

Short-term effects of timber harvest and forest edges on ground-layer mosses and liverworts

Cara R. Nelson and Charles B. Halpern

Abstract: Limited information exists on the effects of forest management practices on bryophytes, despite their importance to forest ecosystems. We examined short-term responses of ground-layer bryophytes to logging disturbance and creation of edges in mature *Pseudotsuga* forests of western Washington (USA). The abundance and richness of species were measured in four 1-ha forest aggregates (patches of intact forest) and in surrounding logged areas before and after structural retention harvests. One year after treatment, species richness, total cover, and frequency of most moss and liverwort taxa declined within harvest areas. Within forest aggregates, mosses did not show significant edge effects; however, richness and abundance of liverworts declined with proximity to the aggregate edge. Our results suggest that, over short time frames, 1-ha-sized aggregates are sufficient to maintain most common mosses through structural retention harvests but are not large enough to prevent declines or losses of liverworts. Thus, current standards for structural retention, which allow for aggregates as small as 0.2 ha, may be inadequate to retain the diversity and abundance of species found in mature, undisturbed forests.

Key words: bryophyte, edge effects, forest borders, forest management, logging effects, structural retention harvest.

Résumé : Il existe peu d'information sur les effets des pratiques d'aménagement forestier sur les bryophytes, en dépit de leur importance pour les écosystèmes forestiers. Les auteurs examinent les réactions à court terme des bryophytes du parterre forestier, suite à la perturbation par la récolte et la création de bordures dans des forêts matures de *Pseudotsuga*, dans l'ouest de l'état de Washington (USA). Ils ont mesuré l'abondance et la richesse en espèces dans quatre superficies de 1 ha (ouvertures et forêt intacte), et des superficies avoisinantes exploitées, avant et après des récoltes avec rétention structurale. Une année après le traitement, la richesse en espèces, la couverture totale et la fréquence de la plupart des mousses et hépatiques déclinent sur les surfaces récoltées. Au contraire, on observe des changements minimaux dans les superficies forestières intactes. Les mousses montrent peu d'effets de bordure, cependant, la richesse et l'abondance des hépatiques déclinent à l'approche des bordure de la forêt intacte. Les résultats suggèrent que, sur de courtes périodes de temps, des superficies intactes de 1 ha sont suffisantes pour maintenir la plupart des mousses communes, suite à des récoltes avec rétention structurale, mais ne sont pas suffisamment grandes pour prévenir le déclin ou la perte d'hépatiques. Ainsi, les standards actuels de rétention structurale, qui permettent la rétention de superficies aussi petites que 0.2 ha, ne serait possiblement pas adéquats pour maintenir la diversité et l'abondance des espèces qui se retrouvent dans les forêts matures non perturbées.

Mots clés : bryophyte, effets de bordure, bordures forestières, aménagement forestier, effets de la récolte des arbres, récolte avec rétention structurale.

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Introduction

There is global interest in the effects of timber harvest, forest fragmentation, and the resultant increase in edge environments in forest ecosystems. Although there have been many investigations of vascular plant responses to harvest (e.g., Halpern 1989; Duffy and Meier 1992) and edges (Murcia 1995), bryophytes (mosses and liverworts) have received limited attention. This gap in information is conspicuous given that bryophytes contribute greatly to biodiversity in forest ecosystems (FEMAT 1993). For instance, over 450

species of mosses and 170 species of liverworts inhabit old-growth forests of the Pacific Northwestern United States (Lawton 1971), with roughly 20% endemic to the region (Christy and Wagner 1996). In addition to comprising a large proportion of the forest flora, bryophytes contribute substantially to net primary productivity (Binkley and Graham 1981; Longton 1984; den Ouden and Alaback 1996), enhance retention of nutrients and moisture (Rieley et al. 1979), provide food and habitat for invertebrates (Gerson 1982), are used as nesting materials for small mammals and birds (Schofield 1985; FEMAT 1993), and are economically important as special forest products (Peck and McCune 1997). Thus, understanding the consequences of timber harvest and forest fragmentation for bryophytes is a critical conservation and management concern.

Several aspects of the biology and ecology of forest bryophytes contribute to their sensitivity to disturbance. First, because of their small stature, bryophytes on the forest floor are highly susceptible to the direct effects of timber

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harvest, including mechanical damage or burial under logging slash (Fenton et al. 2003). Second, because they lack true roots and protective leaf cuticles, bryophytes have limited control over water uptake and loss. Although species of some habitats are tolerant of desiccation (Proctor 1981; Bewley and Krochko 1982), shade-adapted bryophytes have limited capacity to recover from prolonged periods of drying (Proctor 2000). Thus, individuals that survive the direct effects of timber harvest may not tolerate the indirect effects: the warmer, drier conditions found in post-harvest environments. Third, if forest bryophytes are locally extirpated, re-establishment of some species may be slow (Alaback 1982) because of poor dispersal (Söderström 1990; Miles and Longton 1992; Ross-Davis and Frego 2004) or limited representation in the buried propagule bank (Ross-Davis and Frego 2004). Although little is known about bryophyte responses to logging in temperate forests, harvest-related declines have been reported for boreal (Hannerz and Hånell 1997; Jalonen and Vanha-Majamaa 2001; Newmaster and Bell 2002) and Acadian-mixedwood forests (Fenton et al. 2003).

