Persistence of ground-layer bryophytes in a structural retention experiment: initial effects of level and pattern of overstory retention

Martin Dovčiak, Charles B. Halpern, James F. Saracco, Shelley A. Evans, and Denise A. Liguori

Abstract: We examined first-year responses of forest-floor bryophytes to structural retention harvests at four locations in western Washington. Treatments represented a range of retention levels (100%, 75%, 40%, and 15% of original basal area) and spatial patterns (dispersed vs. aggregated in 1 ha patches). Declines in bryophyte cover and species' frequencies were comparably large at 40% and 15% retention. Retention pattern had little effect on the magnitude of decline, although declines in richness tended to be greater in aggregated treatments. Changes in cover were small within forest aggregates (comparable to controls). However, richness declined relative to controls within aggregates at 15% retention; rarer taxa in these exposed patches may be susceptible to edge effects. Declines in species' frequencies and richness were consistently greater in "clear-cut" areas of aggregated treatments than in dispersed retention; liverworts were particularly sensitive to harvest. In cut areas, bryophytes responded positively to cover of understory vegetation and negatively to logging slash. The positive correlation of richness (but not cover) to tree basal area may reflect the contribution of tree boles to persistence of rarer corticolous species. Our results suggest that conservation of bryophytes in forests managed with structural retention will require large retention patches and dispersed trees at levels considerably higher than current retention standards.

Résumé : Nous avons étudié les réactions des bryophytes du parterre forestier pendant la première année suivant des coupes à rétention de structurale effectuées à quatre endroits dans l'ouest de l'État de Washington aux États-Unis. Les traitements couvraient une gamme de patrons de rétention (100 %, 75 %, 40 % et 15 % de la surface terrière initiale) et de patrons spatiaux (dispersés et agglomérés en blocs d'un hectare). La diminution du couvert de bryophytes et de la fréquence des espèces était importante et du même ordre de grandeur pour les traitements de rétention à 40 % et 15 %. Les patrons de rétention ont eu peu d'effet sur l'amplitude du déclin quoique la diminution de la richesse en espèces ait eu tendance à augmenter dans les traitements agglomérés. Les changements de couverture étaient faibles dans les agrégats de forêt et similaires aux témoins. Cependant, la richesse en espèces dans les traitements agglomérés à rétention de 15 % a diminué par rapport aux témoins; les taxons rares de ces blocs exposés sont peut-être susceptibles aux effets de bordure. Les diminutions de fréquence et de richesse en espèces dans les aires coupées à blanc des traitements agglomérés étaient généralement plus grandes que celles des traitements dispersés, les hépatiques étant particulièrement sensibles à la coupe. Dans les aires coupées, les bryophytes ont réagi positivement au couvert de la végétation du sous-bois et négativement à celui des débris de coupe. Une corrélation positive entre la richesse (mais pas la couverture) et la surface terrière peut refléter la contribution du tronc des arbres à la persistance d'espèces corticoles plus rares. Nos résultats indiquent que la conservation des bryophytes dans les forêts aménagées avec une rétention structurale exigera de grands îlots de rétention et des arbres dispersés à des niveaux considérablement plus élevés que les normes actuelles de rétention.

[Traduit par la Rédaction]

Introduction

Forest management can have dramatic effects on biological diversity. Clear-cut logging in particular can lead to marked changes in forest structure and function and to local extirpation of plant and animal species (e.g., Duffy and Meier 1992; Halpern and Spies 1995). Over the past decade, structural or variable retention has been adopted in many temperate-zone and boreal forest ecosystems as a less intensive method of regeneration harvest (US Department of Agriculture (USDA) and US Department of the Interior (USDI) 1994; Aubry et al. 1999; Beese and Bryant 1999;

Received 7 February 2006. Accepted 20 June 2006. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 24 January 2007.

M. Dovčiak,[1] C.B. Halpern, J.F. Saracco,[2] S.A. Evans, and D.A. Liguori.[3] College of Forest Resources, University of Washington, Box 352100, Seattle, WA 98195–2100, USA.

[1] Corresponding author (e-mail: mdovciak@u.washington.edu).

[2] Present address: The Institute for Bird Populations, P.O. Box 1346, Point Reyes Station, CA 94956-1346, USA.

[3] Present address: 7839 116th Avenue SE, Newcastle, WA 98056, USA.

Can. J. For. Res. 36: 3039–3052 (2006) doi:10.1139/X06-168

Vanha-Majamaa and Jalonen 2001). The motivation for using this approach is that partial retention of the overstory can moderate the effects of canopy removal, enhancing species' survival and accelerating ecosystem recovery while allowing for timber extraction (Franklin et al. 1997). Furthermore, by manipulating the level or spatial distribution of retained trees, managers have the ability to address particular ecological or silvicultural goals that vary across the landscape. For example, dispersed retention can be used where the objective is to moderate the forest-floor microclimate or to ensure greater soil stability over an entire harvest unit (Franklin et al. 1997). Aggregated retention can be implemented where it is necessary to retain snags, undisturbed ground vegetation, distinctive habitat features, or biologically rich microsites. On federal "matrix" lands allocated for regeneration harvest in the Pacific Northwest, current regulations require that trees are retained over at least 15% of each cutting unit, and that 70% of this retention is in aggregates of 0.2–1.0 ha (USDA and USDI 1994). Whether this minimum level of retention is sufficient to maintain organisms associated with mature or late-seral forests remains an area of active investigation.

Among the taxa likely to be sensitive to level or pattern of overstory retention are forest-floor bryophytes (mosses and liverworts). Because they are small, they can be easily damaged or buried during logging (Fenton et al. 2003; Åström et al. 2005). Physiologically, they are adapted to cool, moist, and shaded environments of the forest understory (Furness and Grime 1982; Proctor and Tuba 2002; Marschall and Proctor 2004). As a consequence, they are susceptible to the stresses induced by canopy removal, including exposure to direct radiation, elevated temperature, and reduced humidity. Liverworts are particularly sensitive to these stresses (Söderström 1988; Frisvoll and Prestø 1997; Fenton et al. 2003; Nelson and Halpern 2005*b*).

Responses of bryophyte communities to intensive forms of forest management are well documented in the literature (e.g., Hannerz and Hånell 1997; Jalonen and Vanha-Majamaa 2001; Ross-Davis and Frego 2002; Hylander et al. 2005). However, limited attention has been devoted to their responses within variable-retention systems (but see Hannerz and Hånell 1997; Jalonen and Vanha-Majamaa 2001). Moreover, there has been no explicit consideration of how the level and pattern of retention may contribute to bryophyte responses. Partial overstory retention has the potential to ameliorate light and temperature stress through shading by residual trees (Barg and Edmonds 1999; Heithecker and Halpern 2006). It can also give rise to spatial heterogeneity in ground conditions (e.g., disturbed soil and logging slash; Halpern and McKenzie 2001) or understory vegetation, to which bryophytes may respond negatively or positively. This spatial variation should be accentuated by retention of trees in aggregates (Franklin et al. 1997; Halpern et al. 2005; Nelson and Halpern 2005*a*, 2005*b*).

In this paper, we examine the initial (first year) responses of bryophytes to experimental manipulation of level and pattern of overstory retention within a larger regional study, Demonstration of Ecosystem Management Options (DEMO; Aubry et al. 1999), designed to evaluate the responses of diverse groups of forest organisms to structural retention harvests in mature forests of western Oregon and Washington (e.g., Luoma et al. 2004; Halpern et al. 2005; Nelson and Halpern 2005*a*; Schowalter et al. 2005). Experimental treatments represent a broad gradient of residual structure (15%–100% of original basal area) and a sharp contrast in pattern (dispersed vs. aggregated in 1 ha patches). We examine bryophyte responses across a range of spatial scales (among treatments, between cut and uncut portions of treatments, and among plots that vary in local postharvest conditions) to understand how level and pattern of retention directly or indirectly influence persistence and potential for recovery. We pose the following questions: (1) How do level and pattern of overstory retention affect treatment-scale changes in the composition, abundance, and richness of forest-floor bryophytes? (2) How does level of retention affect changes in bryophyte abundance and richness in the cut and uncut portions of harvest units? (3) Do species vary in their responses to harvest intensity? Are liverworts more sensitive than mosses? (4) How do postharvest ground conditions, residual forest structure, and understory vegetation mediate local variation in cover and richness of bryophytes?

Methods

Study sites

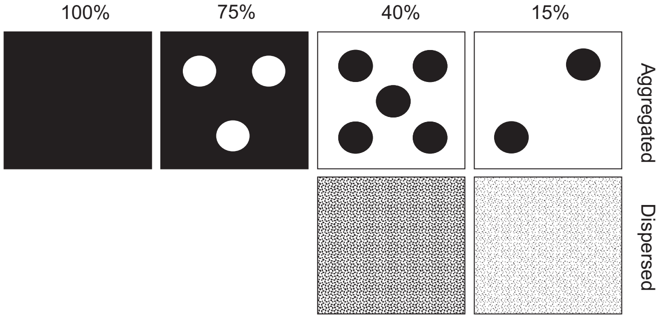
This study was conducted at four locations (experimental blocks) in western Washington State: Butte (BU), Little White Salmon (LW), and Paradise Hills (PH) are in the southern Cascade Range and Capitol Forest (CF) is in the Black Hills, southwest of Olympia. Locations were chosen to represent a range of physical environments and forest types. Elevations range from 210 to 1280 m. The climate is maritime with warm, dry summers and cool, wet winters. Among blocks, annual precipitation ranges from ~1860 to 2970 mm, falling mainly between October and April (Franklin and Dyrness 1973). Mean minimum temperatures in January range from –5.5 to –0.1 °C and mean maxima in August range from 21.5 to 24.1 °C (see Halpern et al. 2005). Soils are moderately deep, well-drained loams to loamy sands derived from volcanic parent materials (Pringle 1990; Wade et al. 1992).

