

Decaying Logs and Habitat Heterogeneity: Implications for Bryophyte Diversity in Western Oregon Forests

Abstract

Bryophytes were inventoried on eight different substrates in plots in the Coast and Cascade Ranges of western Oregon. The relative contribution of each type of substrate towards bryophyte richness was evaluated. Of all substrates, logs in advanced stages of decay had the richest bryophyte flora and supported the greatest percentage of bryophyte landscape-level diversity. Such logs also contributed the greatest number of liverworts unique to a substrate type, while mineral soil contributed the greatest number of unique mosses. Hardwood bases, humus, and rocks also added bryophytes not found on any other substrate type. Habitat heterogeneity increases bryophyte diversity in western Oregon forests. Fostering biological and structural legacies characteristic of old growth in young, managed stands would contribute toward forest management from an ecosystem approach by fostering habitat complexity and biodiversity in the course of harvesting timber.

Introduction

Forest managers in the U.S. Pacific Northwest have been directed to take an ecosystem approach to forest management to maintain and restore biological diversity in late successional and old-growth forests (USDA and USDI 1994). Old-growth forests are recognized as reservoirs of biodiversity in this region (Franklin 1989, Norse 1990), and other areas of the world (e.g., Gustafsson et al. 1992). As of 1990, as little as 13% of old growth remained in Oregon and Washington (Norse 1990), and cutting of that age class has continued. The most important conservation impact of cutting old growth is the resulting loss of biodiversity (Dudley 1992). A majority of the members of the International Association of Bryologists cited forestry practices as the greatest contributor to the decline of species and ecological groups of bryophytes (Christy 1992). Epixylic and epiphytic bryophytes have been particularly negatively impacted (Andersson and Hytteborn 1991, Christy 1992). The continued existence of some bryophytes in the Pacific Northwest may well depend on old-growth forest habitat, and forest managers in this region have been directed to protect many designated old growth-associated bryophytes (FEMAT 1993) through surveying and management strategies (USDA and USDI 1994).

Old-growth forest preserves alone are inadequate for protecting our remaining legacy of biological diversity (Harris 1984, Franklin 1989, Wilcove 1989). To accomplish such protection, the effort to conserve biodiversity must be expanded into younger, managed stands on multiple-use public lands (Thomas and Salwasser 1989, Wilcove 1989). Managed stands in the Pacific Northwest are usually plantations devoted to monocultures of economic importance and high productivity. Such stands do not support a level of biodiversity comparable to that of ecologically complex, natural forests (Acharya 1996). Young, managed stands generally lack the complexity of structural features upon which old growth-associated species may depend (Hansen et al. 1991, McComb et al. 1993). Timber-producing stands should be managed not only for their commercial productivity, but also for those structural, compositional, and functional attributes typically associated with old growth (Franklin et al. 1981, Hansen et al. 1991).

Decaying logs are recognized as one important structural component of old growth in the Pacific Northwest (Franklin et al. 1981, Spies et al. 1988). Such coarse woody debris is important in many ecological and physical processes in these ecosystems, influencing species composition, nutrient cycling, productivity, and stream geomorphology (Maser et al. 1979, Franklin et al. 1981, Harmon et al. 1986, Spies et al. 1988). Decaying logs also contribute to biological diversity (Franklin et al. 1981, Hansen et al. 1991, Esseen et al. 1992)

¹Current address: Department of Environmental Horticulture, University of California, Davis, CA 95616-8587; e-mail: ttrambo@ucdavis.edu

by providing essential habitat for many plant and animal species (Maser et al. 1979, Franklin and Spies 1991). A large number of bryophytes depend upon decaying logs for habitat in Swedish forests (Andersson and Hytteborn 1991, Berg et al. 1993).