Opportunities for recovery of bryophyte communities following timber harvest may be enhanced by retention of undisturbed forest patches (Söderström et al. 1992) such as those left as part of structural or variable retention harvests (for information on retention harvests, see Franklin et al. 1997). However, the extent to which forest remnants provide refugia for bryophyte species will depend on the degree to which they are compromised by edge effects. Light, temperature, wind speed, humidity, and soil moisture can differ substantially between forest-margin and interior environments; these effects can vary in depth and magnitude and with edge orientation (aspect) (Chen et al. 1993, 1995). Although relationships between vascular plant composition or abundance and proximity to edge have been examined in some forest ecosystems (e.g., Brothers and Spingarn 1992; Fraver 1994; Matlack 1994; Nelson and Halpern 2005), similar studies of bryophytes are rare (Luczaj and Sadowska 1997; Moen and Jonsson 2003).

The current study is part of a larger experiment, Demonstration of Ecosystem Management Options (DEMO), which is testing the effects of varying levels and patterns of overstory retention on diverse groups of organisms in mature coniferous forests of the Pacific Northwestern United States (Aubry et al. 1999; Halpern et al. 1999, 2005). We examined first-year responses of bryophytes across steep environmental gradients within aggregated retention treatments and related these responses to the direct and indirect effects of harvest, including ground disturbance, changes in light availability, and cover of residual vascular plants. We addressed three questions. (1) Do bryophyte species richness and abundance decline immediately after timber harvest, and if so, are declines correlated with harvest-related ground disturbance or elevated light levels, or moderated by cover of residual herbs or shrubs? (2) Do 1-ha forest aggregates within harvested areas provide short-term refugia for bryophytes? (3) Within forest aggregates, does proximity to edge or edge orientation (aspect) explain variation in bryophyte richness or abundance, and if so, are these spatial patterns correlated with ground disturbance, light availability, or cover of herbs or shrubs?

Materials and methods

Study sites

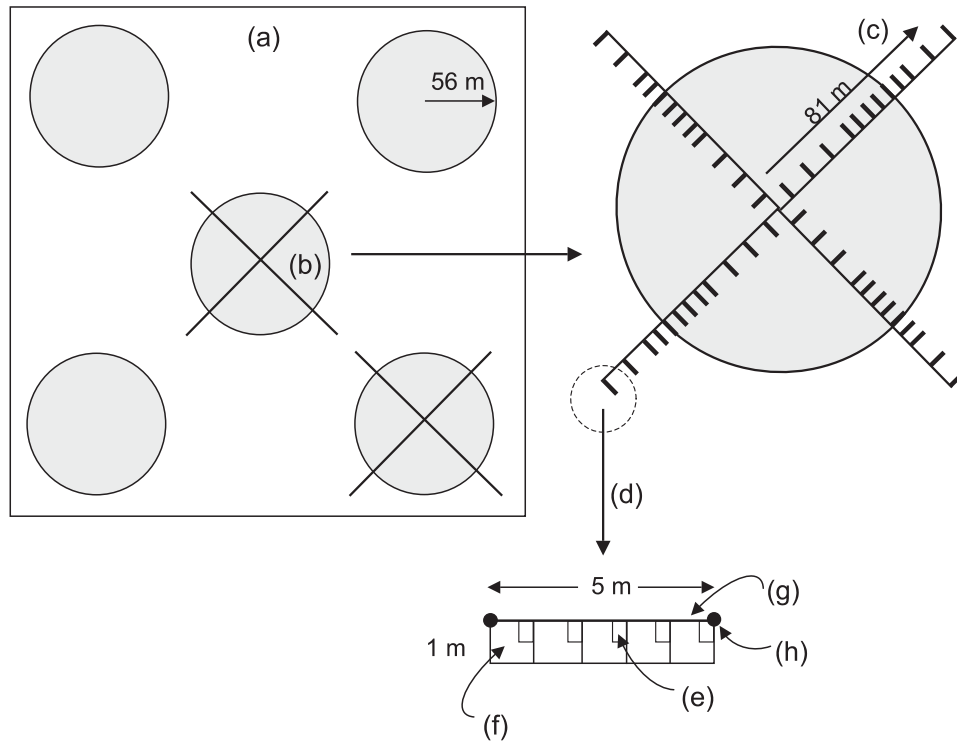
Our study sites, Butte and Paradise Hills, are on the west slope of the Cascade Range in southern Washington in the Gifford Pinchot National Forest. Butte (46°22'07"N, 121°34'40"W) is located at an elevation of 1012–1122 m in the *Tsuga heterophylla* zone (Franklin and Dyrness 1973). Slopes average 40% and face southeast. Soils are well drained and fairly shallow, consist of loamy sands derived from residuum and colluvium, and are covered by a shallow surface layer of volcanic ash originating from the 1980 eruption of Mount St. Helens (Wade et al. 1992). Forests are ca. 70–80 years old and are dominated by *Pseudotsuga menziesii*; *Tsuga heterophylla* and *Thuja plicata* are also common (Halpern et al. 1999). Prior to treatment, canopy height, stem density (trees ≥ 5 cm diameter at breast height), and basal area averaged 36 m, 1150 trees/ha, and 56 m²/ha, respectively; common understory species included *Tsuga heterophylla*, *Thuja plicata*, *Acer circinatum*, *Berberis nervosa*, *Pteridium aquilinum*, *Achlys triphylla*, and *Chimaphila umbellata*. Ground-layer bryophytes averaged approximately 9% cover, with *Rhytidiopsis robusta* and *Eurhynchium oregonum* the most common species; in a systematic sample of the site (888 0.1-m² microplots), 46 bryophyte taxa were recorded (Halpern, unpublished data).

Paradise Hills (46°00'46"N, 121°56'34"W) is located at an elevation of 957–1000 m in the *Abies amabilis* zone (Franklin and Dyrness 1973). Slopes are gentle (averaging 18%) and primarily face east to northeast. Soils are deep sandy loams derived from volcanic ash and pumice, till, and residuum (Wade et al. 1992). Forests are 110–140 years old and are dominated by *Pseudotsuga menziesii*; *Tsuga heterophylla*, *Thuja plicata*, and *Abies amabilis* are common associates (Halpern et al. 1999). Prior to treatment, canopy height, stem density, and basal area averaged 39 m, 740 trees/ha, and 73 m²/ha, respectively; species common in the understory included *Tsuga heterophylla*, *Abies amabilis*, *Vaccinium membranaceum*, *Vaccinium ovalifolium*, *Xerophyllum tenax*, *Achlys triphylla*, and *Cornus canadensis*. Ground-layer bryophytes averaged approximately 23% cover, with *Rhytidiopsis robusta* and *Hypnum circinale* the most common species; in contrast with Butte, a systematic sample of the site yielded 37 bryophyte taxa, with 31 common to both sites (Halpern, unpublished data).

Harvest treatments

Within a 13-ha harvest unit at each site, five 1-ha (56-m radius) circular forest aggregates were retained (Fig. 1). In the surrounding area, all merchantable trees (>18 cm diameter at breast height) were cut and removed; logs were yarded with a helicopter at Butte and a combination of tracked shovel loaders and rubber-tired skidders at Paradise Hills. Nonmerchantable subcanopy trees were retained in harvest areas at Butte but were felled at Paradise Hills. Compacted soil in skid trails (present between aggregates at Paradise Hills) was loosened with a tracked excavator, then covered with logging slash; elsewhere, slash was left in place. Yarding was completed in July 1997 at Butte and in September 1997 at Paradise Hills (for details see Halpern and McKenzie 2001).

Fig. 1. Sampling design within each 13-ha harvest unit (a). Sampling was conducted in and adjacent to two aggregates (b) at each site. Transects (c), oriented in cardinal directions, originated at the center of each aggregate, and extended 25 m into the adjacent harvest area. Twelve $1\text{ m} \times 5\text{ m}$ bands (d) were established at 5- to 10-m intervals along each transect. Each band consisted of five 0.1-m^2 microplots (e) for sampling bryophytes and five 1-m^2 subplots (f) for sampling vascular plants. Harvest-related disturbance (cover of logging slash and disturbed soil) was sampled along the interior edge of each band (g), and cover of open sky at the two endpoints (h).



Sampling

Pretreatment sampling was conducted from 1 July to 9 September 1996 and posttreatment sampling from 5 July to 15 September 1998. Four circular aggregates (two at each site) that were marked for retention were randomly selected for sampling. In each of these, we established four perpendicular transects, 81 m in length, extending in cardinal directions from the aggregate center and ending 25 m past the aggregate edge (Fig. 1). Twelve bands of permanent plots were established along each transect, eight in the area marked for retention (at distances of 0, 5, 10, 15, 20, 30, 40, and 50 m from the edge) and four in the area marked for harvest (at distances of 5, 10, 15, and 25 m from the edge). Thus, bands were spaced at 5-m intervals on both sides of the forest edge, where we expected steeper gradients in vegetation response, and at 10-m intervals elsewhere.

Each band consisted of five, 0.1-m^2 microplots within which we estimated total cover of ground-layer mosses and liverworts and cover of individual species, including epilithic, epixylic, and epigeic taxa (but not epiphytic taxa present as litter fall). Cover was estimated by measuring plant dimensions. Where microplots fell on coarse woody debris or on the bases of shrubs or trees, sampling was limited to within 1 m of the forest floor. When species could not be reliably identified in the field, specimens were collected from outside the sample bands (collections could not be taken from sample bands without compromising future measurements), identified in the lab, and archived for future reference. *Brachythecium* (represented by six species) was

analyzed at the genus level because several species that cannot be identified on gross morphological characteristics co-occurred within microplots and could not be distinguished without destructive sampling. Nomenclature follows Anderson et al. (1990) for mosses and Stotler and Crandall-Stotler (1977) for liverworts.

At each sample band, we collected additional data on ground disturbance and "habitat" conditions. Disturbance variables included cover of logging slash and disturbed soil, measured along the interior edge of each band using the line-intercept method (Fig. 1). Habitat variables included: (1) cover of open sky, determined at the two endpoints of each band using a CI-110 digital canopy imager with 150-degree lens (CID Inc., Camas, Washington, USA) and (2) total cover of herbaceous species (ferns, forbs, graminoids, and low-growing woody taxa) and tall shrubs, visually estimated within five 1-m^2 subplots at each band (Fig. 1). Detailed analyses of ground-disturbance and habitat variables are reported in Nelson and Halpern (2005).

Statistical analyses

Because mosses and liverworts exhibited considerable spatial variation in richness (number of taxa per sample band) and abundance (total cover and species' frequencies) prior to timber harvest, we used changes (post- minus pre-treatment values) in these variables as measures of response. Means of these changes were computed for each of the four aggregates and adjacent harvest areas, and for each sample distance within an aggregate. Statistical tests of species' re-

sponses were limited to taxa that, prior to treatment, occurred in and adjacent to at least three of the four aggregates and had >10% frequency (percentage of bands).

Responses within harvest areas and forest aggregates

Paired *t* tests (Sokal and Rohlf 1981) were used to compare pre- and post-treatment values of moss and liverwort richness and cover, and individual species' frequencies within each environment (forest aggregates vs. adjacent harvest areas) (questions 1 and 2). To explore the possible correlates of change in harvest areas, we computed Spearman rank correlations (Sokal and Rohlf 1981) between changes in richness or abundance and ground-disturbance (cover of logging slash and disturbed soil) or habitat variables (cover of open sky, herbs, and tall shrubs).

Gradients within forest aggregates

To assess relationships between bryophyte responses and proximity to aggregate edge (question 3), we computed Spearman rank correlations between changes in richness or abundance and distance from edge (bands within forest aggregates only). We then explored the possible correlates of these changes by computing Spearman rank correlations between these same bryophyte response variables and ground-disturbance and habitat variables (see above). To test whether responses within forest aggregates varied with edge orientation, we used analysis of variance (ANOVA; Sokal and Rohlf 1981) to compare mean changes in richness and abundance for transects representing the four cardinal directions ($n = 4$ transects per direction); transect means were computed from the eight bands representing the forested portion of each transect.

All statistical analyses were conducted using Systat 10.0 (SPSS 2001), with an alpha level of 0.05 as the criterion for reporting statistical significance.

Results

Prior to treatment, a total of 36 bryophyte taxa (28 mosses and 8 liverworts) were identified in sample bands (Table 1). Eight taxa (six mosses and two liverworts) were sufficiently abundant to meet our criteria for statistical analysis: presence prior to treatment in and adjacent to at least three of the four aggregates and >10% frequency (percentage of bands); we refer to these as "common taxa". Species richness (number of taxa per band) and total cover of mosses and liverworts did not differ significantly between areas marked for retention and those marked for harvest (Table 2); except for very infrequent taxa, species occurrences were similar in these environments (Table 1).

Responses within harvest areas

Within harvest areas, richness and cover of mosses and liverworts declined significantly one year after treatment (Fig. 2, open symbols). Nearly 90% of taxa declined in frequency; of the eight common taxa tested, declines were significant for five (Fig. 3a). Seven infrequent taxa (*Blepharostoma trichophyllum*, *Eurhynchium pulchellum*, *Trachybryum megaptium*, *Orthotrichum* sp., *Plagiomnium insigne*, *Plagiothecium laetum*, and *Rhytidiadelphus loreus*; each with 2%–5% frequency) disappeared completely from

sample bands, but four new taxa were observed after harvest (*Ditrichum montanum*, *Hygrohypnum bestii*, *Pleurozium schreberi*, and *Polytrichum juniperinum*; each with 1%–2% frequency).

Changes in species richness were negatively correlated with logging slash and open sky, and changes in total cover were negatively correlated with logging slash, disturbed soil, and open sky (Table 3). However, these declines were significantly reduced at higher levels of vascular plant cover (Table 3). Similarly, for four of eight common taxa, changes in frequency showed a significant negative correlation with cover of logging slash or disturbed soil, and for five taxa, changes showed a significant positive correlation with cover of herbs or tall shrubs (Table 3).

Responses within forest aggregates

In contrast to patterns in harvest areas, species richness and total cover changed minimally within forest aggregates (Fig. 2, closed symbols), as did frequency of common taxa (Fig. 3b). One infrequent species (*Ditrichum montanum*, 1% frequency) disappeared from sample bands within forest aggregates, but four new species were observed after harvest (*Lepidozia reptans*, *Plagiothecium undulatum*, *Pleurozium schreberi*, and *Racomitrium heterostichum*; each with 1% frequency).

Gradients within forest aggregates

Mosses showed limited short-term response to forest edges. We did not observe significant relationships between proximity to edge and changes in richness or cover of mosses, or between proximity to edge and changes in the frequency of common moss taxa (Fig. 4, Table 4). In addition, there were few significant correlations between moss responses and ground-disturbance, or between moss responses and habitat variables (Table 4). In contrast, liverworts were more sensitive: richness, cover, and frequency of *Scapania bolanderi* (one of two common species) declined significantly with proximity to edge (Table 4, Fig. 5). Change in liverwort species richness was negatively correlated with percent open sky and positively correlated with cover of herbs and tall shrubs; change in cover was negatively correlated with slash and positively correlated with cover of tall shrubs (Table 4).

Edge orientation did not have an effect on the responses of mosses or liverworts within forest aggregates; changes in richness, cover, and species' frequencies were comparable among transects representing contrasting edge orientations (one-way ANOVAs: $0.116 < P < 0.963$).

Discussion

Our results clearly show the sensitivity of ground-layer bryophytes to logging disturbance. One year after treatment, species richness, total cover, and frequency of most taxa declined within harvest areas. Similar responses have been observed in *Picea* and mixedwood forests: one year after clearcut logging, Jalonen and Vanha-Majamaa (2001) observed 60% and 94% declines in richness and total cover, respectively; four years after logging, Fenton et al. (2003) observed extirpations of 72% of liverwort species from quadrats directly affected by timber harvest; and seven to

Table 1. Abundance of bryophyte taxa found prior to treatment.

Taxon ^b	Forest aggregates		Harvest areas ^a	
	Constancy ^c	Frequency ^d	Constancy ^c	Frequency ^d
<i>Rhytidiopsis robusta</i>	4	85	4	80
<i>Dicranum fuscescens</i>	4	51	4	38
<i>Brachythecium</i> spp. ^e	4	43	4	48
<i>Hypnum circinale</i>	4	36	3	30
<i>Eurhynchium oreganum</i>	4	28	4	28
<i>Dicranum tauricum</i>	4	20	4	31
<i>Scapania bolanderi</i> *	4	15	4	20
<i>Ptilidium californicum</i> *	4	14	3	18
<i>Pseudoleskea stenophylla</i>	3	6	3	11
<i>Pseudotaxiphyllum elegans</i>	3	20	2	11
<i>Aulacomnium androgynum</i>	2	17	2	16
<i>Rhizomnium glabrescens</i>	2	6	2	8
<i>Pohlia nutans</i>	2	5	2	13
<i>Cephalozia lunulifolia</i> *	2	2	2	5
<i>Trachybryum megaptilum</i>	2	2	1	5
<i>Lophozia</i> spp.*	2	2	1	2
<i>Cephalozia bicuspidata</i> *	2	2		
<i>Hylocomium splendens</i>	2	2		
<i>Mnium spinulosum</i>	2	2		
<i>Plagiothecium laetum</i>	1	2	2	5
<i>Blepharostoma trichophyllum</i> *	1	2	1	2
<i>Scapania umbrosa</i> *	1	2		
<i>Claopodium bolanderi</i>	1	1		
<i>Ditrichum montanum</i>	1	1		
<i>Isothecium stoloniferum</i>	1	1		
<i>Lophocolea heterophylla</i> *	1	1		
<i>Drepanocladus aduncus</i>			1	2
<i>Eurhynchium pulchellum</i>			1	2
<i>Orthotrichum</i> sp.			1	2
<i>Plagiomnium insigne</i>			1	2
<i>Rhytidiadelphus loreus</i>			1	2

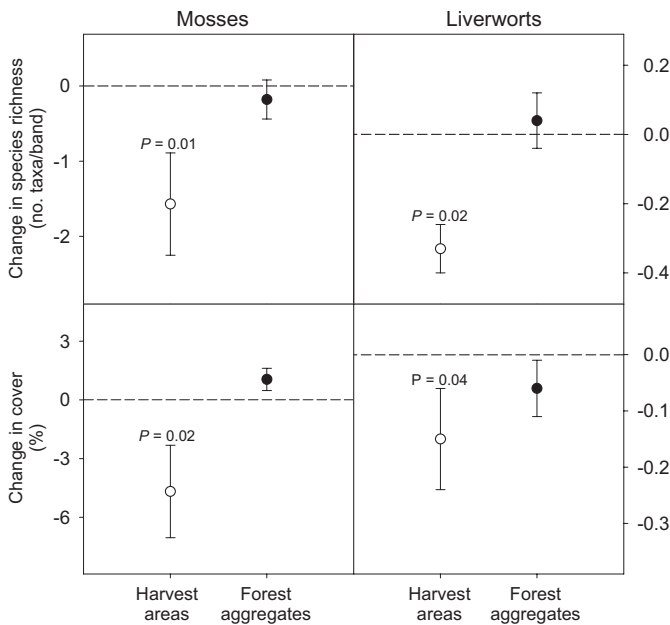
^aPrior to logging.^bLiverworts are followed by asterisks.^cThe number of forest aggregates or harvest area locations in which a species was present (maximum of 4).^dThe percentage of sample bands in which a species was present; each aggregate contained 32 bands, and each harvest area contained 16 bands.^eIncludes *Brachythecium leibergii*, *B. starkei*, *B. velutinum*, *B. asperrimum*, *B. hylotapetum*, and *B. albicans* (in descending order of abundance based on frequency of collections).**Table 2.** Results of two-sample *t* tests (df = 6) comparing species richness and abundance of bryophytes in forest aggregates (*n* = 4) and harvest areas (*n* = 4) prior to treatment.

	Mean (SE)		<i>t</i>	<i>P</i>
	Forest aggregates	Harvest areas		
Richness (no. taxa/band)				
All bryophytes	3.9 (0.4)	3.9 (0.5)	-0.079	0.940
Mosses	3.5 (0.5)	3.5 (0.5)	0.002	0.999
Liverworts	0.4 (0.1)	0.4 (0.1)	-0.380	0.717
Cover (%)				
All bryophytes	9.6 (2.9)	9.5 (3.2)	0.024	0.982
Mosses	9.4 (2.9)	9.3 (3.1)	0.017	0.987
Liverworts	0.2 (<0.1)	0.2 (<0.1)	0.267	0.798

eight years after harvest, Hannerz and Hånell (1997) observed 64%–89% reductions in cover of common bryophyte species. On our sites, as well as those studied by Fenton et

al. (2003), species were more sensitive to the direct effects of timber harvest (burial by logging slash and soil disturbance) than to the indirect effects of overstorey removal, such

Fig. 2. Mean changes (± 1 SE) in richness and total cover of mosses and liverworts in harvest areas (\circ) and forest aggregates (\bullet) one year after treatment. *P* values are shown where pre- and post-treatment means differed significantly based on a paired *t* test ($n = 4$).

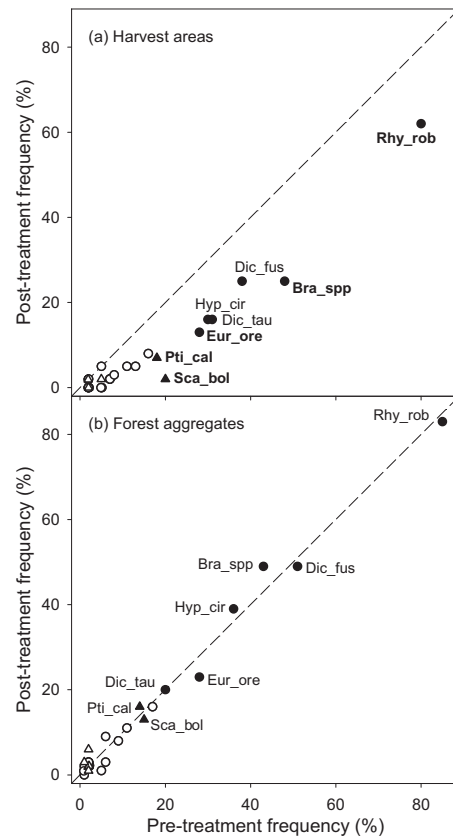


as increased exposure to light (Table 3). However, changes in microclimate (e.g., temperature or humidity) associated with increased radiation may result in longer term declines in bryophyte abundance. Reduction in the quality of substrates, particularly moist, well-decayed coarse woody debris, may also contribute to further declines (Söderström 1988; Rambo and Muir 1998; Newmaster et al. 2003).

In disturbed areas, populations of forest bryophytes may require long periods of time to recover (e.g., Alaback 1982; Zobel and Antos 1997). Although spore production may be prolific in suitable habitats (Miles and Longton 1992), it requires adequate moisture, which may be limited in the warmer, drier postharvest environment. Recolonization also may be constrained by a poorly developed buried-propagule bank (Ross-Davis and Frego 2004); limited dispersal ability (Wyatt 1982) or spore lifespan (Tan and Pocs 2000); or inability of spores to survive desiccation, extreme temperatures, or exposure to ultraviolet radiation (van Zanten and Pocs 1981; Miles and Longton 1992; Tan and Pocs 2000). Moreover, recovery may not be possible until adequate microclimatic conditions and substrates develop within the regenerating forest (Edwards 1986; Söderström 1988; Lesica et al. 1991; Frisvoll and Prestø 1997; Newmaster et al. 2003).

In comparison to harvest areas, bryophyte communities within forest aggregates changed minimally. Although edge environments were characterized by increased light availability and ground disturbance to a distance of 15 m (Nelson and Halpern 2005), richness, cover, and frequency of common mosses did not show strong edge-related responses one year after timber harvest. In contrast, liverworts, which were considerably less abundant than mosses, showed significant declines with proximity to edge. These results support previ-

Fig. 3. Mean frequency ($n = 4$) of individual bryophyte taxa before and after treatment in harvest areas (25 taxa) (a) and forest aggregates (28 taxa) (b). Only taxa present before treatment are plotted. \circ and \bullet represent mosses; \triangle and \blacktriangle represent liverworts. Open symbols represent infrequent taxa; filled symbols represent common taxa (see Methods), with species codes as follows: Bra_spp., *Brachythecium* spp.; Dic_fus, *Dicranum fuscescens*; Dic_tau, *Dicranum tauricum*; Eur_ore, *Eurhynchium oregonum*; Hyp_cir, *Hypnum circinale*; Pti_cal, *Ptilidium californicum*; Rhy_rob, *Rhytidiopsis robusta*; Sca_bol, *Scapania bolanderi*. Species in bold font exhibited significant declines in abundance (based on paired *t* tests, $n = 4$) with probability values as follows: Bra_spp = 0.014, Eur_ore = 0.042, Pti_cal = 0.048, Rhy_rob = 0.007, and Sca_bol = 0.007.



ous suggestions that, as a group, liverworts are more sensitive to changes in humidity and temperature than are mosses (Söderström 1988; Frisvoll and Prestø 1997; Fenton et al. 2003).

Because it was not possible to test for changes in the frequency of infrequent or rare species, it is likely that we have underestimated the breadth and magnitude of edge effects. It is these uncommon species that should be more susceptible to disturbance or to stochastic effects that lead to local extirpation. Furthermore, the general absence of immediate, edge-related declines in richness or abundance of mosses does not preclude the possibility of future declines. Although the contrast in microclimatic conditions is most extreme immediately after edges are formed (Williams-Linera 1990; Matlack 1993), plant responses are likely to lag behind environmental changes. We observed this trend with forest herbs on these sites: the proportion of species that

Table 3. Spearman rank correlation coefficients (r), and probabilities of significance (P), between bryophyte responses in harvest areas and post-treatment cover of ground-disturbance or habitat variables.

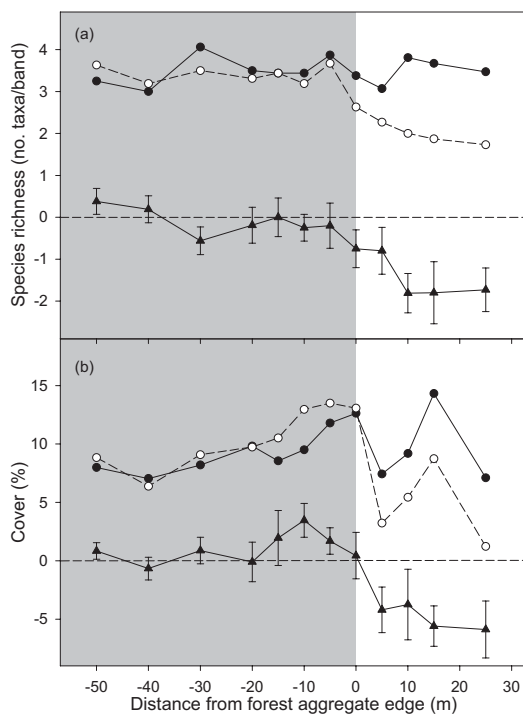
	Logging slash		Disturbed soil		Open sky		Herbs		Tall shrubs	
	r	P	r	P	r	P	r	P	r	P
Change in species richness (no. of taxa/band)										
Mosses	-0.48	0.001	-0.22		-0.41	0.004	0.12		0.39	0.006
Liverworts	-0.44	0.002	-0.09		-0.53	<0.001	0.36	0.011	0.29	0.045
Change in cover (%)										
Mosses	-0.60	<0.001	-0.45	0.001	-0.40	0.005	0.25		0.33	0.024
Liverworts	-0.39	0.006	-0.25		-0.35	0.014	0.11		0.29	0.044
Change in species frequency ^a (% of bands)										
<i>Brachythecium</i> spp. ^b	-0.14		0.05		-0.09		-0.11		0.17	
<i>Dicranum fuscescens</i>	-0.34	0.019	-0.31	0.029	-0.34		-0.04		-0.07	
<i>Dicranum tauricum</i>	-0.20		0.10		-0.10		-0.08		0.38	0.007
<i>Eurhynchium oregonum</i>	-0.28		-0.13		-0.36		0.42	0.003	0.02	
<i>Hypnum circinale</i>	-0.22		-0.36	0.012	-0.18		0.03		-0.10	
<i>Ptilidium californicum</i>	-0.32	0.027	-0.18		-0.33		0.20		0.36	0.013
<i>Rhytidiopsis robusta</i>	-0.57	<0.001	-0.46	0.001	-0.40		0.18		0.36	0.012
<i>Scapania bolanderi</i>	-0.21		-0.17		-0.19		0.10		0.35	0.016

Note: Probability of statistical significance is given only for $P \leq 0.05$; $n = 16$ for all tests.

^aCommon taxa only, that is, those present prior to treatment in and adjacent to at least three of the four forest aggregates and >10% frequency (percentage of bands).

^bIncludes *Brachythecium leibergii*, *B. starkei*, *B. velutinum*, *B. asperimum*, *B. hylotapetum*, and *B. albicans* (in descending order of abundance based on frequency of collections).

Fig. 4. Changes in richness (a) and cover (b) of mosses with proximity to forest aggregate edge. Triangles (\blacktriangle) represent mean differences (± 1 SE) ($n = 16$) between pre- and post-treatment values (\bullet and \circ , respectively) at each distance. Points in the shaded region represent bands within forest aggregates.



showed significant edge-related declines increased from 10% to 28% over two years (Nelson and Halpern 2005). A similar pattern may develop over time in the bryophyte community.

Orientation or aspect can influence vascular plant responses to forest edges (Wales 1972; Palik and Murphy 1990; Brothers and Spingarn 1992), with south and west exposures characterized by greater direct radiation and greater potential for physiological stress. In this study, however, we did not detect a significant effect of orientation on bryophyte responses, a pattern consistent with the responses of vascular plants at these sites (Nelson and Halpern 2005). More pronounced responses along south- and west-facing edges may be more common at lower elevations and at lower latitudes where the effects of summer drought are more intense. However, it is also possible that these effects will develop with time.

Implications for conservation and management

Structural retention harvest is now a common silvicultural practice in many northern temperate and boreal regions (e.g., USDA and USDI 1994; Arnott and Beese 1997; Coates et al. 1997; Vanha-Majamaa and Jalonen 2001), reflecting greater emphasis on the conservation of biodiversity in managed landscapes. Maintenance of undisturbed patches of forest as temporary refugia and dispersal sources for forest-dwelling species is integral to this practice. Although longer term measurements are needed to fully understand the consequences of aggregated retention harvest for forest bryophyte communities, our results document initial responses and provide insights into the physical and biotic factors that mediate changes in the distribution and abundance of mosses and liverworts.

On our sites, most bryophytes were highly sensitive to timber harvest. Once extirpated, considerable time may be required for communities to regain initial composition, abundance, and diversity (Alaback 1982; Zobel and Antos 1997). Thus, silvicultural strategies that minimize local loss of species and that provide for sources of dispersal into

Table 4. Spearman rank correlation coefficients (*r*), and probabilities of significance (*P*), between bryophyte responses within forest aggregates and proximity to forest edge, or ground-disturbance cover, or habitat variables.

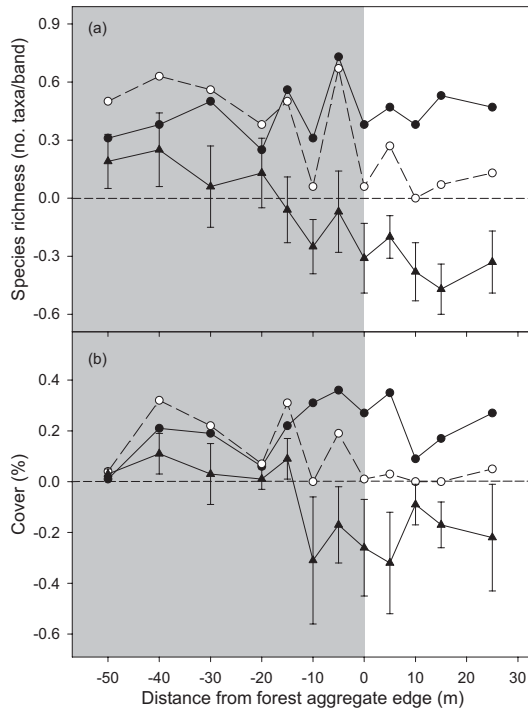
	Proximity to forest edge			Ground-disturbance cover						Habitat variables					
				Logging slash		Disturbed soil		Open sky		Herbs		Tall shrubs			
	<i>r</i>	<i>P</i>		<i>r</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>		
Change in species richness (no. of taxa/band)															
Mosses	-0.22			-0.17		-0.11		0.06		-0.16		0.43	0.014		
Liverworts	-0.50	0.004		-0.32		0.13		-0.41	0.022	0.39	0.029	0.36	0.044		
Change in cover (%)															
Mosses	0.29			-0.14		-0.27		0.34		0.05		0.05			
Liverworts	-0.50	0.008		-0.44	0.012	-0.07		-0.29		0.01		0.35	0.050		
Change in species frequency ^a (% of bands)															
<i>Brachythecium</i> spp. ^b	0.00			-0.05		0.19		0.21		-0.20		0.27			
<i>Dicranum fuscescens</i>	-0.14			-0.26		-0.15		-0.17		-0.20		-0.23			
<i>Dicranum tauricum</i>	0.00			-0.12		0.22		0.20		-0.21		0.43			
<i>Eurhynchium oregonum</i>	-0.29			-0.12		-0.09		-0.41	0.019	0.50		-0.08			
<i>Hypnum circinale</i>	0.08			-0.03		-0.31		0.16		-0.08		-0.25			
<i>Ptilidium californicum</i>	-0.23			-0.11		-0.01		-0.09		0.04		0.35			
<i>Rhytidopsis robusta</i>	0.25			-0.12		-0.22		0.30		-0.15		0.16			
<i>Scapania bolanderi</i>	-0.38	0.033		-0.26		-0.03		-0.11		0.23		0.43			

Note: Negative coefficients indicate declines with proximity to forest aggregate edge. Probability of statistical significance listed only for $P \leq 0.05$; $n = 32$ for all tests.

^aCommon taxa only, that is, those present prior to treatment in and adjacent to at least three of the four forest aggregates and >10% frequency (percentage of bands).

^bIncludes *Brachythecium leibergii*, *B. starkei*, *B. velutinum*, *B. asperinum*, *B. hylotapetum*, and *B. albicans* (in descending order of abundance based on frequency of collections).

Fig. 5. Changes in richness (a) and cover (b) of liverworts with proximity to forest aggregate edge. Triangles (\blacktriangle) represent mean differences (± 1 SE) ($n = 16$) between pre- and post-treatment values (\bullet and \circ , respectively) at each distance. Points in the shaded region represent bands within forest aggregates.



har vest areas are necessary for adequate protection of forest bryophytes in managed landscapes. Dispersed retention of live trees may moderate the effects of clearcut logging (Hannerz and Hånell 1997; Jalonen and Vanha-Majamaa 2001); however, some forest-floor bryophytes may require conditions that are only met in undisturbed forest and may disappear from areas where even a moderate amount of timber is extracted (Söderström 1988).

Aggregated retention of live trees may provide a refugium for disturbance-sensitive species and a local source for dispersal of propagules into adjacent harvested areas once microclimatic conditions become suitable for establishment. However, the efficacy of remnant forest patches for conserving bryophyte diversity will depend on their size, shape, and the degree to which habitat conditions are not compromised by edge phenomena (Moen and Jonsson 2003). In the temperate, coniferous forests that we studied, 1-ha circular forest patches appear sufficiently large in the short term to buffer common ground-layer mosses from the effects of timber harvest. However, our data suggest that they are not large enough to prevent decline or loss of liverworts that are particularly sensitive to changes in substrate quality, humidity, or temperature resulting from increased radiation. Disturbed soil, deposition of logging slash, and elevated levels of light were found at distances of up to 15 m from the edge, thus influencing ca. 50% of the aggregate area (Nelson and Halpern 2005). In boreal forests, remnant patches smaller than 1 ha (or larger, irregularly shaped patches) are strongly influenced by edge phenomena (Moen and Jonsson 2003)

and show declines in bryophyte richness or abundance (Jalonen and Vanha-Majamaa 2001). In combination, these results suggest that current standards for structural retention on federal lands in the Pacific Northwestern United States (USDA and USDI 1994), which allow for aggregates as small as 0.2 ha, may be inadequate to retain the diversity and abundance of bryophyte species found in older, undisturbed forests. Longer term studies in these and other fragmented forests will be critical for improving standards for bryophyte protection in managed landscapes.

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