Blocks represent three forest zones (Franklin and Dyrness 1973) — *Tsuga heterophylla* (Raf.) Sarg. (BU and CF), *Abies grandis* (Dougl. ex D. Don) Lindl. (LW), and *Abies amabilis* (Dougl. ex Loud) Dougl. ex Forbes (PH). However, all were dominated by mature *Pseudotsuga menziesii* (Mirb.) Franco before harvest. Three blocks (BU, LW, and PH) were mature, undisturbed forests, whereas CF was second growth that regenerated naturally following clear-cut logging in the 1930s. Stand age and pre-treatment basal area varied among blocks (65–170 years and 48–87 $m^2 \cdot ha^{-1}$, respectively), as did the pre-treatment abundance of understory vegetation (19%–52% cover of herbs and 13%–69% cover of shrubs >1 m tall). Details on the physical and biological characteristics of the blocks can be found in Aubry et al. (1999) and Halpern et al. (2005).

Experimental design

The experimental design consists of six treatments (including a control) randomly assigned to 13 ha harvest units at each of four blocks (Fig. 1). Treatments vary in the proportion of overstory basal area retained and (or) the spatial

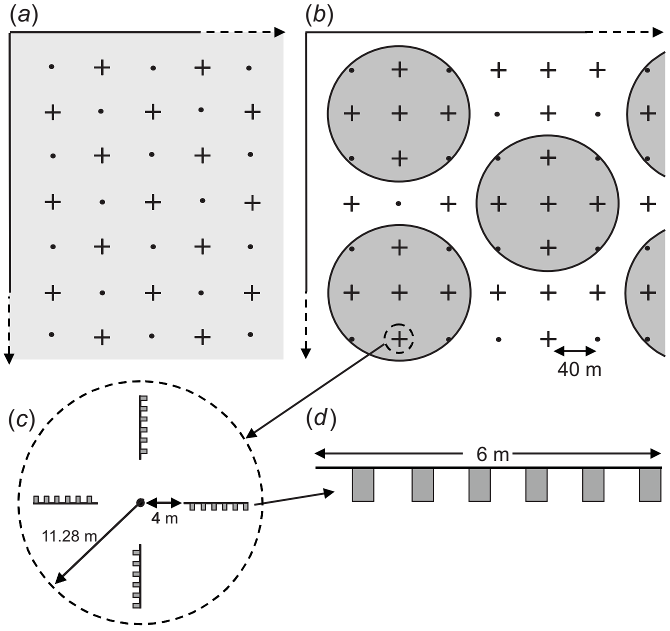
Fig. 1. Schematic diagram of the six experimental treatments replicated at each block. Black areas represent uncut forest (100% and 75%A) or 1 ha forest aggregates (40%A and 15%A) and stippled areas represent dispersed retention (40%D and 15%D; A and D denote aggregated and dispersed, respectively). (From Halpern and McKenzie 2001, reproduced with permission of Elsevier, For. Ecol. Manage., Vol. 154, pp. 215–225, © 2001 Elsevier.)



pattern of retention (aggregated vs. dispersed) as follows: 100% retention (control; 100%), 75% aggregated retention (75%A), 40% aggregated retention (40%A), 40% dispersed retention (40%D), 15% aggregated retention (15%A), and 15% dispersed retention (15%D). In 15%A and 40%A, trees were retained in 1 ha (56 m radius) circular patches (Fig. 1) with all merchantable trees (>18 cm diameter at breast height (DBH)) removed from adjacent harvested areas. In 75%A, all merchantable trees were removed from three 1 ha circular "gaps". In the dispersed treatments (40%D and 15%D), dominant and codominant trees were evenly dispersed, leaving a total basal area equivalent to that of the corresponding aggregated treatment (Aubry et al. 1999).

Although attempts were made to maximize the proximity of experimental units within a block, site selection was constrained by topography and past management (e.g., harvest units and roads). As a result, harvest units were not always adjacent. The greatest distance between units within a block was ~10 km (PH); otherwise distances were <3 km. Harvest treatments were completed within each block within a period of 3–7 months (1997 or 1998). Yarding methods varied among blocks depending on topography — helicopters at BU and LW, tracked or rubber-tired skidders at PH, and suspension cables at CF. Additional details on experimental design and harvest implementation are provided in Aubry et al. (1999), Halpern and McKenzie (2001), and Halpern et al. (2005).

Fig. 2. Sampling design with portions of two treatment units shown for illustration. (*a*) Sampling points (+) for dispersed treatments (15%D and 40%D) and the control (100%). (*b*) Sampling points for aggregated treatments (40%A and 15%A); a similar design was used for 75%A. (*c*) Circular 0.04 ha overstory plot with four 6 m long transects for sampling woody understory vegetation, logging disturbance, and other ground conditions. (*d*) Microplots (0.2 m × 0.5 m) for sampling herbaceous species and forest-floor bryophytes. For details see the text (Methods: Field sampling).



Field sampling

Prior to harvest, a systematic grid of sampling points (7 × 9 or 8 × 8, with 40 m spacing) was surveyed in each treatment unit (Fig. 2). Permanent plots were established at alternate points in the control and dispersed treatments ($n = 32$; Fig. 2*a*). To sample the two distinct postharvest environments of the aggregated treatments, plots were established at all grid points in the forest aggregates ($n = 24$–25 in 40%A; $n = 10$ in 15%A) and at a subset of points (chosen to represent all distances from the aggregates) in adjacent clear-cut areas ($n = 12$ in 40%A; $n = 22$ in 15%A). This yielded a total of 36–37 (40%A) or 32 (15%A) plots per treatment (Fig. 2*b*). In 75%A, plots were established at all grid points in the "gaps" ($n = 15$) and at a subset of points in the forest matrix ($n = 17$), yielding a total of 32 plots. Grid points on the edges of forest aggregates or gaps were not sampled (in a related study, gradients of bryophyte response across aggregate edges were examined; Nelson and Halpern 2005*b*). Each permanent plot consisted of a 0.04 ha circular overstory plot with four radial transects (6 m), each with six microplots (0.2 m × 0.5 m) spaced 1 m apart (yielding 24 microplots per plot; Figs. 2*c*, 2*d*). Pre-treatment sampling was conducted in summer 1994 or 1995 and post-treatment sampling in summer 1998 or 1999 (the growing season after harvest). Thus, 3–4 years passed between pre- and post-treatment sampling of each treatment unit. Observers differed between pre- and post-treatment sampling (although some were the same); the two teams were comparably trained and surveyed all experimental units during their respective sampling years.

Microplots were used to estimate total cover of bryophytes and presence of individual bryophyte species. In microplots with coarse woody debris, stumps, or bases of shrubs or trees, sampling was limited to a height of 1 m from the forest floor. Bryophytes were identified in the field if possible. However, if field identification could not be made, a sample was collected and subsequently identified in the laboratory. Several species of *Brachythecium*, *Lophozia*, *Calypogeia*, and *Scapania* could not be distinguished in the field from gross morphological traits, but co-occurred within

Table 1. Overstory, understory, and ground-surface/disturbance variables included in multiple regression models of bryophyte cover and species richness in cut portions of treatments.

Variable	Definition
Overstory	
TREEBA	Overstory tree basal area ($m^2 \cdot ha^{-1}$) (trees ≥5 cm DBH)
Cover of understory vegetation (%)	
HERB	Herbaceous and low-growing (<1 m) woody species
SHRUB	Tall shrubs (≥1 m tall)
CONIF	Understory conifers (<5 cm DBH)
HDWD	Understory hardwoods (<5 cm DBH)
Cover of ground substrates and soil disturbance (%)	
DISTURB	Disturbed soil resulting from harvest operations
INTACT	Intact forest floor (supporting original litter layer)
SLASH	Foliage and branches (<10 cm diameter) resulting from harvest operations
RTWAD	Rootwads (bases of uprooted trees supporting mineral soil or litter)
LTREEB	Bases of live trees, including exposed roots
SHSTEM	Bases of live shrubs (≥5 cm diameter)
STUMP	Stumps, including exposed roots
Volume of coarse woody debris ($m^3 \cdot ha^{-1}$)	
F_LOG	Fresh logs (decay classes I–II of Fogel et al. 1973)
D_LOG	Decayed logs (decay classes III–V of Fogel et al. 1973)
Other	
SLASH_D	Slash depth (cm)

microplots; these taxa are treated at the generic level. Vouchers of all species are retained at the College of Forest Resources, University of Washington. Nomenclature follows Schofield (2002) for liverworts and Anderson et al. (1990) for mosses.

Additional variables were sampled to quantify understory vegetation, logging disturbance, and other ground conditions that potentially mediate bryophyte responses to harvest. Microplots were used to estimate total cover of herbaceous and low-growing woody species (<1 m tall). The line-intercept method was used along the four transects to estimate cover of taller growth forms, ground substrates, and soil disturbance. Separate estimates were made for tall shrubs (≥1 m tall), understory hardwoods or conifers (<5 cm DBH), logging slash, soil disturbance, and various woody substrates (for a complete list of variables see Table 1). In addition, volume of coarse woody debris (≥10 cm DBH) was estimated from the diameters of logs that intersected transects using the method of Brown (1974). Volume was estimated separately for "fresh" and "decayed" wood (decay classes I–II and III–V, respectively; Fogel et al. 1973) to distinguish between material generated by harvest and that which was present initially (Halpern and McKenzie 2001). Transects were also used to estimate depth of slash (12 evenly spaced points per transect). Finally, all overstory trees (≥5 cm DBH) in each 0.04 ha circular plot were tagged and identified to species, and DBH was measured.

Data aggregation and statistical analyses

For bryophytes, three types of plot-level statistics were computed from the pre- and post-treatment microplot data: mean total cover of bryophytes, frequencies of individual species (number of microplots in which a species occurred in a given plot), and species richness (number of species per plot). Treatment means were then computed from plot-level values. For aggregated treatments, however, treatment means were computed as weighted averages to account for the unequal area and sampling intensity of the two postharvest environments (forest aggregates and adjacent clear-cut areas; Fig. 2). To standardize for variation in pre-treatment abundance and richness among experimental units (Table 2), we subtracted pre-treatment from post-treatment means to compute changes in cover, frequency, and richness; these "change variables" served as the measures of response to treatments. In addition to the frequencies of individual species, we computed a community-level index of decline, "proportion of declining species". Although this index does not quantify the decline, it provides an unbiased estimate of the proportion of species that declined in frequency, allowing for comparisons among treatments (including the control). Plot-level statistics were also computed for overstory, understory, and ground-surface/disturbance variables (see Table 1); these were used as predictors in models of bryophyte response to local variation in postharvest environment (see below).

Changes in composition

To compare changes in species composition among treatments representing different levels and patterns of retention (question 1), we conducted a nonparametric form of ordination, non-metric multidimensional scaling (NMS) using PC-ORD version 4.0 (McCune and Mefford 1999). Mean pre- and post-treatment frequencies were used as measures of species' abundance, with post-treatment means for aggregated treatments computed as weighted averages (as described above). Sørensen's distance was used as the measure

Table 2. Pre-treatment total bryophyte cover and richness by block and treatment.

	BU		LW		PH		CF	
Treatment[a]	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Total cover (%)								
100% (control)	4.7	1.0	7.0	0.7	29.3	3.3	14.9	1.3
75%A	8.3	1.0	11.7	0.9	20.4	1.6	10.4	1.6
40%D	7.5	1.2	14.6	2.1	22.9	2.2	18.8	1.9
40%A	8.9	1.0	9.3	0.9	23.4	1.7	21.6	2.1
15%D	3.5	0.5	8.8	1.3	20.1	2.5	10.7	1.3
15%A	7.1	0.7	11.4	1.2	19.0	2.0	11.8	1.7
Richness (number of taxa per plot)								
100% (control)	9.2	0.6	7.8	0.5	9.2	0.3	7.2	0.4
75%A	9.6	0.4	10.6	0.5	9.1	0.6	10.3	0.5
40%D	6.9	0.5	9.4	0.4	9.5	0.3	6.5	0.4
40%A	11.1	0.5	9.2	0.4	7.7	0.4	8.1	0.4
15%D	8.2	0.5	8.1	0.5	9.1	0.5	5.2	0.4
15%A	11.6	0.5	10.1	0.4	9.2	0.2	8.8	0.6

Note: BU, Butte; LW, Little White Salmon; PH, Paradise Hills; CF, Capitol Forest.

[a] Treatments are designated by the level of retention (%) and spatial pattern (aggregated (A) or dispersed (D)).

of dissimilarity. Separate ordinations were run for individual blocks because floristic variation was considerably greater among blocks than among treatments. For each analysis we constructed a sample-by-species matrix with 12 samples — the average pre- and post-treatment composition for each of the six treatments. Initial configurations were derived from detrended correspondence analysis of the same data matrix with rare species down-weighted. Stress reduction was determined after 100 iterations using Monte Carlo tests of one- and two-dimensional solutions. In all instances, solutions were stable and two dimensions provided considerable reduction in stress over one dimension. Final two-dimensional stress values were acceptable (2.4–8.6, $P = 0.01$–0.03; McCune and Grace 2002). We did not attempt to fit additional dimensions; these could have marginally improved the results for some blocks, but would have made it difficult to compare and interpret ordinations with different numbers of axes (cf. Kruskal and Wish 1978).

Changes in abundance and richness

Analysis of variance (ANOVA) models were used to compare changes in abundance (total cover of bryophytes and proportion of declining species) and richness among treatments (question 1) or among postharvest environments within treatments (question 2). Three single-factor randomized block designs were employed (Neter et al. 1990). The first design was used to test for overall treatment differences, and utilized data from all plots to represent each treatment. The second design was used to test for differences among the uncut portions of treatments (100%, forest matrix of 75%A, and aggregates of 40%A and 15%A); these models did not include dispersed treatments. The third design was used to test for differences among the cut portions of treatments (40%D, 15%D, “gaps” in 75%A, and clear-cut portions of 40%A and 15%A); these models did not include the control. Because these designs used different treatments, the degrees of freedom varied: block (3), treatment (5, 3, or 4, respectively), and error (15, 9, or 12, respectively). For models that showed a significant main effect ($P \le 0.05$), differences in treatment means were identified with a Tukey’s HSD test. In several instances where variance differed among treatments (Levene’s test, $P \le 0.05$) an arcsine square root transformation was used, otherwise all model assumptions were met.

Responses of individual species

The uneven distributions of species among blocks and experimental units within blocks necessitated the use of a simpler model to analyze species’ responses to harvest (question 3) — one that reflected a simple gradient of harvest intensity. Reflecting increasing overstory removal, plots were pooled into three broader treatment categories: (1) uncut forest (100%, forest matrix of 75A%, and aggregates of 40%A and 15%A); (2) dispersed retention (40%D and 15%D); and (3) clear-cut areas (gaps of 75%A and the cut matrix of 40%A and 15%A). Tests were conducted separately within each block, with plots treated as replicates. Comparisons were limited to 27 taxa (35% of the flora) present in at least 5% of plots in at least two of these harvest-intensity classes within a block; this yielded a total of 56 species-by-block comparisons. Response was measured as the change in species frequency. Tests were implemented in one of two ways: when variance among treatment categories was equal (Levene’s test, $P > 0.05$), a single-factor ANOVA with unequal sample sizes was used (most tests); when variance was unequal, a Kruskal–Wallis test was used. Where a significant main effect was detected ($P \le 0.05$), differences in means were identified with a Tukey’s HSD test or its nonparametric equivalent (Siegel and Castellan 1988).

Relationships with residual vegetation and postharvest ground conditions

We used multiple linear regression to assess how ground conditions, residual forest structure, and understory vegetation influenced local variation in bryophyte cover and richness among plots undergoing harvest (question 4). As with species-specific analyses, plots were considered to be independent samples; examination of semi-variograms computed for responses within individual treatment units showed no evidence of spatial autocorrelation, which supported this assumption (Cressie 1993). Plots from all blocks were analyzed jointly ($n = 441$). Post-treatment cover (transformed as arcsine square root) and post-treatment richness (number of species per plot) served as response variables. Potential predictors for each model included pre-treatment cover (or richness); overstory basal area; cover of herbs, tall shrubs, conifer saplings, and hardwood saplings; and ground-condition variables (Table 1). To avoid multi-collinearity among ground-condition variables in the regression models, principal components analysis (PCA) was used to reduce a set of four highly correlated measures of ground disturbance (cover of intact forest floor, disturbed soil, slash, and depth of slash) to two orthogonal variables. The first two PCA axes accounted for 83% of the variation in the original data. The first axis (PCA1; 57% of the variation) represented a slash-accumulation gradient, with high positive loadings for slash cover and depth (eigenvector coefficients 0.634 and 0.475, respectively). The second axis (PCA2; 26% of the variation) represented a soil-disturbance gradient, with high positive loadings for cover of disturbed soil and high negative loadings for cover of intact forest floor (eigenvector coefficients 0.886 and –0.462, respectively). Final models were selected using a backward stepwise procedure, with 0.05 as the probability for removing a variable. Model assumptions and presence of outliers were evaluated through plots of predicted values and predictors versus residuals, and index plots of Cook's distance (Chatterjee et al. 2000). All ANOVA, PCA, and regression analyses were performed with JMP for Windows version 5.0 (SAS Institute Inc. 2002).

Results

We recorded a total of 78 bryophyte taxa (56 mosses and 22 liverworts) in the initial pre-treatment sample. Representation of liverworts varied among blocks, ranging from 9 species at LW (19% of the bryophyte flora) to 16 at PH (36%). Twenty-three species (30%) of bryophytes were common to all blocks, but 22 were unique to a single block. Among experimental units prior to harvest, mean cover of bryophytes ranged from 3.5% to 29.3% and mean richness from 5.2 to 11.6 species per plot (Table 2).

Treatment-scale responses to level and pattern of retention

Changes in composition

The magnitude of compositional change, expressed in ordination space, declined with increasing retention in all blocks (Fig. 3); changes at 15% retention were much larger than in other treatments. Responses to retention pattern, however, were not consistently different. At lower levels of retention (15% and 40%), compositional changes were generally similar in direction among treatments regardless of retention pattern. At higher retention (100% and 75%A), changes were relatively small (Fig. 3).

Changes in abundance and richness

Significant treatment effects were found for all community-level response variables (Fig. 4). Declines in total cover were larger at 15% and 40% retention than at 75% or 100% retention, but only the 40% treatments differed significantly from the control (Fig. 4*a*). Losses of cover were comparable at 15% and 40% retention and among dispersed and aggregated treatments. Relative to initial abundance (~3% to 23% cover; Table 2), declines in these treatments represented losses of half to nearly all of the original bryophyte cover.

The proportion of species declining in frequency within plots was also greater at lower levels of retention (Fig. 4*b*). In 100% and 75%A, ~40% of species declined (i.e., ~60% showed no change or an increase). In contrast, at lower levels of aggregated retention (15%A and 40%A) and in 15%D, 77%–91% of species declined. Although proportions appeared to be greater in aggregated than in dispersed treatments, means did not differ statistically.

Changes in richness were positive in 100% and 75%A but negative at lower levels of retention (Fig. 4*c*). Mean losses were consistently greater in aggregated than in dispersed treatments, but not significantly so. Among treatments, declines were significantly greater in 15%A than in 40%D (~4 vs. <1 species per plot, respectively). Relative to the original species pool (~5 to 12 species per plot; Table 2), species losses represented local extirpations of a large proportion of the flora.

Responses in the uncut portions of treatments

In uncut plots, changes in bryophyte cover and proportion of declining species were comparable among treatments (Figs. 5*a, 5b*). In contrast, retention level had a significant effect on changes in species richness (Fig. 5*c*). In 100% and the forest matrix of 75%A, richness increased by ~2 species per plot in the 3–4 years between pre- and post-treatment sampling, but no change was observed in the forest aggregates of 15%A (a significant decline in relative terms).

Responses in the cut portions of treatments

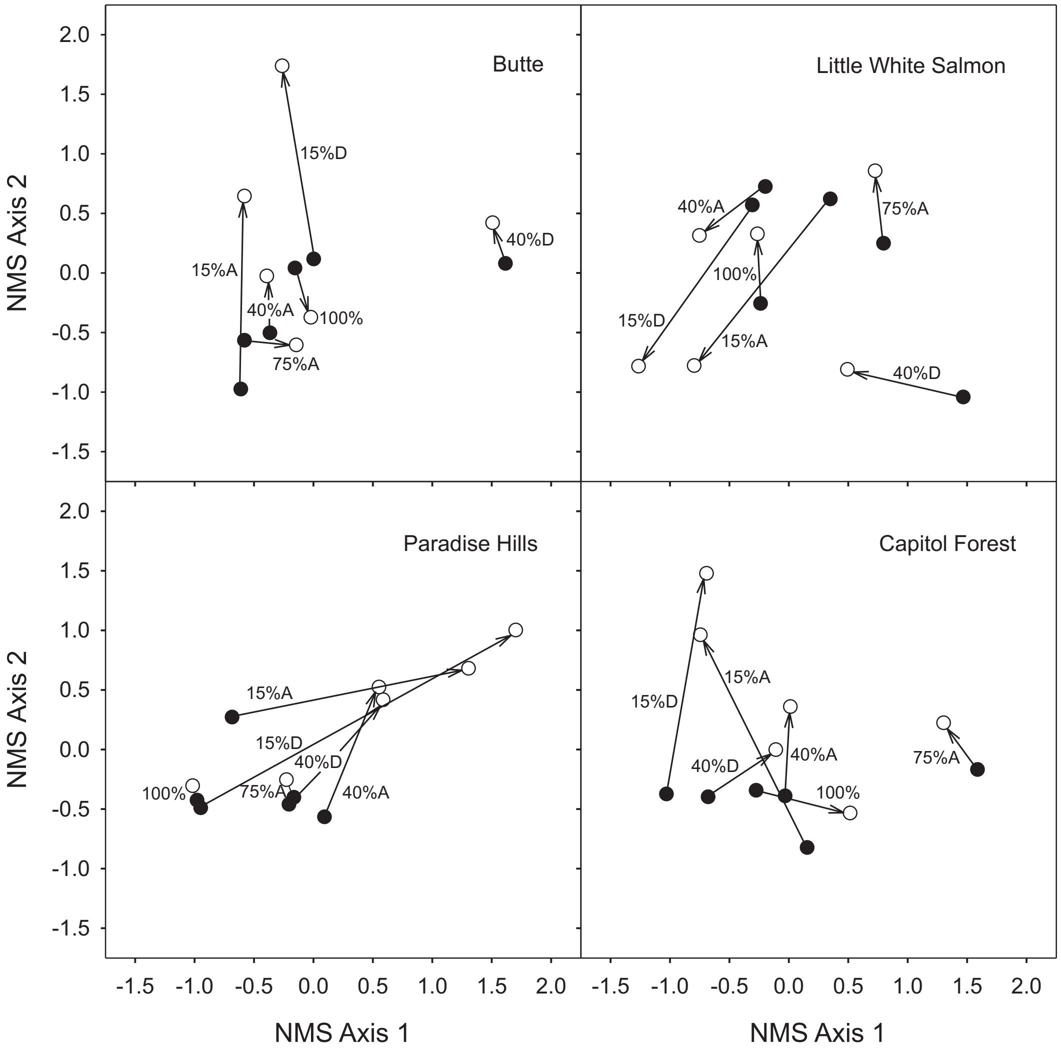
Changes in abundance and richness

Declines in bryophyte cover were much greater in the cut portions of treatments than in adjacent, intact forest (cf. Figs. 5*a* and 6*a*). However, declines did not vary with level or pattern of retention (Fig. 6*a*). The proportion of species showing declines in frequency was consistently high in the cut areas of treatments (63%–93%; Fig. 6*b*). Declines were more frequent in clear-cut areas than in dispersed retention, but this difference was significant only at 40% retention (Fig. 6*b*). Species richness also declined in the cut portions of treatments (Fig. 6*c*). Declines tended to increase with decreasing retention, but this effect was not consistent among treatments (Fig. 6*c*). Losses tended to be greater in clear-cut areas of aggregated treatments than under corresponding levels of dispersed retention (>4 vs. <1–2 species per plot, respectively), but this difference was significant only at 40% retention.

Responses of individual species

Among the 27 species tested, 22 (81%) exhibited significantly greater declines in frequency in cut plots (dispersed

Fig. 3. Non-metric multidimensional scaling (NMS) ordinations portraying changes in bryophyte species composition among the six experimental treatments in each block (preharvest compositions (●) and postharvest compositions (○)). The mean frequency (number of microplots in which a species occurred within a plot) was used as the measure of species abundance (see the text (Methods: Data aggregation and statistical analyses)).



retention or clear-cut areas) than in uncut plots (Table 3). Of 56 species-by-block tests, 38 (68%) yielded significantly greater declines in cut plots. In 24 of these, declines were comparable in dispersed retention and clear-cut areas, but in 13, declines were significantly greater in clear-cut areas. In only one test was the decline greater in dispersed retention.

As a group, liverworts were more sensitive to harvest intensity than were mosses: 80% of tests yielded significantly greater declines in frequency in cut than in uncut plots (compared with 63% for mosses). Declines were significantly greater in clear-cut areas than in dispersed retention in 33% of tests for liverworts and 20% for mosses (Table 3).

Relationships with residual vegetation and postharvest ground conditions

Within cut areas, variation in bryophyte cover and richness correlated strongly with cover of residual vegetation and postharvest ground conditions. Multiple regression models explained 36%–43% of the variation in post-treatment cover and richness (Table 4). For both models, post-treatment values were positively correlated with pre-treatment values, positively correlated with cover of residual herbs and tall shrubs, and negatively correlated with PCA1 (increasing cover and depth of slash). In addition, bryophyte cover showed a negative correlation with PCA2 (increasing soil disturbance) and bryophyte richness and positive correlations with overstory basal area and stump cover (although effect sizes were relatively small; Table 4).

Discussion

The initial responses of forest bryophytes to conventional forms of timber harvest can be dramatic, and characterized by significant loss of cover and species diversity (e.g., Hannerz and Hånell 1997; Jalonen and Vanha-Majamaa 2001; Fenton et al. 2003). These initial declines may explain the differences in richness observed between second-growth and primary forests in the Pacific Northwest and elsewhere (Gustafsson and Hallingback 1988; Lesica et al. 1991; Rambo and Muir 1998*a*). In this study we evaluated whether

Fig. 4. Treatment-level responses (mean +1 SE) of bryophytes. (*a*) Absolute change in percent cover. (*b*) Proportion of species showing declines in frequency. (*c*) Change in species richness. Means for aggregated treatments are weighted averages of plot values (see the text (Methods: Data aggregation and statistical analyses)). *P* values represent the significance of the main effect in a single-factor randomized-block ANOVA. Different letters indicate treatment means that differ significantly ($P \leq 0.05$) using Tukey's HSD test.

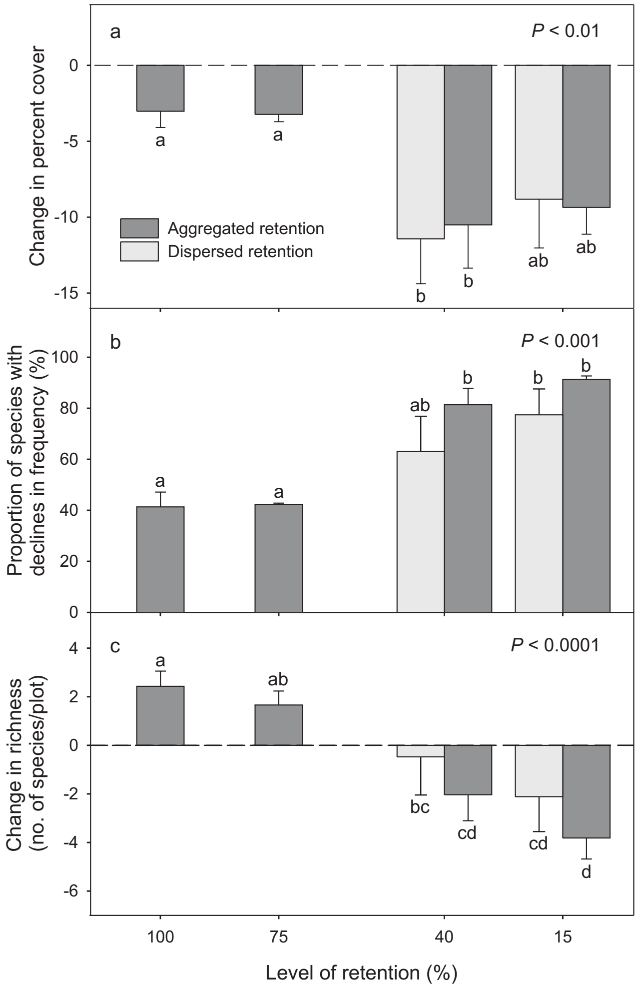
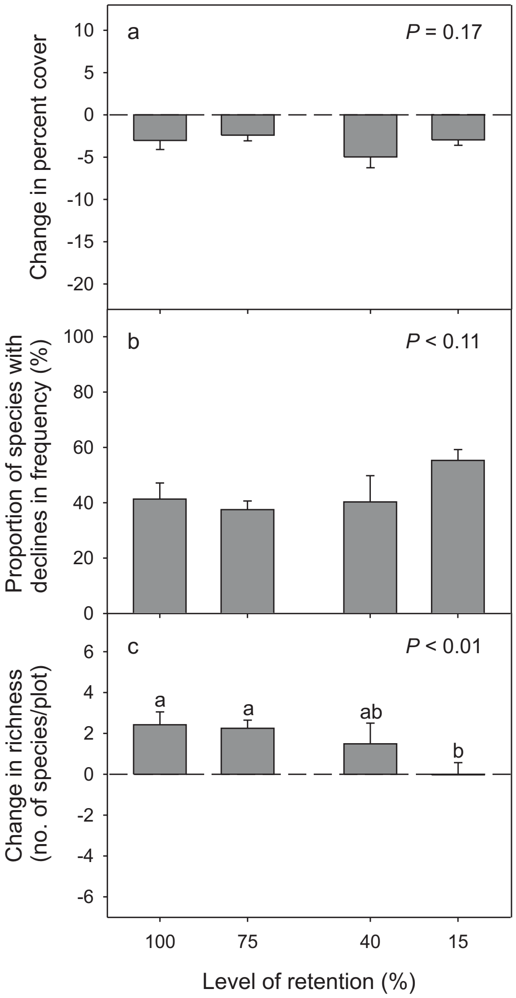


Fig. 5. Responses (mean +1 SE) of bryophytes in the uncut portions of treatments (forest matrix in 100% and 75%A and forest aggregates in 40%A and 15%A). (*a*) Absolute change in percent cover. (*b*) Proportion of species showing declines in frequency. (*c*) Change in species richness. *P* values represent the significance of the main effect in a single-factor randomized-block ANOVA. Different letters indicate treatment means that differ significantly ($P \leq 0.05$) using Tukey's HSD test.



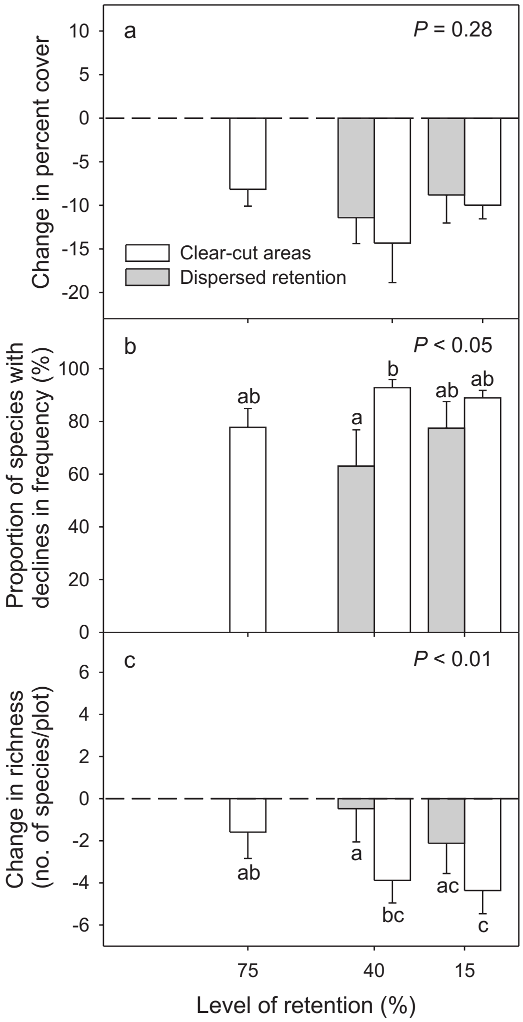
the effects of timber harvest could be tempered by partial overstory retention, and to what extent the level and pattern of retention contribute to these effects. Although we report only initial responses, they are nevertheless critical for documenting the magnitude of decline and predicting the potential for recovery. Even if forest-floor conditions become conducive to growth, bryophyte recruitment can be limited by dispersal (Söderström 1990; Miles and Longton 1992); thus, initial postharvest distribution and abundance may be indicative of longer trends in recovery.

Effects of level and pattern of retention

At the scale of harvest units (13 ha), bryophytes clearly responded to level of retention but less so to spatial pattern. Loss of cover and the proportion of species showing declines in frequency were comparably large at 40% and 15% retention, suggesting a threshold response to overstory removal. In contrast, changes in community composition (expressed in ordination space) and declines in local richness were proportional to the amount of basal area removed. The fact that richness continued to decline while cover did not suggests that relatively uncommon species were lost at lower levels of retention; these rarer taxa typically have lower thresholds for extinction and are more likely to be lost as a result of disturbance or stochastic processes (e.g., Hanski and Ovaskainen 2002; Nelson and Halpern 2005*b*). Similar patterns of response have been observed in boreal spruce forests in Finland (Jalonen and Vanha-Majamaa 2001); bryophyte cover decreased by 50% and species richness by as much as 24% at moderate retention levels (50%–67% as gap felling or single-tree selection), but nearly all cover was lost and richness decreased by 60% at low retention levels (7% as forest aggregates of 0.01–0.02 ha).

Despite strong contrasts in the spatial distribution of re-

Fig. 6. Responses (mean +1 SE) of bryophytes in the cut portions of treatments (40%D, 15%D, “gaps” in 75%A, and “clear-cut” areas of 40%A and 15%A). Note that data for 40%D and 15%D are the same as in Fig. 4. For other details see Fig. 5.



sidual trees in dispersed and aggregated treatments, we were unable to detect significant effects of retention pattern on community-level responses. An explanation for this general result becomes apparent when the variation in response between the uncut (forest aggregates) and cut portions of harvest units is examined, as discussed in the following sections.

Forest aggregates as short-term refugia

Within individual treatments, changes in bryophyte abundance and richness were considerably smaller in uncut forest (forest matrix or 1 ha aggregates) than in adjacent clear-cut or patch-cut areas. Moreover, for most measures of community response, changes were no greater in the aggregates than in the larger, more contiguous tracts of undisturbed forest of the 75%A or 100% treatments. Thus, although richness and cover changed measurably within aggregates, similar changes were recorded in control plots. These changes may reflect a variety of factors: the natural dynamics of communities over the period of study (3–4 years) (Økland 1994; Fenton et al. 2003), annual variation in weather or phenology, and (or) sampling error. It is not possible to tease apart the effects of these factors; nevertheless, these changes should be viewed in relative terms: all treatments were sampled similarly and experienced the same weather conditions. Moreover, if increases in richness in the aggregates and controls reflect sampling error (species missed prior to treatment), our estimates of decline in the harvested areas would be conservative, suggesting even stronger effects of treatments.

Although forest aggregates were largely effective in preserving the original abundance and diversity of bryophytes, declines in richness in the two patches of 15%A (relative to controls) suggest a diminished capacity to retain the full complement of species at low retention levels. It is likely that the greater exposure of these patches leaves them more susceptible to edge effects. In companion studies at BU and PH, Nelson and Halpern (2005*a*, 2005*b*) documented significant edge-related declines in the richness of liverwort species, as well as elevated light levels to distances up to 15 m from the edge.

Others have described the contributions of remnant forest patches to the maintenance of bryophyte diversity in managed forest landscapes (Jalonen and Vanha-Majamaa 2001; Fenton et al. 2003; Hylander et al. 2005). Patches as small as 10–40 m^2 can support species that are absent from disturbed areas of forests (Fenton and Frego 2005). However, the ecological benefits of these forest remnants must be viewed cautiously. Small patches are susceptible to further fragmentation or deterioration resulting from wind-induced damage or mortality (e.g., Moore et al. 2003). Moreover, edge effects not apparent in the short term may become more apparent over time (Baldwin and Bradfield 2005; Nelson and Halpern 2005*a*), as plant responses to stress lag behind abrupt changes in environment. As a result, extinctions may be delayed, preceded by gradual decline or by stochastic loss of rarer species (Tilman et al. 1994; Hanski and Ovaskainen 2002). If extirpations occur before populations can successfully disperse to disturbed areas, the role of forest aggregates as biological “lifeboats” (Franklin et al. 1997) is greatly diminished. Experimental studies of habitat fragmentation and its consequences for larger scale patterns of species’ abundance and diversity are fairly limited (Debinski and Holt 2000), and have not been undertaken for forest bryophytes. Clearly, the potential for forest aggregates to retain the flora characteristic of mature, undisturbed forest will be enhanced by increasing the size, number, or cumulative area of undisturbed patches within a harvested landscape (Pharo et al. 2004).

Declines in the cut portions of treatments

As expected, bryophytes showed significant declines in the cut portions of treatments. However, declines in abundance (total cover or proportion of declining species) were relatively insensitive to the level of retention in dispersed treatments or to the cumulative harvest area in aggregated treatments, thus supporting the use of “harvest intensity” (clear-cut areas vs. dispersed retention) as a reasonable model to assess species’ responses. Although we were unable to detect a consistent effect of harvest intensity on community-level responses in the cut portions of treatments, declines tended to be greater where trees were fully cleared

Table 3. Changes in species' frequencies (ΔFrq; maximum 24) in plots representing uncut forest, dispersed retention, and "clear-cut" areas of aggregated treatments.

		Uncut forest		Dispersed retention		Clear-cut areas		
Taxon[a]	Block[b]	*n*	ΔFrq	*n*	ΔFrq	*n*	ΔFrq	*P*[c]
Aulacomnium androgynum	BU	71	–0.4±0.2a	34	–2.3±0.4b	41	–3.2±0.4b	<0.0001
*Blepharostoma trichophyllum**	PH	15	0.3±0.7a	11	–3.7±0.9b	6	–1.5±0.3ab	0.007
Brachythecium spp. [d]	BU	49	0.1±0.5a	41	–3.0±0.5b	15	–4.2±0.9b	<0.0001
	LW	45	–4.1±0.6	25	–3.9±1.0	22	–6.6±1.0	ns
Calypogeia spp.*[e]	CF	43	–1.0±0.6a	15	–0.9±0.3a	11	–4.2±1.0b	0.005
*Cephalozia bicuspidata**	PH	19	–4.2±0.8	21	–4.7±0.6	0	0.0±0.0	ns
*Cephalozia lunulifolia**	PH	45	0.3±0.3a	21	–3.1±0.4b	27	–2.2±0.3b	<0.0001
Dicranum fuscescens	BU	71	2.5±0.3a	37	–0.2±0.3b	41	–1.5±0.4b	<0.0001
	LW	50	–0.2±0.3	23	–0.2±0.3	23	–0.7±0.3	ns
	PH	81	–0.2±0.3a	61	–4.0±0.6b	43	–2.8±0.5b	<0.0001
	CF	24	0.2±0.2	16	0.1±0.3	16	–0.4±0.3	ns
Dicranum scoparium	BU	52	–2.2±0.2	17	–2.9±0.7	35	–2.4±0.3	ns
	LW	38	–1.2±0.2	28	–1.9±0.4	16	–1.2±0.3	ns
	PH	47	–0.5±0.5a	23	–2.4±0.4b	38	–4.5±0.5c	<0.0001
	CF	29	–1.0±0.2	6	–0.5±0.6	14	–1.6±0.2	ns
Dicranum tauricum	BU	73	–0.4±0.2a	43	–1.4±0.3b	39	–3.0±0.4c	<0.0001
	LW	58	0.7±0.3a	42	–0.1±0.4ab	38	–0.7±0.3b	0.006
	PH	40	–0.6±0.3	41	–1.4±0.2	26	–1.7±0.2	ns
Eurhynchium oreganum	BU	73	0.6±0.3a	31	–1.9±0.3b	45	–2.6±0.4b	<0.0001
	LW	63	–1.4±0.4a	51	–4.7±0.7b	41	–2.8±0.5b	0.003
	PH	41	–3.8±0.6	41	–3.2±0.4	19	–4.6±0.9	ns
	CF	83	1.5±0.5a	64	–5.8±0.7b	41	–4.3±1.2b	<0.0001
Hypnum circinale	BU	75	0.9±0.2a	32	–1.8±0.3b	41	–2.7±0.4b	<0.0001
	LW	76	1.0±0.3a	56	–1.0±0.4b	45	–2.2±0.5b	<0.0001
	PH	82	0.6±0.2a	63	–4.9±0.5b	41	–4.1±0.4b	<0.0001
	CF	57	0.4±0.2a	20	–1.2±0.5b	34	–1.8±0.4b	<0.0001
Isopterygium elegans	BU	29	–0.3±0.7a	5	–1.6±0.6ab	16	–4.5±0.8b	0.002
	LW	42	–2.7±0.6	20	–3.4±0.8	24	–3.7±0.8	ns
	CF	23	1.6±0.8a	10	–0.9±0.4a	10	–4.1±1.2b	0.002
Isothecium stoloniferum	LW	14	–0.3±0.3a	12	–1.2±0.3ab	15	–2.9±1.1b	0.023
	CF	79	3.1±0.6a	39	2.1±0.7a	39	–1.0±0.9b	0.0003
*Lepidozia reptans**	CF	18	–0.4±0.4a	12	–1.2±0.5a	11	–3.8±1.1b	0.002
Lescuraea stenophylla	BU	20	–0.6±0.3	22	–0.4±0.3	12	–1.3±0.4	ns
	LW	83	2.1±0.3a	59	–2.4±0.6b	47	–4.3±0.7c	<0.0001
*Lophocolea heterophylla**	LW	15	–1.3±0.7	11	–2.0±0.4	14	–2.6±0.6	ns
	PH	25	–0.6±0.4a	23	–3.3±0.5b	18	–2.3±0.4b	<0.0001
	CF	30	–0.2±0.8a	11	–1.8±0.4b	19	–4.2±0.7c	0.0002
Lophozia spp.*[f]	PH	22	–1.1±0.4a	15	–2.9±0.4b	10	–1.2±0.2a	0.006
Mnium spinulosum	BU	21	–0.6±0.3a	9	–1.6±0.2ab	21	–2.0±0.4b	0.019
	LW	52	–0.2±0.2a	32	–2.2±0.4b	28	–2.0±0.3b	<0.0001
Plagiothecium laetum	LW	11	–1.4±0.8	14	–3.3±1.0	8	–3.4±0.7	ns
Plagiothecium undulatum	CF	68	0.2±0.2a	51	–1.0±0.3b	36	–2.3±0.4c	<0.0001
Pohlia nutans	BU	32	–1.4±0.4	19	–1.9±0.6	12	–1.3±0.2	ns
*Ptilidium californicum**	LW	59	0.1±0.3a	44	–1.3±0.3b	41	–1.7±0.3b	<0.0001
	PH	73	–0.5±0.3a	57	–3.2±0.3b	41	–4.2±0.5b	<0.0001
Rhizomnium glabrescens	BU	17	–0.8±0.2	10	–1.1±0.8	11	–1.0±0.4	ns
	CF	66	0.0±0.3a	41	–1.0±0.3b	25	–3.0±0.4c	<0.0001
Rhytidiadelphus loreus	LW	18	–0.8±0.3	5	–1.0±0.0	11	–1.4±0.4	ns
Rhytidiadelphus triquetrus	LW	12	–1.2±0.4	15	–2.1±0.6	8	–1.2±0.3	ns
Rhytidiopsis robusta	BU	78	0.8±0.3a	48	–0.5±0.4b	47	–3.4±0.3c	<0.0001
	LW	70	–0.2±0.2a	57	–3.6±0.6b	38	–1.8±0.4b	<0.0001
	PH	84	0.4±0.2a	63	–7.5±0.7b	48	–8.4±0.7b	<0.0001
Scapania spp.*[g]	BU	56	0.0±0.2a	13	–1.9±0.4b	37	–2.6±0.4b	<0.0001
	LW	12	–0.6±0.3	10	–1.1±0.3	7	–0.7±0.3	ns

Table 3 (*concluded*).

Taxon[a]	Block[b]	Uncut forest *n*	Uncut forest ΔFrq	Dispersed retention *n*	Dispersed retention ΔFrq	Clear-cut areas *n*	Clear-cut areas ΔFrq	*P*[c]
	PH	60	–1.2±0.2a	58	–3.9±0.4b	31	–2.2±0.3c	<0.0001
	CF	46	–0.4±0.3a	11	–1.0±0.4a	33	–3.8±0.6b	<0.0001

Note: Tests were run for species present in ≥5% of plots in at least two postharvest environments within a block; *n* is the number of plots in which a species was found before treatment. Maxima for each postharvest environment within a block were *n* = 84–85 for uncut forest, *n* = 64 for dispersed retention, and *n* = 41–48 for clear-cut areas.

[a] An asterisk denotes liverworts.

[b] BU, Butte; LW, Little White Salmon; PH, Paradise Hills; CF, Capitol Forest.

[c] From one-way ANOVA models when variance among environments was equal and Kruskal–Wallis tests when variance was unequal; "ns" denotes nonsignificant differences ($P > 0.05$). Within a row, different letters indicate significant differences between environments, based on a Tukey's HSD test or its nonparametric equivalent.

[d] Includes *Brachythecium albicans, Brachythecium frigidum, Brachythecium hylotapetum, Brachythecium leibergii, Brachythecium salebrosum*, and *Brachythecium velutinum*.

[e] Includes *Calypogeia fissa* and *Calypogeia muelleriana.*

[f] Includes *Lophozia incisa, Lophozia guttulata*, and *Lophozia ventricosa.*

[g] Primarily *Scapania bolanderi*, but also includes *Scapania umbrosa*.

Table 4. Results of multiple regression models for post-treatment bryophyte cover and species richness (number of species per plot) in cut areas.

Predictor	Estimate Mean	Estimate SE	*P*
Total bryophyte cover[a]			
PRECOV[b]	0.042	0.003	<0.0001
SHRUB	0.027	0.004	<0.0001
HERB	0.017	0.004	<0.0001
PCA1[c]	–0.033	0.003	<0.0001
PCA2[d]	–0.020	0.003	<0.0001
Species richness[e]			
PRESR[f]	0.235	0.049	<0.0001
SHRUB	0.994	0.155	<0.0001
HERB	1.012	0.164	<0.0001
TREEBA	0.308	0.149	0.0395
STUMP	0.330	0.145	0.0229
PCA1	–0.741	0.150	<0.0001

Note: Post-treatment bryophyte cover was arcsine square root transformed; predictor variables were standardized to zero mean and unit variance (for definitions of variables see Table 1). Models were selected using a backward stepwise procedure, with 0.05 as the probability for removing a variable.

[a] Full model: $R^2 = 0.43$; $P < 0.0001$; $n = 441$.

[b] Pre-treatment cover.

[c] Score on PCA axis 1 (high positive loadings for slash cover (SLASH) and slash depth (SLASH_D)).

[d] Score on PCA axis 2 (high positive loading for cover of disturbed soil (DISTURB) and high negative loading for cover of intact forest floor (INTACT)).

[e] Full model: $R^2 = 0.36$; $P < 0.0001$; $n = 441$).

[f] Pre-treatment species richness.

than under dispersed retention. These tendencies in clear-cut areas, balanced by relatively small changes in forest aggregates, thus contributed to the general result that retention pattern had a limited effect on treatment-level responses.

A combination of disturbance, substrate, and microclimatic differences may have contributed to the greater persistence of bryophytes in areas of dispersed retention. First, ground-surface conditions may have been more conducive to survival: cover of intact forest floor was significantly greater and accumulation of logging slash was significantly lower in dispersed treatments (Halpern and McKenzie 2001). Second, corticolous species (associated with live tree boles) were more likely to be present, persisting at the bases of live stems. Finally, solar radiation and air temperature declined with increased retention (Heithecker and Halpern 2006); these microclimatic contrasts were most extreme between 40%D and the clear-cut portions of 15%A — treatments that showed significant differences in species loss. Because loss of bryophyte cover was uniformly high within cut areas, it appears that the immediate benefit of dispersed retention is in increasing the survival of rarer taxa. This conclusion is also supported by the results of species-level comparisons: in 34% of tests for which species declined in frequency in cut areas, the decline was significantly smaller under dispersed retention. This differential response was more frequent among liverworts than mosses, consistent with previous observations that liverworts are more sensitive to overstory removal and environmental stress than are mosses (e.g., Söderström 1988; Frisvoll and Prestø 1997; Fenton et al. 2003; Nelson and Halpern 2005*b*).

Role of residual vegetation and ground conditions in moderating responses

Declines in bryophyte abundance and richness were not uniform within cut areas, but were influenced, to various degrees, by residual understory vegetation, soil disturbance, accumulations of logging slash, and other substrates. Multiple regression models suggested that residual herbs and tall shrubs moderated initial losses of bryophyte cover and richness. In the absence of overstory shade, understory vegetation can reduce direct exposure of the forest floor, moderating surface temperatures (Heithecker and Halpern 2006) and increasing humidity and surface soil moisture. Under low levels of overstory retention, herb and shrub strata may exert stronger controls on bryophyte response than do the relatively sparse distributions of residual trees. In studying the conservation value of remnant forest patches in a recently logged Acadian forest, Fenton and Frego (2005) concluded that patches with low canopies (<1.5 m) moderate microclimatic conditions as well as those with taller canopies, thus providing comparable benefits to bryophytes. Care must be taken, however, in inferring a causal relationship in the current study: it is possible that the positive correlations of bryophytes with herbs and tall shrubs derive from co-occurrence in areas of lesser ground disturbance (note however, that soil disturbance also was significant in the cover model).

Interestingly, tree basal area was not a significant predictor of bryophyte cover, whereas it did have a weak positive relationship to richness (as did cover of stumps). This contrast may underscore a potentially important function of "green trees" in partially harvested stands — not in providing shade, but in increasing habitat heterogeneity and thus diversity of corticolous species associated with the bases of trees (Lawton 1971). McGee and Kimmerer (2002) have observed that large or old, thick-barked residual hardwood stems can fulfill this function in northern hardwood forests. In contrast, decayed logs, an important substrate for many forest bryophytes (e.g., Söderström 1988; Rambo and Muir 1998*b*), did not emerge as a significant predictor in models of bryophyte cover or richness. Fragmentation and exposure of decayed wood in harvest areas may have severely reduced substrate quality.

While bryophyte cover and richness were positively correlated with vegetation structure, they were negatively correlated with soil disturbance and cover/depth of logging slash (PCA2 and PCA1, respectively). Greater loss of cover in areas of disturbed soil was expected, and is consistent with the results of previous studies (e.g., Fenton et al. 2003; Baldwin and Bradfield 2005); however, the negative correlation with slash loading is less intuitive. Residual woody debris reduces wind velocity, exposure to solar radiation, and fluctuations in soil temperature (Proe et al. 2001; Heithecker and Halpern 2006) and thus may serve the same function as residual ground vegetation. In an experimental study of slash removal, Bråkenhielm and Liu (1998) documented poorer survival of bryophytes in plots from which slash was removed, and suggested that slash reduced environmental extremes and protected species sensitive to desiccation. Positive effects of slash on bryophytes in forest clearcuts were documented also by Åström et al. (2005). It is possible that on our sites, accumulations of slash may have been excessive. Cover in excess of 80% and mean depths >15 cm were common (Halpern and McKenzie 2001), likely leading to burial rather than beneficial shading of the forest-floor community.

Implications for forest management

Structural retention is intended to moderate the ecological impacts of clear-cut logging and is now a common method of regeneration harvest in northern temperate-zone and boreal forests (Coates et al. 1997; Aubry et al. 1999; Beese and Bryant 1999; Vanha-Majamaa and Jalonen 2001). However, standards for its implementation on public lands in the Pacific Northwest are largely based on expert opinion and inference, and thus reflect considerable uncertainty. Large-scale experiments such as ours provide critical tests of current retention standards. Clearly, in operational settings the dispersion of residual trees and the sizes, shapes, and distribution of forest aggregates can differ considerably from these simple and highly structured configurations. The value of our design, however, is that it allows for simple inferences to be drawn about the roles of level and pattern of retention in shaping ecological responses. With an understanding of these simple relationships, forest structure can then be manipulated in more natural or complex ways to target particular ecological goals.

Our results suggest that 15% retention, the current minimum standard on federal forestlands within the range of the northern spotted owl (USDA and USDI 1994), is not sufficient to prevent immediate and dramatic declines in the abundance and richness of forest-floor bryophytes. Treatment-scale responses, consistent with patterns observed in other forest ecosystems (e.g., Jalonen and Vanha-Majamaa 2001), suggest that retention well in excess of 40% is required to retain the abundance and diversity of species found in mature, undisturbed forest. In fact, given the size of our experimental units (13 ha) it is likely that we have underestimated the loss of diversity in the form of rarer taxa that are more difficult to detect through systematic sampling of permanent plots.

Although bryophyte abundance can recover fairly rapidly following logging in some forest ecosystems (e.g., Hannerz and Hånell 1997), this is often due to a relatively limited set of species that can colonize disturbed ground or to those capable of rapid vegetative spread. Recovery of diversity, on the other hand, can be comparatively slow (Ross-Davis and Frego 2002), limited by microclimatic conditions, species requirements for specialized substrates, or dispersal. Our results suggest that a dispersed overstory, particularly at higher retention levels, can reduce local extirpations. Clearly, there is also potential for conserving bryophyte cover and diversity, at least in the short term, through aggregated retention of trees. The effectiveness of this strategy in the long term will depend, however, on numerous factors: placement of forest patches in areas with a rich representation of bryophytes, the structural integrity of these patches, the degree to which they are compromised by edge effects, and the abilities of species to disperse to adjacent harvest areas. To date, forest aggregates on our sites appear structurally stable: after 6 years, cumulative tree mortality has been markedly lower than in dispersed treatments, but no greater than in adjacent controls (Maguire et al. 2006). However, even after one growing season, edge-related declines of liverworts on these sites were apparent (Nelson and Halpern 2005*b*). The poorer performance of bryophytes in aggregates of 15%A suggests that edge effects are increasingly likely as the cumulative area or sizes of forest aggregates are reduced. Current standards for structural retention in the Pacific Northwest allow for aggregates as small as 0.2 ha. Although these relatively small patches can support species lost from adjacent harvest areas (e.g., Fenton and Frego 2005), they may be inadequate to retain the full diversity of species found in older forests. Thus, the more quickly the microclimate in adjacent cut areas becomes conducive to germination and growth, the greater the likelihood that dispersal events will lead to successful colonization. This microclimatic amelioration can be achieved, in part, by dispersed retention and by yarding methods that minimize damage to understory strata. A combination of large aggregates and dispersed trees — at levels considerably greater than current retention standards — may be the most viable strategy for conserving local diversity of forest-floor bryophytes while allowing for some extraction of timber. Ultimately, retention strategies that minimize loss of disturbance-sensitive taxa such as bryophytes are likely to confer broader ecological benefits, including maintenance of other species and processes associated with mature and late-seral forests.

Acknowledgements

We thank our field crews and Chris Oakley, David Phillips, and Tammy Stout in particular for assistance with data collection; David Board, Judith Harpel, and David Wagner for identifying or verifying bryophyte collections; and Gody Spycher for database management in support of the DEMO study. For logistical help we thank Rick Abbott, Dave Allaway, Richard Bigley, Sue Macmeeken, Jon Nakae, Ed Tompkins, and Jim White. Cara Nelson and two anonymous reviewers provided helpful comments on earlier drafts of the manuscript. This is a product of the DEMO Study, a joint effort of the USDA Forest Service Region 6 and the Pacific Northwest Research Station (http://www.cfr.washington.edu/research.demo/). Research partners include the University of Washington, Oregon State University, University of Oregon, Gifford Pinchot and Umpqua National Forests, and the Washington State Department of Natural Resources. Funds were provided by the USDA Forest Service Pacific Northwest (PNW) Research Station (PNW-93–0455, PNW-97–9021–1-CA, and PNW-01-CA-11261993–091).

References

Anderson, L.E., Crum, H.A., and Buck, W.R. 1990. List of the mosses of North America north of Mexico. Bryologist, **93**: 448–499.

Åström, M., Dynesius, M., Hylander, K., and Nilsson, C. 2005. Effects of slash harvest on bryophytes and vascular plants in southern boreal forest clear-cuts. J. Appl. Ecol. **42**: 1194–1202.

Aubry, K.B., Amaranthus, M.P., Halpern, C.B., White, J.D., Woodard, B.L., Peterson, C.E., Lagoudakis, C.A., and Horton, A.J. 1999. Evaluating the effects of varying levels and patterns of green-tree retention: experimental design of the DEMO study. Northwest Sci. **73** (Spec. Issue): 12–26.

Baldwin, L.K., and Bradfield, G.E. 2005. Bryophyte community differences between edge and interior environments in temperate rain-forest fragments of coastal British Columbia. Can. J. For. Res. **35**: 580–592.

Barg, A.K., and Edmonds, R.L. 1999. Influence of partial cutting on site microclimate, soil nitrogen dynamics, and microbial biomass in Douglas-fir stands in western Washington. Can. J. For. Res. **29**: 705–713.

Beese, W.J., and Bryant, A.A. 1999. Effect of alternative silvicultural systems on vegetation and bird communities in coastal montane forests of British Columbia, Canada. For. Ecol. Manage. **115**: 231–242.

Bråkenhielm, S., and Liu, Q. 1998. Long-term effects of clear-felling on vegetation dynamics and species diversity in a boreal pine forest. Biodiversity Conserv. **7**: 207–220.

Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA For. Serv. Gen. Tech. Rep. INT-16.

Chatterjee, S., Hadi, A.S., and Price, B. 2000. Regression analysis by example. 3rd ed. John Wiley and Sons, New York.

Coates, K.D., Banner, A., Steventon, J.D., LePage, P., and Bartemucci, P. 1997. The Date Creek silvicultural systems study in the interior cedar–hemlock forests of northwestern British Columbia: overview and treatment summaries. Land Management Handb. 38, British Columbia Ministry of Forests, Victoria, B.C.

Cressie, N.A.C. 1993. Statistics for spatial data. John Wiley and Sons, New York.

Debinski, D.M., and Holt, R.D. 2000. A survey and overview of habitat fragmentation experiments. Conserv. Biol. **14**: 342–355.

Duffy, D.C., and Meier, A.J. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? Conserv. Biol. **6**: 196–201.

Fenton, N.J., and Frego, K.A. 2005. Bryophyte (moss and liverwort) conservation under remnant canopy in managed forests. Biol. Conserv. **122**: 417–430.

Fenton, N.J., Frego, K.A., and Sims, M.R. 2003. Changes in forest floor bryophyte (moss and liverwort) communities 4 years after forest harvest. Can. J. Bot. **81**: 714–731.

Fogel, R.M., Ogawa, M., and Trappe, J.M. 1973. Terrestrial decomposition: a synopsis. US IBP Coniferous Forest Biome Rep. 135. Coniferous Forest Biome, College of Forest Resources, University of Washington, Seattle, Wash.

Franklin, J.F., and Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. USDA Gen. Tech. Rep. PNW-8.

Franklin, J.F., Berg, D.R., Thornburgh, D.A., and Tappeiner, J.C. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. *In* Creating a forestry for the 21st century: the science of ecosystem management. *Edited by* K.A. Kohm and J.F. Franklin. Island Press, Washington, D.C. pp. 111–139.

Frisvoll, A.A., and Prestø, T. 1997. Spruce forest bryophytes in central Norway and their relationship to environmental factors including modern forestry. Ecography, **20**: 3–18.

Furness, S.B., and Grime, J.P. 1982. Growth rate and temperature responses in bryophytes: II. A comparative study of species of contrasted ecology. J. Ecol. **70**: 525–536.

Gustafsson, L., and Hallingback, T. 1988. Bryophyte flora and vegetation of managed and virgin coniferous forests in south-west Sweden. Biol. Conserv. **44**: 283–300.

Halpern, C.B., and McKenzie, D. 2001. Disturbance and post-harvest ground conditions in a structural retention experiment. For. Ecol. Manage. **154**: 215–225.

Halpern, C.B., and Spies, T.A. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecol. Appl. **5**: 913–934.

Halpern, C.B., McKenzie, D., Evans, S.A., and Maguire, D.A. 2005. Initial responses of forest understories to varying levels and patterns of green-tree retention. Ecol. Appl. **15**: 175–195.

Hannerz, M., and Hånell, B. 1997. Effects on the flora in Norway spruce forests following clearcutting and shelterwood cutting. For. Ecol. Manage. **90**: 29–49.

Hanski, I., and Ovaskainen, O. 2002. Extinction debt at extinction threshold. Conserv. Biol. **16**: 666–673.

Heithecker, T.D., and Halpern, C.B. 2006. Variation in microclimate associated with dispersed-retention harvests in coniferous forests of western Washington. For. Ecol. Manage. **226**: 60–71.

Hylander, K., Dynesius M., Jonsson, B.G., and Nilsson, C. 2005. Substrate form determines the fate of bryophytes in riparian buffer strips. Ecol. Appl. **15**: 674–688.

Jalonen, J., and Vanha-Majamaa, I. 2001. Immediate effects of four different felling methods on mature boreal spruce forest understorey vegetation in southern Finland. For. Ecol. Manage. **146**: 25–34.

Kruskal, J.B., and Wish, M. 1978. Multidimensional scaling. Sage Publications, Beverly Hills, Calif.

Lawton, E. 1971. Moss flora of the Pacific Northwest. Hattori Botanical Laboratory, Tokyo, Japan.

Lesica, P., McCune, B., Cooper, S.V., and Hong, W.S. 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. Can. J. Bot. **69**: 1745–1755.

Luoma, D.L., Eberhart, J.L., Molina, R., and Amaranthus, M.P. 2004. Response of ectomycorrhizal fungus sporocarp production to varying levels and patterns of green-tree retention. For. Ecol. Manage. **202**: 337–354.

Maguire, D.A., Mainwaring, D.B., and Halpern, C.B. 2006. Stand dynamics after variable-retention harvesting in mature Douglas-fir forests of western North America. Allg. Forst Jagdztg. **177**: 120–131.

Marschall, M., and Proctor, M.C.F. 2004. Are bryophytes shade plants? Photosynthetic light responses and proportions of chlorophyll a, chlorophyll *b* and total carotenoids. Ann. Bot. **94**: 593–603.

McCune, B., and Grace, J.B. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Ore.

McCune, B., and Mefford, M.J. 1999. PC-ORD. Multivariate analysis of ecological data. Version 4. MjM Software Design, Gleneden Beach, Ore.

McGee, G.G., and Kimmerer, R.W. 2002. Forest age and management effects on epiphytic bryophyte communities in Adirondack northern hardwood forests, New York, U.S.A. Can. J. For. Res. **32**: 1562–1576.

Miles, C.J., and Longton, R.E. 1992. Deposition of moss spores in relation to distance from parent gametophytes. J. Bryol. **17**: 355–368.

Moore, J.R., Mitchell, S.J., Maguire, D.A., and Quine, C.P. 2003. Wind damage in alternative silvicultural systems: review and synthesis of previous studies. *In* Proceedings of the International Conference on Wind Effects on Trees. *Edited by* B. Ruck, C. Kottmeier, C. Mattheck, C. Quine, and G. Wilhelm. pp. 191–198.

Nelson, C.R., and Halpern, C.B. 2005*a*. Edge-related responses of understory plants to aggregated retention harvest in the Pacific Northwest. Ecol. Appl. **15**: 196–209.

Nelson, C.R., and Halpern, C.B. 2005*b*. Short-term effects of timber harvest and forest edges on ground-layer mosses and liverworts. Can. J. Bot. **83**: 610–620.

Neter, J., Wasserman, W., and Kutner, M.H. 1990. Applied linear statistical models. Irwin Press, Homewood, Ill.

Pharo, E.J., Lindenmayer, D.B., and Taws, N. 2004. The effects of large-scale fragmentation on bryophytes in temperate forests. J. Appl. Ecol. **41**: 910–921.

Pringle, R.F. 1990. Soil survey of Thurston County, Washington. USDA Soil Conservation Service, Washington State Department of Natural Resources, and Washington State University Agricultural Research Center, Pullman, Wash.

Proctor, M.C.F., and Tuba, Z. 2002. Poikilohydry and homoihydry: antithesis or spectrum of possibilities? New Phytol. **156**: 327–349.

Proe, M.F., Griffiths, J.H., and McKay, H.M. 2001. Effect of whole-tree harvesting on microclimate during establishment of second rotation forestry. Agric. For. Meteorol. **110**: 141–154.

Rambo, T.R., and Muir, P.S. 1998*a*. Bryophyte species associations with coarse woody debris and stand ages in Oregon. Bryologist, **101**: 366–376.

Rambo, T.R., and Muir, P.S. 1998*b*. Forest floor bryophytes of *Pseudotsuga menziesii – Tsuga heterophylla* stands in Oregon: influences of substrate and overstory. Bryologist, **101**: 116–130.

Ross-Davis, A.L., and Frego, K.A. 2002. Comparison of plantations and naturally regenerated clearcuts in the Acadian Forest: forest floor bryophyte community and habitat features. Can. J. Bot. **80**: 21–33.

SAS Institute Inc. 2002. JMP statistics and graphics guide. SAS Institute Inc., Cary, N.C.

Schofield, W.B. 2002. Field guide to liverwort genera of Pacific North America. Global Forest Institute, Banff, Alta., and University of Washington Press, Seattle, Wash.

Schowalter, T.D., Zhang, Y., and Progar, R.A. 2005. Canopy arthropod response to density and distribution of green trees retained after partial harvest. Ecol. Appl. **15**: 1594–1603.

Siegel, S., and Castellan, N.J. 1988. Nonparametric statistics for the behavioral sciences. McGraw–Hill, New York.

Söderström, L. 1988. The occurrence of epixylic bryophyte and lichen species in an old natural and a managed forest stand in northeast Sweden. Biol. Conserv. **45**: 169–178.

Söderström, L. 1990. Dispersal and distribution patterns in patchy, temporal habitats. *In* Spatial processes in plant communities. *Edited by* F. Krahulec, A.D.Q. Agnew, S. Agnew, and J.H. Willems. SPB Academic Publishing, The Hague, the Netherlands. pp. 103–113.

Tilman, D., May, R.M., Lehman, C.L., and Nowak, M.A. 1994. Habitat destruction and the extinction debt. Nature (Lond.), **371**: 65–66.

USDA and USDI. 1994. Record of decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owl. USDA Forest Service, Pacific Northwest Research Station, Portland, Ore.

Vanha-Majamaa, I., and Jalonen, J. 2001. Green tree retention in Fennoscandian forestry. Scand. J. For. Res. **3**(Suppl.): 79–90.

Wade, J., Herman, L., High, T., and Couche, D. 1992. Soil resource inventory, Gifford Pinchot National Forest. USDA Forest Service, Pacific Northwest Region, Gifford Pinchot National Forest, Portland, Ore.

Økland, R. 1994. Bryophyte and lichen persistence patterns in a Norwegian boreal coniferous forest. Lindbergia, **91**: 50–62.