Bryophyte diversity increased with increasing number of suitable habitats, such as logs and rocks, in New York State forests (Slack 1977). In North Wales, bryophyte richness was positively correlated with the availability of diverse woodland habitats such as rocks (Edwards 1986). Likewise, bryophyte richness was positively correlated with the number of different substrates in forest communities of Jasper National Park, Canada (Lee and La Roi 1979). However, quantitative information on the relative contributions of different substrates towards bryophyte richness in the Pacific Northwest is generally lacking. For bryophyte species conservation, it is important that those habitats with high bryological value be identified so that they may be protected in the course of forest management.

This study examines bryophyte richness on a variety of forest substrates, including decaying logs, mineral soil, rocks, and hardwood tree bases. Study objectives were: 1) to inventory bryophytes and survey for species designated for federal agency protection, 2) to quantify and evaluate the relative contributions of the range of bryophyte substrates towards bryophyte richness, and 3) to examine whether bryophyte richness was associated with stand age. The study provides information that will aid efforts to implement an ecosystem approach to forest management and conserve bryophyte diversity in older stands. It will also be of value to forest managers when developing strategies to encourage old growth-associated bryophyte diversity in younger managed stands.

Study Area

Sites were in the Coast and Cascade mountain ranges of central western Oregon on federal lands managed by the Eugene District, Bureau of Land Management (BLM), and the Willamette National Forest (Figure 1). Plot longitudes fell between $122^{\circ} 22.8' W$ on the western slope of the Cascade Range and $123^{\circ} 43.3' W$ on the western slope of the Coast Range, while latitudes fell between $43^{\circ} 36.8'$ and $44^{\circ} 25.5' N$. Plots were in forest stands from 50 to over 200 years old, typically

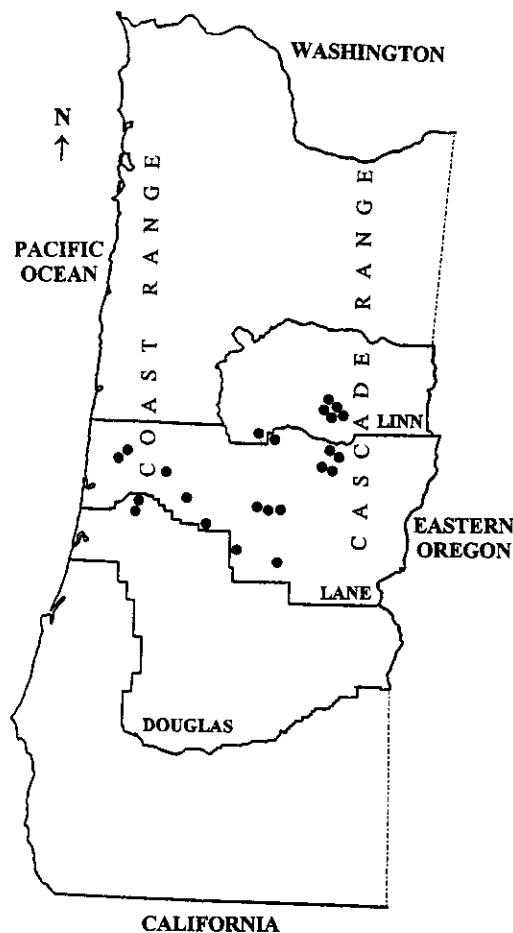


Figure 1. Distribution of study plots in western Oregon, showing the three counties in which they were located.

situated on lower to upper slopes with a full range of aspects. Elevations ranged between 215 and 795 m, with one exception (1220 m). Average annual rainfall for the vicinities of these plots ranges from approximately 180 cm in the western Coast Range to 110 cm on its east slope, increasing again easterly to 160 cm in the Cascade Range (Owenby and Ezell 1992). Mean annual temperatures range from $10.2^{\circ} C$ (interior), to $12.0^{\circ} C$ (coastal). Mean temperatures for the coldest month (January) range from $3.4^{\circ} C$ (interior) to $5.0^{\circ} C$ (coastal), while those for the warmest month (August) range between $17.6^{\circ} C$ and $19.3^{\circ} C$ (Owenby and Ezell 1992).

Overstorey vegetation was generally dominated by Douglas-fir (*Pseudotsuga menziesii*), with

Pacific yew (*Taxus brevifolia*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*) also present. Hardwoods included bigleaf maple (*Acer macrophyllum*), cascara buckthorn (*Rhamnus purshiana*), and red alder (*Alnus rubra*). Understory shrubs typically included hazel (*Corylus cornuta*), red huckleberry (*Vaccinium parvifolium*), ocean spray (*Holodiscus discolor*), and vine maple (*Acer circinatum*). Conifer basal areas ranged between 23.9 and 76.2 m² ha⁻¹ with the exception of one plot, dominated by red alder, that had no live conifers. Hardwood basal areas were 0.0–20.2 m² ha⁻¹.

Methods

Locations for 18 plots on BLM lands were randomly selected using their Geographic Information System database. Use of this system enabled us to minimize edge effects by restricting plots to stands ≥ 4 ha. Five more plots on Willamette National Forest lands were placed using criteria to achieve broad characteristics consistent with those of the randomly selected plots (e.g., elevation, stand age, minimum stand area). Plots were square, 35 x 35 m (0.1225 ha). Surveys for presence of bryophytes were limited to two hours per plot. Shrubs and tree boles and branches were surveyed up to two meters in height.

Bryophyte richness was inventoried on eight different substrates: 1) shrubs, 2) hardwood tree bases, 3) conifer bases, 4) logs in early stages of decay (decay classes I & II, Maser et al. 1988), 5) logs in advanced stages of decay (decay classes III–V), 6) humus, including incorporated litterfall, 7) mineral soil, and 8) rock, including soil over rock. Logs in early stages of decay had much intact bark, were at least somewhat elevated above the forest floor by branch stubs, and had wood that remained mostly hard. Logs in advanced stages of decay were largely decorticated, rested in contact with the forest floor, and had wood that was softened from decomposition. These substrates represent the diversity of habitats made available for bryophytes by the compositional and structural heterogeneity that can characterize western Oregon forests.

Two levels of richness are discussed: 1) average plot-level richness (α diversity), and 2) landscape-level richness across all plots (γ diversity). The percentage of bryophyte γ diversity contributed by a substrate type was calculated by divid-

ing the richness (for either mosses or liverworts) found on a substrate across all plots by the γ diversity of either mosses or liverworts.

Regression analyses with untransformed data were used to evaluate associations between bryophyte richness by substrate type and stand age (SPSS 1994). Residual scatter plots were examined for normality and acceptable distribution. Nomenclature for mosses and liverworts follows Anderson et al. (1990) and Stotler and Crandall-Stotler (1977), respectively. Voucher specimens are in the author's herbarium at the University of California, Davis.

Results and Discussion

Eighty-seven bryophyte species were found across the 23 plots: 58 mosses and 29 liverworts (Appendix). Three of the mosses, *Antitrichia curtispindula*, *Buxbaumia viridis*, and *Uloa megalospora*, have been designated for protection in this region through survey and management standards and guidelines (USDA and USDI 1994). The average plot-level bryophyte richness (α diversity) was 32.1 species: 21.7 mosses and 10.4 liverworts (std. errors = 1.52, 1.09, 0.68, respectively).

Decaying Logs and Humus

Logs in advanced stages of decay contributed the greatest average richness of both mosses (10.9 species, std. error = 0.67) and liverworts (6.8 species, std. error = 0.56) to plot-level α diversity (Figure 2). Likewise, the greatest percentage of landscape-level bryophyte richness across all plots (γ diversity) contributed by a substrate type was found on logs in advanced stages of decay (Figure 3, Appendix). Such logs were habitat for 82.8% of all liverwort species and 55.2% of all moss species.

Twenty-six bryophytes (17 mosses, 9 liverworts; 29.9% of γ diversity) were restricted to one substrate type (Figure 4, Appendix). Many of these species are also known to occur on other substrates in the Pacific Northwest (Lawton 1971; Schofield 1976, 1992; Jonsson 1996). The presence of a species on a substrate type may be influenced by its more common occurrence on another nearby type. For example, the establishment of *Neckera douglasii* on humus is commonly associated with its occurrence as an epiphyte in the overstory. Establishment of this and other usually epiphytic

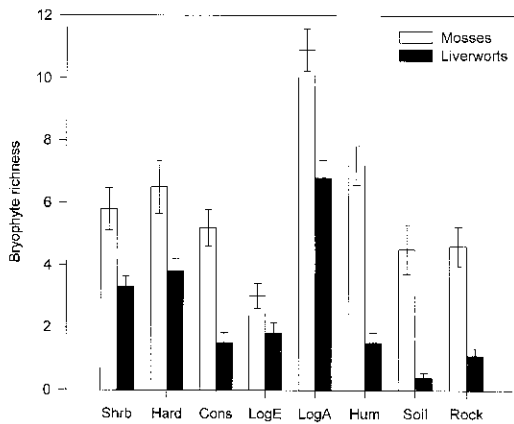


Figure 2. Average moss and liverwort richness contributed by a substrate type, with standard error bars. Shrb = shrubs (20), Hard = hardwoods (17), Cons = conifers (22), LogE = logs in early decay (12), LogA = logs in more advanced decay (21), Hum = humus (23), Soil = mineral soil (17), Rock = rock & soil over rock (19). Parentheses indicate the number of plots in which a substrate occurred ($n = 23$).

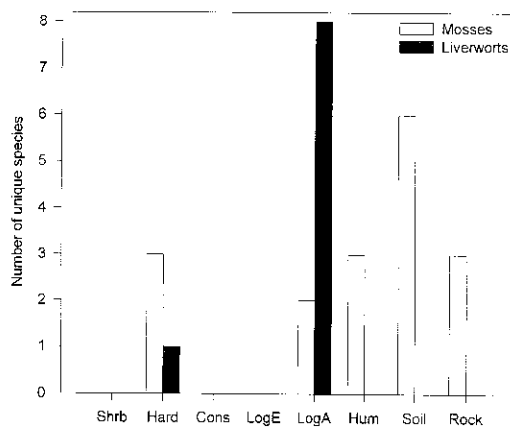


Figure 4. Number of species unique to a substrate type. Shrb = shrubs, Hard = hardwoods, Cons = conifers, LogE = logs in early decay, LogA = logs in more advanced decay, Hum = humus, Soil = mineral soil, Rock = rock & soil over rock.

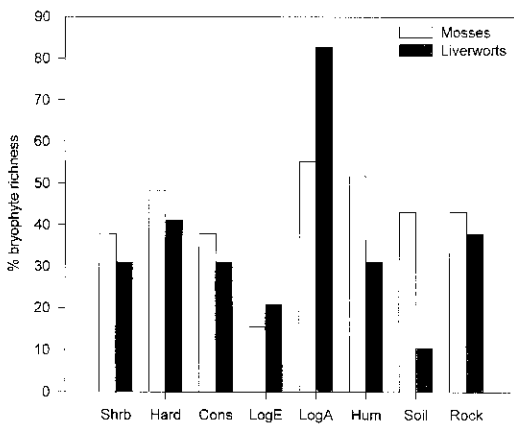


Figure 3. Percentage of bryophyte richness (γ) found on a substrate type across all plots ($n = 23$), calculated by dividing the richness (for either mosses or liverworts) found on a substrate across all plots by the γ diversity of either mosses or liverworts. Shrb = shrubs, Hard = hardwoods, Cons = conifers, LogE = logs in early decay, LogA = logs in more advanced decay, Hum = humus, Soil = mineral soil, Rock = rock & soil over rock.

species on humus or soil in the Pacific Northwest has been previously reported (Peck et al. 1995, Rambo and Muir 1998a). However, we found three mosses only on humus: *Eurhynchium pulchellum*, *Plagiomnium insigne*, and *Trachybryum megaptilum*.

Logs in advanced stages of decay supported the greatest number of species that were unique to a substrate type (Figure 4): two mosses (*Buxbaumia piperi* and *B. viridis*) and eight liverworts (*Calypogeia muelleriana*, *C. suecica*, *Cephalozia bicuspudata*, *Lophozia incisa*, *Plagiochila asplenioides*, *Riccardia latifrons*, *R. palmata*, and *Scapania umbrosa*). Thus, logs in advanced decay had the richest bryophyte flora, and the greatest number of unique bryophytes, and supported the greatest percentage of bryophyte γ diversity of all substrate types. These results are consistent with other studies in Pacific Northwest forests that have found higher bryophyte richness with greater amounts of decaying wood (Jonsson 1997, Rambo and Muir 1998a), and where there was a full range of log decay stages (Rambo and Muir 1998b). Similarly, the abundance of coarse woody debris in all stages of decay was important for bryophyte diversity, especially liverworts, in Swedish forests (Andersson and Hytteborn 1991, Ohlson et al. 1997).

The particular importance of logs in advanced decay for liverwort richness is emphasized by the large number of hepatics found only on this substrate (Figure 4). Decaying logs provide favorable bryophyte substrate and a humid microclimate particularly favorable for hepatics (Gustafsson and Hallingbäck 1988, Andersson and Hytteborn 1991). Logs in advanced stages of decay are generally decorticated, their wood has become spongy,

and they are in close contact with the forest floor. Such characteristics enable these logs to absorb and retain moisture better than logs in earlier stages of decay, thus increasing available moisture for cryptogams. More decayed wood is also better able to buffer the humidity of its microenvironment during periods without precipitation, and influences the general forest environment by contributing to more equable stand humidity (Franklin et al. 1981).

Regression analysis did not show a significant correlation between stand age and bryophyte richness on logs in advanced decay ($P = 0.26$). However, greater availability of this substrate favors liverworts (Söderström 1988a), and decaying wood generally accumulates as stands age (Bingham and Sawyer 1991, Franklin et al. 1981). Decaying wood-associated bryophytes, especially liverworts, differentiated old growth from young stands in western Oregon (Rambo and Muir 1998b), and other published accounts have also found more bryophytes and rare epixylic liverworts associated with old growth than with young, managed stands (e.g., Gustafsson and Hallingbäck 1988, Söderström 1988b, Lesica et al. 1991).

Sample and plot sizes in this study may have been too small to allow demonstration of a significant relationship between stand age and richness on decaying logs. Of the four plots in stands older than 170 years, one had no logs in advanced decay. Western Oregon forests can have continuity without major disturbance for 1,000 years and only be initiating development of old-growth characteristics at 200 years (Spies and Franklin 1988, Norse 1990). The few 200 year-old stands in this study likely did not have enough time for development of the bryophyte richness associated with old-growth stands in other studies (e.g., Gustafsson and Hallingbäck 1988, Söderström 1988b, Lesica et al. 1991, Rambo and Muir 1998a). Stand continuity without major disturbance promotes diversity of dispersal-limited organisms by allowing more time for their successful colonization and establishment (Edwards 1986). Forest floor bryophytes generally have limited dispersal abilities (Khanna 1964, Crum 1972, Söderström 1987).

Hardwoods

Of the three epiphytic substrates, only hardwoods contributed unique species to γ diversity (Figure 4). Three mosses (*Homalothecium aeneum*,

Metaneckera menziesii, and *Orthotrichum striatum*) and one liverwort (*Porella cordaeana*) were only found on hardwood tree bases. Hardwood tree bases also had higher average moss and liverwort richness (Figure 2), and were habitat for a higher percentage of landscape-level richness (Figure 3) than shrubs or conifer tree bases.

In a prior study in western Oregon, forest floor bryophyte richness increased with the diversity and number of hardwoods present (Rambo and Muir 1998a). This was attributed to hardwood-associated epiphytic bryophytes that were either temporarily incorporated into the ground layer via litterfall, or established in the humus. Hardwoods also influence their environment through variations in light, leachate nutrients, and pH of precipitation throughfall, all of which potentially affect bryophyte communities.

Rocks and Mineral Soil

Rocks contributed three unique mosses to γ diversity: *Brachythecium frigidum*, *Heterocladium procurrens*, and *Racomitrium obesum*. Tree uprooting exposes rocks and mineral soil in the resulting tip-up mounds and pits (Beatty and Stone 1986, Jonsson and Esseen 1990). Such habitats were important for maintaining high bryophyte diversity in a Swedish boreal forest, doubling the bryophyte diversity compared to undisturbed forest matrix (Jonsson and Esseen 1990). Infrequent rock substrate, apparently exposed by mechanical disturbance from logging operations, also contributed appreciably to bryophyte richness in western Oregon forests, especially for mosses (Rambo and Muir 1998a).

Mineral soil stands out as the substrate that contributed the greatest number of unique mosses to γ diversity (Figure 4). Six acrocarpous mosses were found only on mineral soil: *Bryum capillare*, *Dicranella heteromalla*, *D. varia*, *Polytrichum juniperinum*, *P. longisetum*, and *Timmiella crassinervis*. In mature Scots pine (*Pinus sylvestris*) stands in the Netherlands, pioneer acrocarpous mosses were negatively affected by litter accumulation. Moss community composition changed when soil was exposed by removing litter and humus layers, with an increase in pioneer species and an accompanying decrease in species characteristic of later seral communities (DeVries et al. 1995). Similarly, disturbance by litter raking changed moss community composition in a

Norway spruce (*Picea abies*) stand in southwest Finland (Lindholm and Nummelin 1983).

Bryophyte richness on mineral soil was positively correlated with stand age ($r^2 = 0.40$, $P = 0.006$). Bryophytes dependent upon temporary habitats, such as mineral soil or decaying logs, must continuously disperse to newly generated habitat as their former ones degrade (Söderström 1993). In order for such species to colonize new, suitable habitat, it must be within their effective dispersal range. With relatively limited dispersal abilities, many forest floor pioneer bryophytes depend upon disturbances of low to intermediate intensity and frequency to furnish a continuing supply of nearby habitats suitable for colonization. As these habitats degrade over time, they host intermediate-seral bryophyte communities. Long-term forest continuity provides the time necessary for both successful colonization by dispersal-limited species and development of the disturbance-generated habitat heterogeneity upon which they depend.

Evidence from other studies supports the role that moderate disturbance plays in enhancing bryophyte diversity (e.g., Jonsson and Esseen 1990). For example, low to moderate severity wind disturbance enhances forest structural and habitat diversity by converting green trees to snags and coarse woody debris, and by exposing soil and rocks from tree uprooting. Such features are often found more commonly in old growth than in managed stands (Hansen et al. 1991). A comparison of mature (100-150 yrs) and old-growth (> 200 yrs) Douglas-fir and western hemlock stands in western Oregon found that tree mortality by uprooting was more than twice as common in the old growth (Spies et al. 1990). In another comparison between young (55 yrs) and old-growth stands (> 400 yrs) in western Oregon forests, four mosses occurring on mineral soil of root tip-ups were restricted to the old growth (Rambo and Muir 1998a). Bryophyte diversity on a riparian cliff in southwestern Wisconsin similarly increased with the amount of patchiness caused by flooding, with highest diversities at moderate levels of flood disturbance (Kimmerer and Allen 1982). Bryophyte richness in riparian areas of a western Oregon forest also peaked where soil disturbance from flooding was moderate in intensity (Jonsson 1997). Such examples are consistent with the intermediate disturbance hypothesis, which suggests that

highest levels of diversity are maintained at intermediate scales of disturbance (Connell 1978).

To optimize bryophyte richness in young, managed stands, structural and compositional features characteristic of older stands should be maintained and fostered when harvesting timber. The importance of decaying wood to other forest ecosystem components in the Pacific Northwest has been well established. This study shows that logs in advanced stages of decay are also particularly important for bryophyte richness. Forest management should encourage and protect unique habitats such as decaying logs, hardwood trees, and rock outcrops. Additionally, retention of some mature overstory conifers will ensure future treefall disturbance, contributing a continuing supply of coarse woody debris to the forest floor, and creating patches of disturbed mineral soil and rocks, thus renewing temporary habitats critical for many bryophyte species. Retention of such biological and structural legacies in young, managed stands would contribute towards forest management from an ecosystem approach by fostering habitat complexity and bryophyte diversity in the course of harvesting timber.

This work provides insights into those structural characteristics of older forests that may be of particular importance to bryophyte diversity. However, inferences are limited by the number of stands sampled. More region-wide analyses of this type are needed to elaborate and strengthen these insights, and improve ecological understanding of bryophytes and their habitat requirements. Federally mandated protection of late successional-associated species makes the gathering of such information all the more important.

Acknowledgements

Jeri Peck contributed greatly to the research and analysis; only her modesty kept her from being co-author. Funding was provided through a cost-share agreement between the Oregon State office of the Bureau of Land Management (BLM) and Oregon State University. Nancy Wogen of the Eugene District, BLM, Jenny Dimling of the Willamette National Forest, and Patricia Muir of Oregon State University were instrumental in arranging this agreement and providing other assistance. Thanks also to Patricia Muir, Jeri Peck, and Steve Sillett for constructive criticisms of earlier drafts.

Literature Cited

- Acharya, A. 1996. Forest loss continues. Pages 122-123 *In* L. Starke (editor), *Vital Signs 1996*, W. W. Norton & Co., New York, USA.
- Anderson, L. E., H. A. Crum, and W. R. Buck. 1990. List of the mosses of North America north of Mexico. *Bryologist* 93:448-499.
- Andersson, L. I., and H. Hyttborn. 1991. Bryophytes and decaying wood - a comparison between managed and natural forest. *Holarctic Ecology* 14:121-130.
- Beatty, S. W., and E. L. Stone. 1986. The variety of soil microsites created by tree falls. *Canadian Journal of Forest Research* 16:539-548.
- Berg, Å., B. Ehnström, L. Gustafsson, T. Hallingbäck, M. Jonsell, and J. Weslien. 1993. Threatened plant, animal, and fungus species in Swedish forests: distributions and habitat associations. *Conservation Biology* 8:718-731.
- Bingham, B. B., and J. O. Sawyer, Jr. 1991. Distinctive features and definitions of young, mature, and old-growth Douglas-fir/hardwood forests. USDA Forest Service General Technical Report PNW-GTR-285. Pacific Northwest Research Station, Portland, Oregon.
- Christy, J. A. 1992. Global perspective on endangered bryophytes. *Northwest Science* 66:129.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310.
- Crum, H. 1972. The geographic origins of the mosses of North America's eastern deciduous forest. *Journal of Hattori Botanical Laboratory* 35:269-298.
- De Vries, B. W. L., E. Jansen, H. F. Van Dobben, and Th. W. Kuyper. 1995. Partial restoration of fungal and plant species diversity by removal of litter and humus layers in stands of Scots pine in the Netherlands. *Biodiversity and Conservation* 4:156-164.
- Dudley, N. 1992. *Forests in Trouble: a Review of the Status of Temperate Forests Worldwide*. WWF (World Wide Fund for Nature), Gland, Switzerland.
- Edwards, M. E. 1986. Disturbance histories of four Snowdonian woodlands and their relation to Atlantic bryophyte distributions. *Biological Conservation* 37:301-320.
- Esseen, P. -A., B. Ehnström, L. Ericson, and K. Sjöberg. 1992. Boreal forests - the focal habitats of Fennoscandia. Pages 252-325 *In* L. Hansson (editor), *Ecological Principles of Nature Conservation*. Elsevier Science Publishers, New York, USA.
- FEMAT (Forest Ecosystem Management Assessment Team). 1993. *Forest ecosystem management: an ecological, economic, and social assessment*. U.S. Government Printing Office, Washington D.C.
- Franklin, J. 1989. Toward a new forestry. *American Forests* 95:37-44.
- Franklin, J. F., and T. A. Spies. 1991. Composition, function, and structure of old-growth Douglas-fir forests. USDA Forest Service General Technical Report PNW-GTR-285. Pacific Northwest Research Station, Portland, Oregon.
- Franklin, J. F., K. Cromack, Jr., W. Denison, A. Mckee, C. Maser, J. Sedell, F. Swanson, and G. Juday. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA Forest Service General Technical Report PNW-GTR-118. Pacific Northwest Research Station, Portland, Oregon.
- Gustafsson, L., and T. Hallingbäck. 1988. Bryophyte flora and vegetation of managed and virgin coniferous forests in South-West Sweden. *Biological Conservation* 44:283-300.
- Gustafsson, L., A. Fiskesjö, T. Hallingbäck, T. Ingelög, and B. Pettersson. 1992. Semi-natural deciduous broadleaved woods in southern Sweden - habitat factors of importance to some bryophyte species. *Biological Conservation* 59:175-181.
- Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests: lessons from natural forests. *BioScience* 41:382-392.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133-302.
- Harris, L. D. 1984. *The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity*. University of Chicago Press, Chicago, USA.
- Jonsson, B. G. 1996. Riparian bryophytes of the H. J. Andrews Experimental Forest in the Western Cascades, Oregon. *Bryologist* 99:226-235.
- Jonsson, B. G. 1997. Riparian bryophyte vegetation in the Cascade mountain range, Northwest U.S.A.: patterns at different spatial scales. *Canadian Journal of Botany* 75:744-761.
- Jonsson, B. G., and P. -A. Esseen. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. *Journal of Ecology* 78:924-936.
- Khanna, K. R. 1964. Differential evolutionary activity in bryophytes. *Evolution* 18:652-670.
- Kimmerer, R. W., and T. F. H. Allen. 1982. The role of disturbance in the pattern of a riparian bryophyte community. *American Midland Naturalist* 107:370-383.
- Lawton, E. 1971. *Moss Flora of the Pacific Northwest*. Hattori Botanical Laboratory, Tokyo, Japan.
- Lec, T. D., and G. H. La Roi. 1979. Gradient analysis of bryophytes in Jasper National Park, Alberta. *Canadian Journal of Botany* 57:914-925.
- Lesica, P., B. McCune, and W. S. Hong. 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. *Canadian Journal of Botany* 69:1745-1755.
- Lindholm, T., and M. Nummelin. 1983. Changes in the community structure of forest floor vegetation after repeated litter disturbance by raking. *Silva Fennica* 17:289-300.

- Maser, C., R. G. Anderson, K. Cromack, Jr., J. T. Williams, and R. E. Martin. 1979. Dead and down woody material. Pages 78-95 In J. W. Thomas (editor), *Wildlife Habitats in Managed Forests the Blue Mountains of Oregon and Washington*. Agriculture Handbook 553. USDA Forest Service, Wildlife Management Institute, and USDI Bureau of Land Management, Washington D.C.
- