ** at the 0.01 level.

	CWD richness	Shrub density	Bryophyte Cover	Rock Cover	Leaf litter cover	CWD cover	Light	Herb richness	Herb cover
Shrub density	−.104		−.004	.033	−.019	.011	−.019	.074	.093
Bryophyte cover	−.027	−.049		−.083	**−.535****	−.008	.043	.019	−.037
Rock cover	−.069	−.117	.030		**−.192***	.123	.082	.032	.084
Leaf litter cover	−.082	.105	**−.488****	**−.504****		**−.704****	−.049	−.081	−.065
CWD cover	.170*	−.028	−.094	.193**	**−.667****		.032	.146	.084
Light	.367**	.131	.080	−.111	−.162*	.125		.178*	.244**
Herb richness	.199**	.137*	.122	−.129	−.026	.008	.314**		.168**
Herb cover	.255**	.189**	.131	−.059	−.121	.091	.470**	**.465****	

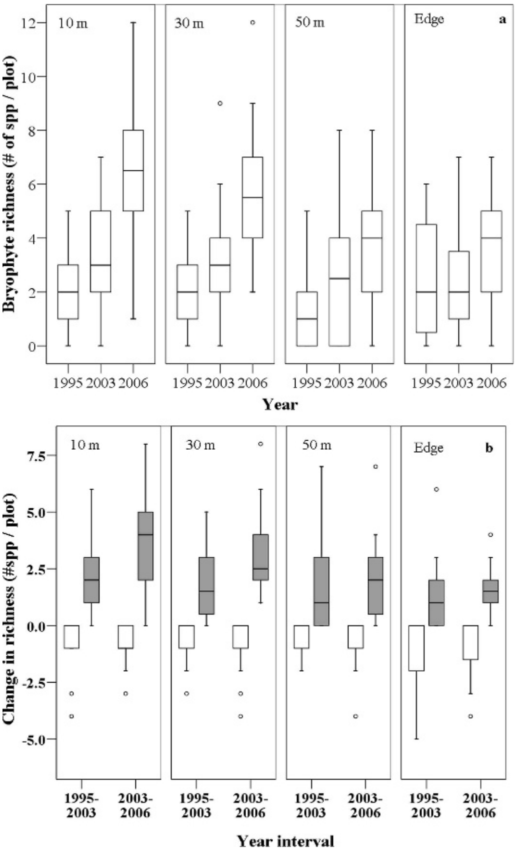

FIG. 1. Bryophyte species response shown by box plots as: (a) number of species by position in ravine over the three sample years and (b) number of species gained (positive values) and number of species lost (negative values) by position in ravine over two sampling intervals. Horizontal lines represent the median values, while the boxes show the interquartile range (middle 50% of the data; i.e., from 25th to 75th quantile). Vertical lines extend to show the spread of 80% of the data. Circles indicate outliers (data beyond three quartiles).

number of herbaceous species. Explanatory variables not included in the model were ravine, original number of bryophyte species, change in light availability, change in shrub density, change in leaf litter cover, and change in herbaceous species cover.

Table 3. The "best" regression model describing bryophyte richness in the permanent plots. Details of the model: df = 205, ratio of residual deviance = 1.25, and log likelihood = 271.49. In comparison, details for the "full" model containing all main effects and all two-way interactions: df = 173, ratio of residual deviance = 1.39, and log likelihood = 293.47.

Source	df	X^2	*P*-value
Bryophyte species on CWD	1	26.26	< 0.0001
Position in ravine	3	11.72	0.0084
Shrub density	1	5.89	0.0152
Leaf litter cover	1	8.64	0.0033
Light	1	0.88	0.3476
Herbaceous species	1	3.81	0.0508
Light * Leaf litter cover	1	5.07	0.0244
Light * Herbaceous species	1	5.77	0.0163

In regression analysis, losses of bryophyte species from plots were best predicted by an interaction between the original number of bryophyte species in the plot and change in shrub density (df = 1; $X^2 = 3.95$; $P = 0.047$). More species were lost from plots that had a greater number of original species regardless of shrub density (df = 1; $X^2 = 12.83$; $P = 0.0003$); however, this relationship was strongest in plots where shrub density increased. Explanatory variables not included in the model were year interval, ravine, position in ravine, change in light availability, change in leaf litter cover, and change in herbaceous species richness and cover.

SPECIFIC BRYOPHYTE RESPONSE BY SUBSTRATUM TYPE AND SPECIES. Significant increases were observed over time in bryophyte frequency on CWD (slope: 9.41 plots/sample time; 95% CI: 1.95–16.87) and bare soil (slope: 4.96; 95% CI: 3.29–6.62) while frequency on rock (slope: 0.95; 95% CI: 0.67–1.22) and tree roots/bases (slope: 1.21; 95% CI: −0.11–2.52) remained relatively constant (Fig. 2). The mean number of species on each substratum type increased slightly on CWD and tree roots/bases, but the majority of richness response was through increased frequency of common species that occur on multiple substrata.

From logistic regression analysis, plots had a higher probability of containing species on CWD if they were closer to the stream (df = 1; Deviance Reduction = 12.53; Wald = 11.63, $P = 0.001$), had higher light levels (df = 1; Dev. Red. = 20.21; Wald = 16.48, $P < 0.001$), higher cover of herbaceous plants (df = 1; Dev. Red. = 6.79; Wald = 4.27, $P = 0.039$) or lower shrub density (df = 1; Dev. Red. = 4.64; Wald = 4.56, $P = 0.033$) (Fig. 3). Plots were more likely to have species occurring on exposed soil if they were located at 30 m or edge position with high herbaceous species richness (significant interaction term: df = 1; Dev. Red. = 22.99; Wald = 8.15, $P = 0.004$), and had lower cover of leaf litter (df = 1; Dev. Red. = 7.79; Wald = 6.98, $P = 0.008$) or

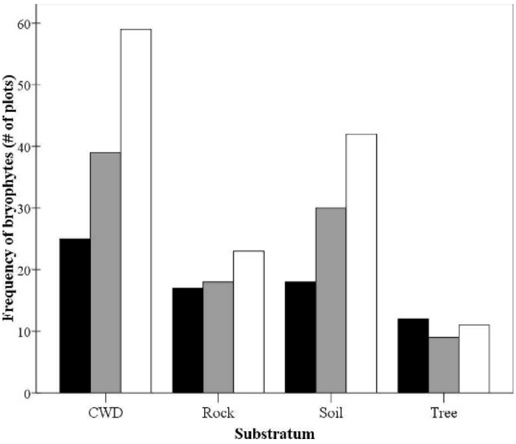

FIG. 2. Frequency of bryophytes on four substrata at three sample times as bar plot of total count of species (72 plots maximum possible at each sample time).

higher light levels (df = 1; Dev. Red. = 4.92; Wald = 4.54, $P = 0.033$) (Fig. 4).

There were 16 bryophyte species that occurred in 10% or more of the plots for at least one sample time including three liverworts, five acrocarpous mosses, and eight pleurocarpous mosses (Table 4). *Orthodicranum montanum* and *Lophocolea heterophylla* were by far the most frequent species (Fig. 5a). Considering substratum preferences, species with 50% or more of total occurrences on CWD were *Nowellia curvifolia*, *L. heterophylla*, *Ptillidium pulcherrimum*, *O. montanum*, *Tetraphis pellucida*, *Ulota crispa*, and *Platygyrium repens* (Fig. 5a). Mainly soil species (50% or more of occurrences) were *Dicranella heteromalla*, *Leucobryum glaucum*, *Hypnum imponens*, and *Brachythecium rutabulum*. Generalist species (i.e., occurred on all four substrata and did not have 50% or more of occurrences on any one substratum type) were *Brotherella recurvans*, *Hypnum pallescens*, *Plagiothecium laetum*, *Pseudotaxiphyllum elegans*, and *Thuidium delicatulum* (Fig. 5a).

The pattern of species occurrence in plots over time relates to species persistence and ability of the species to take advantage of changes in the plot environment. *Plagiothecium laetum* and *Pseudotaxiphyllum elegans* were the only two species to have more than 50% of their plots of occurrence date from 1995 (Fig. 5b). These two species had either no response or slightly negative response to changes in the ravines (Fig. 5c). On the other

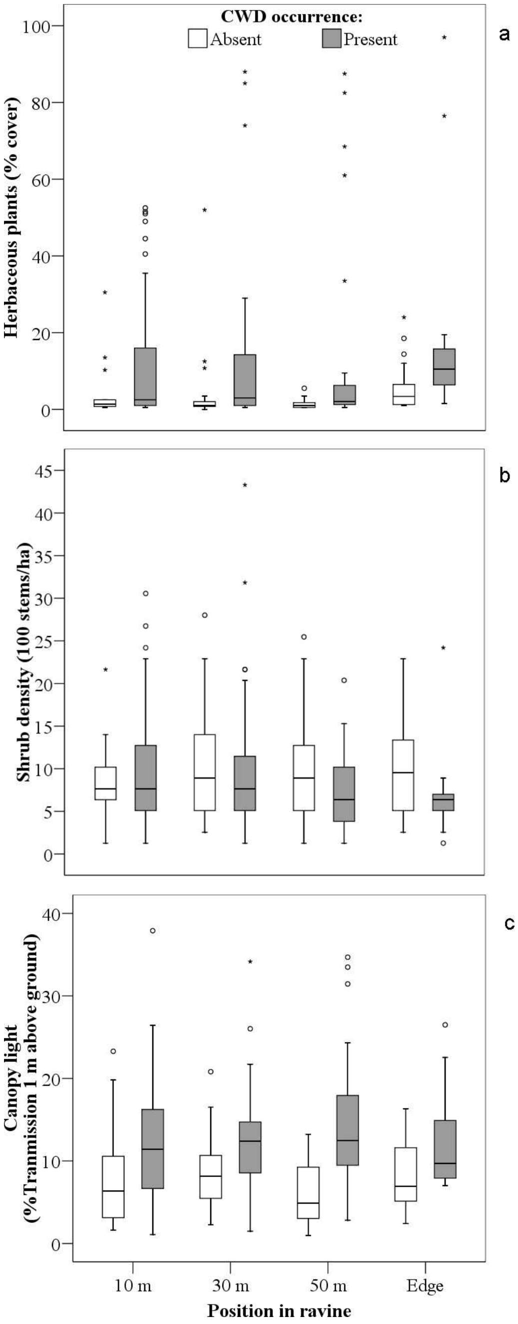

FIG. 3. Boxplots of variables significant in predicting the presence/ absence of species occurring on CWD shown here by position in the ravine and by: (a) herbaceous species cover, (b) shrub density, and (c) light. Horizontal lines represent the median values, while the box shows the interquartile range. Vertical lines extend to show the spread of 80% of the data. Circles indicate outliers (data beyond three quartiles) and asterisks denote extreme values.

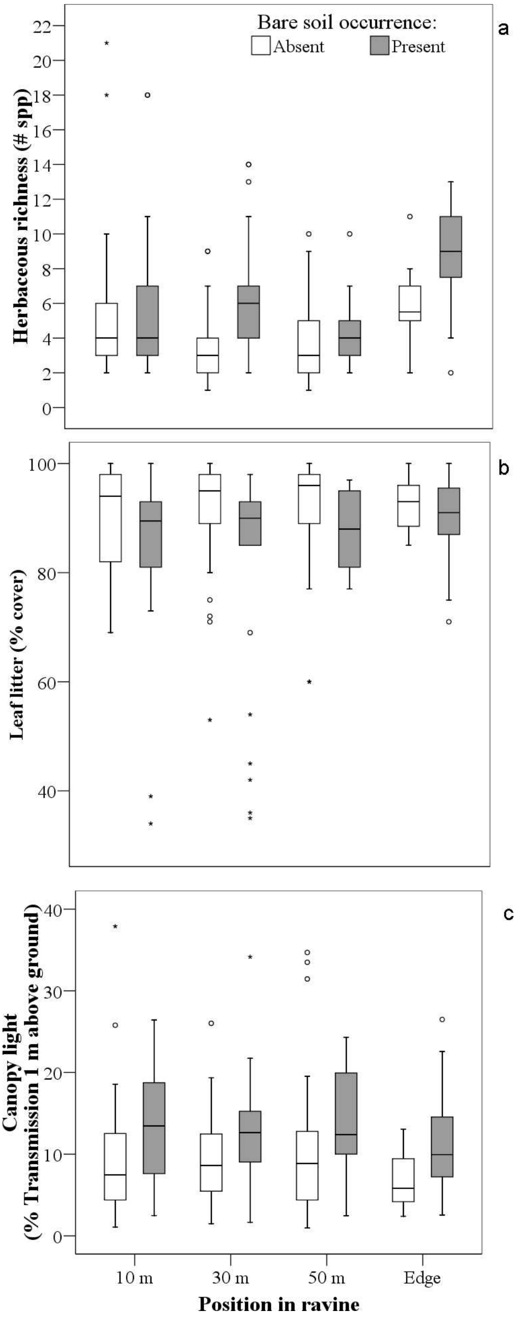

FIG. 4. Boxplots of variables significant in predicting the presence/absence of species occurring on bare soil shown here by position in the ravine and by: (a) herbaceous species richness, (b) forest floor cover, and (c) light. Box displays interquartile range, with horizontal line representing the median. Vertical lines extend to show the spread of 80% of the data. Circles indicate outliers (data beyond three quartiles) and asterisks denote extreme values.

Table 4. List of the 16 bryophyte species occurring in 10% or more of the permanent plots over the study period 1994/5–2006. Plants are arranged by growth form and rough size differences (smaller to larger) to aid in interpretation.

Liverworts
- *Nowellia curvifolia* (Dicks.) Mitt.
- *Lophocolea heterophylla* (Shrad.) Dumort.
- *Ptillidium pulcherrimum* (Weber) Vainio

Acrocarpous mosses
- *Dicranella heteromalla* (Hedw.) Schimp.
- *Othodicranum montanum* (Hedw.) Loeske
- *Tetraphis pellucida* Hedw.
- *Ulota crispa* (Hedw.) Brid.
- *Leucobryum glaucum* (Hedw.) Ångstr.

Pleurocarpous mosses
- *Plagiothecium laetum* Schimp.
- *Pseudotaxiphyllum elegans* (Brid.) Iwats.
- *Hypnum pallescens* (Hedw.) P.-Beauv.
- *Platygyrium repens* (Brid.) Schimp.
- *Hypnum imponens* Hedw.
- *Brotherella recurvans* (Mich.) Fleisch.
- *Brachythecium rutabulum* (Hedw.) Schimp.
- *Thuidium delicatulum* (Hedw.) Schimp.

hand, species that responded positively to the change in plot environments showed a greater percentage of their first occurrences in later sample times. For five species, over 50% of their first occurrences were not until 2006, *Brachythecium rutabulum*, *Brotherella recurvans*, *Platygyrium repens*, *Ulota crispa*, and *Tetraphis pellucida* (Fig. 5b). Of these species, the three pleurocarpous mosses had a strong increase in frequency between sample periods (Fig. 5a, c). Species with high persistence at the plot scale (over 50% of total occurrences in a plot were for 2 or more sample times) were *Othodicranum montanum*, *Leucobryum glaucum*, *Hypnum imponens*, and *Thuidium delicatulum* (Fig. 5d). Of these four species, *O. montanum* showed the strongest increase in frequency and over time the greatest prevalence throughout the plots (Fig. 5a, c).

Infrequent species (present in less than 10% of plots) showed three main patterns of occurrence: (1) six moss species disappeared or were transient in the plots and not present by 2006; (2) five moss species were added to the plots since initial surveys in 1994/5 with transience in some or all plots of occurrence; and (3) six liverwort species and seven moss species appeared in 2003 and were present in 2006 or appeared in 2006 (Table 5).

Discussion. Changes in the forest environment caused by hemlock decline have thus far resulted in a sustained increase in bryophyte

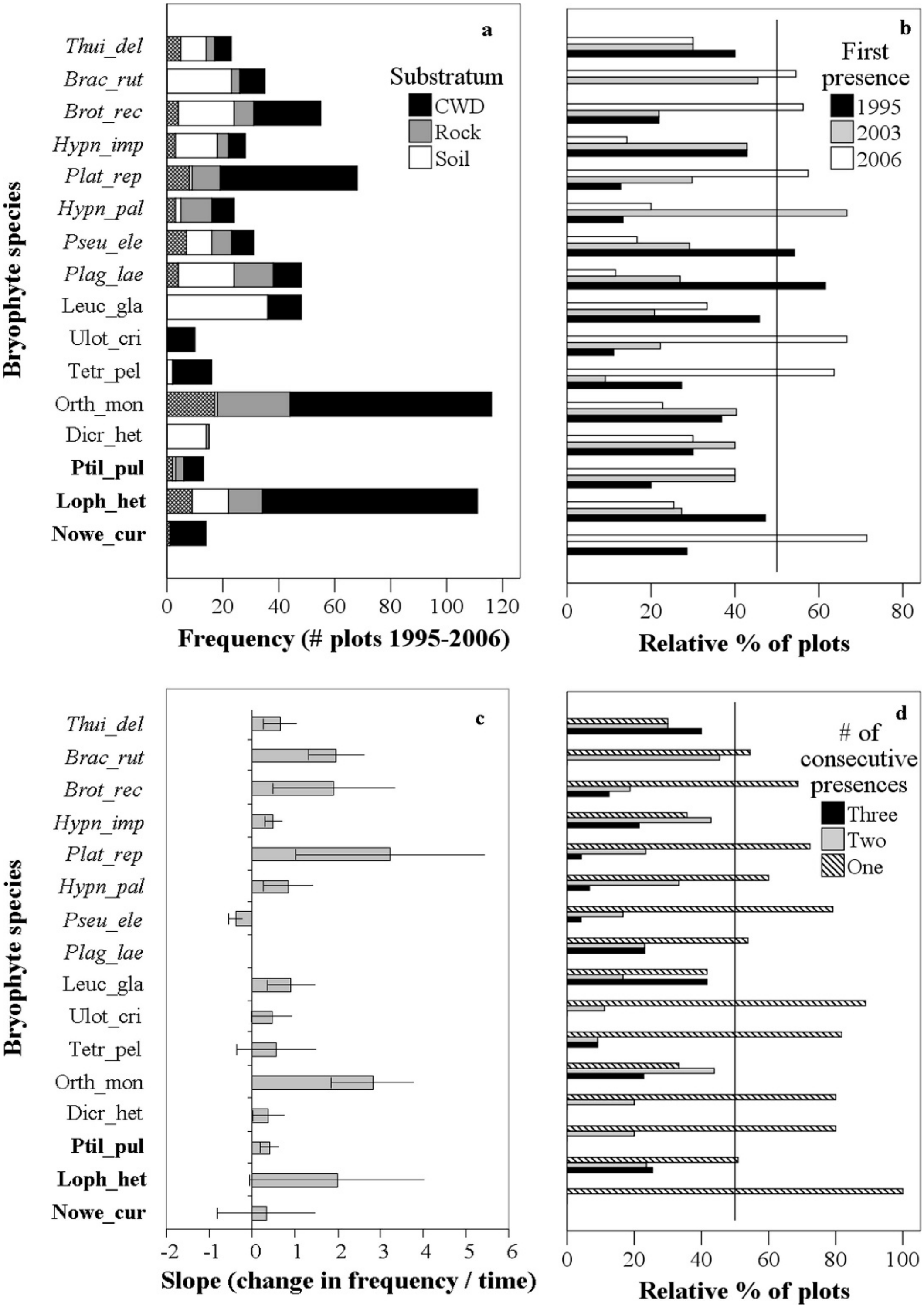

FIG. 5. Patterns of occurrence in plots for 16 bryophyte species over the three sample times by: (a) stacked bar graph of frequency on four substratum types, (b) clustered bar graph of first year of occurrence in plots, (c) bar graph for slope of frequency change over the sample times (error bars are 95% CI), and (d)

cover, frequency, and species richness. Bryophytes responded similarly in experimental plots following the exposure of soil to mimic root tip-up disturbance in the boreal forest (Jonsson and Esseen 1998). A sustained increase in bryophyte richness has also been documented in the absence of any experimental disturbance in monitoring plots in Norway, where bryophytes were thought to have responded positively to longer and/or moister growing seasons (Økland 1995, Økland and Eilertsen 1996, Økland et al. 2004). In our study, the main determinant of bryophyte response appeared to be the increase in CWD, although our study interval also encompassed a number of warmer than average years that may have played a role in the magnitude of the response.

This is the first study to document the response of forest bryophytes to an influx of CWD. The importance of CWD as a notable habitat for forest bryophytes has been repeatedly documented, especially for liverwort species (e.g., Söderström 1988, Ohlson et al 1997, Rambo 2001). The majority of species gains occurred on CWD and species richness on CWD was the most significant predictor of overall richness. However, cover estimates of substratum types, especially for CWD, were not detailed enough to be significant explanatory variables and this should be noted for future studies planning to include bryophytes. For CWD, some index of quality of the substratum needs to be included such as decay stage, moisture status, size, and type (e.g., twigs, bark, stumps, logs). Over one-third of the plots with no recorded CWD cover had species present on CWD in the bryophyte subplot. The presence of less than 1% cover of high quality CWD may support more species in a plot than much higher coverage of suboptimal CWD. In this study, bryophytes on fallen bark pieces were an important component of species diversity on CWD.

Position of the plots in the ravine was the most universally significant explanatory variable in the models of bryophyte response. The importance of slope position is primarily interpreted as a moisture gradient with conditions more conducive to bryophyte growth at 10 m and 30 m plots (Jonsson 1997, Stewart and Mallik 2006).

Unlike vascular plants, the ability of bryophytes to take advantage of increased light availability is tightly linked with ambient moisture conditions (e.g., Cleavitt et al. 2007). In general, the photosynthesis of bryophytes saturates at low light levels and many species may not be capable of benefiting from increased light availability (Hoddinott and Bain 1979, Proctor 2000). However, some bryophytes fail to saturate at high light levels (e.g., Marschall and Proctor 2004), and more recent studies have found evidence of light limitation to growth of forest bryophytes (Gabriel and Bates 2003, Cleavitt et al. 2007). In these hemlock forests, the absolute index of light availability was positively related to richness while the change in light availability was not important in explaining bryophyte losses and gains. These results suggest that while light plays a role in structuring bryophyte assemblages in hemlock forests, its importance is limited by other factors such as substrata availability, moisture regime, and species dispersal.

Given the effects of increased shrub density on species losses, light may be more important in determining species persistence rather than species colonization. Species loss was not directly related to any change in the environment; however, the strength of the relationship between the number of species lost and the original number of bryophytes increased when shrub density increased. Although increased shrub density could affect a number of understory conditions such as soil moisture and animal activities, we interpret a denser shrub layer to most directly correspond with decreased light availability at the ground-level (Pitkin 1975). Change in light from increases in shrub density would not have been captured in our canopy light measurements, but apparently were important to persistence of bryophytes.

In forest canopy manipulation experiments in Canada and Scandinavia, bryophytes re-

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clustered bar graph for the number of consecutive sample times that the species was recorded in a given plot. Species are abbreviated by the first four letters of their genus and first three letters of their specific epithet, and are arranged by growth form and size (within each group smallest are closest to y-axis). Liverworts are in bold, acrocarpous mosses are in regular font, and pleurocarpous mosses are italicized.

Table 5. Details of plot occurrence for bryophyte species that occurred in less then 10% of the plots for all sample periods (1994–2006). Liverworts are marked with an asterisk.

Species occurring only in one year, not present in 2006	Years of occurrence	Number of plots for that period
Anomodon rostratus (Hedw.) Schimp.	1995	1
Herzogiella striatella (Brid.) Iwats.	2003	1
Herzogiella turfacea (Lindb.) Iwats.	2003	1
Pohlia nutans (Hedw.) Lindb.	2003	1
Isopterygiopsis muelleriana (Schimp.) Iwats.	1995	1
Rosulabryum capillare (Hedw.) Spence	2003	1
Species not present in 1994/5, occurring thereafter with some transience		
Anomodon attenuatus (Hedw.) Hüb.	2003	1
	2006	1
Brachythecium velutinum (Hedw.) Schimp.	2003	3
	2003–2006	1
	2006	5
Eurhynchium pulchellum (Hedw.) Jennings	2003–2006	1
Plagiomnium cuspidatum (Hedw.) T. Kop.	2003	2
	2003–2006	1
	2006	3
Rhizomnium punctatum (Hedw.) T. Kop.	2003	2
	2006	1
Species not present in 1994/5, maintained in plots since appearance		
* *Bazzania trilobata* (L.) Gray	2003–2006	1
	2006	1
Buxbaumia aphylla Hedw.	2006	1
* *Colojeunea biddlecomiae* (Aust.) Evans	2006	4
* *Cephalozia bicuspidata* (L.) Dumort.	2006	2
Dicranum fuscescens Turn.	2006	2
* *Lophocolea bidentata* (L.) Dumort.	2003–2006	1
* *Lophocolea minor* Nees.	2006	1
Mnium hornum Hedw.	2006	1
Orthodicranum flagellare (Hedw.) Loeske.	2003–2006	2
	2006	3
Plagiomnium ciliare (Hedw.) T. Kop.	2006	1
* *Radula complanata* (L.) Dumort.	2006	1
Rhynchostegium serrulatum (Hedw.) A. Jaeger	2003–2006	1
	2006	2
Sphagnum sp. (single stranded stem)	2006	1

sponded to canopy disturbance more quickly than the vascular ground vegetation with reduced cover of pre-disturbance species and increased frequency of colonist species in many cases (Gustafsson and Hallingback 1988, Jonsson and Esseen 1990, Haeussler et al. 2002, Ross-Davis and Frego 2002, Fenton et al. 2003). In the hemlock ravines, the relationship between bryophyte richness and herbaceous richness was complex, always occurring as a significant interaction term when present in the models. The most informative of these interactions was based on ravine position. At 10 m and 30 m positions, plots with the greatest gains in bryophyte species had the greatest herbaceous species losses. In contrast, at 50 m and edge positions, there was a positive relationship between gains for the two plant groups. Changes in substratum importance may partially explain this pattern, as the gains of bryophyte richness closer to streams occurred mainly on CWD while away from the stream, soil gains became more prevalent.

Liverworts have repeatedly been shown to suffer greater declines than mosses due to forest canopy opening (Andersson and Hytteborn 1991, Åström et al. 2005, Fenton et al. 2003, Hylander et al. 2005, Nelson and Halpern 2005). In general, HWA disturbance is a more gradual process than the abrupt changes caused by forest harvest because it proceeds gradually through progressive needle loss and resultant canopy thinning (Kizlinski et al. 2002). We did not see a greater loss of liverwort species in our plots relative to moss species. To the contrary, there were no liverwort species lost from the plots and six infrequent liverworts were added. The three common liverworts tended either toward no change in frequency or slight increase in frequency. This difference in response is likely related to the less severe change in light and humidity levels in our plots compared with the cited studies and to the concurrent addition of a key liverwort substratum, CWD.

Two moss species may have been negatively impacted by changes in the hemlock ravines, *Plagiothecium laetum* and *Pseudotaxiphyllum elegans*. Although these two small pleurocarpous mosses appeared to be substrata generalists, they were not able to take advantage of changes in substrata availability suggesting either that they were unable to disperse to or compete for these substrata under changing conditions. In contrast, a second pair of small pleurocarpous mosses, *Hypnum pallescens* and *Platygyrium repens*, were able to increase in frequency in 2003 and 2006, respectively. Further physiological comparisons of these species should reveal interesting differences that may relate to differential ability for growth under higher light conditions. The largest species, *Leucobryum glaucum*, *Hypnum imponens*, *Brotherella recurvans*, *Brachythecium rutabulum*, and *Thuidium delicatulum* were more persistent in the plots than the smaller species (note that *all* of one year occurrences for *B. recurvans* and *B. rutabulum* were the result of appearance in 2006). The common liverwort species appeared to be fairly mobile with all three benefiting from the increased availability of CWD. *Ulota crispa* most often occurred in the plots as an epiphyte on fallen bark, which explains the transient nature of this species here. *Dicranella heteromalla* and *Tetraphis pellucida* were also transient in this study; however, *T. pellucida* appeared in the majority of plots where it occurred in 2006 and may have higher persistence with further resampling.

Notable species additions of nutrient demanding, faster growing members of the Brachytheciaceae (*Brachythecium rutabulum*, *B. velutinum*, and *Rhynchostegium serrulatum*) may indicate that increased light levels are operating in conjunction with high levels of regional nitrogen (N) deposition (or other sources of N related to adelgid effects) to promote conditions suitable for invasion of damaged hemlock forests by these species. In Europe, species of *Brachythecium* usually experience increases in frequency and abundance with nitrogen additions (Kellner and Mårshagen 1991, Dirske and Martakis 1992, Strengbom et al 2001). Similarly, *Orthodicranum montanum*, the species with the greatest increase in frequency in this study, has been shown to indicate elevated nitrogen deposition in Britain (Bates et al. 2004). *Leucobryum glaucum*, another species with significant increase in frequency in our plots, was also found to increase in frequency after N addition (Rodenkirchen 1992). Additional support for this hypothesis comes from tissue analysis of 23 bryophyte species from two sample times in our study area that indicated elevated nitrogen content in bryophyte tissues (Cleavitt unpublished data). These samples had ^{15}N isotope signatures typical of nitrogen from oxidized nitrous compounds from industrial activity (-5 to 10‰) (Pearson et al. 2000).

The dramatic response of bryophytes to increased CWD in declining hemlock stands emphasizes the dynamic nature of these plant assemblages. It will be crucial to further our understanding of bryophyte ecology and HWA impacts by continuing to follow the response of the bryophytes in these ravines as hemlock decline proceeds further, especially since decline accelerates in the later stages of infestation (Eschtruth unpublished data). Important questions that remain for future resurveys include: (1) At what point will bryophyte species richness level off? (2) What will be the main determinant(s) of this leveling off? and (3) How will the effects of continued opening up of the hemlock canopy be balanced with effects of increases in deciduous leaf litter as the forest composition switches to a higher percentage of deciduous canopy trees? The valuable information gained by inclusion of bryophytes in studies of vegetation response to disturbance has been shown in this study and others (e.g., Økland et al. 2004). Truly effective monitoring programs require a whole-flora approach, which includes both bryophytes and vascular plants because the contrasting morphology and physiology of these two plant groups causes them to respond to different perturbation signals (Økland and Eilertsen 1996, Haussler et al. 2002, Økland et al. 2004).

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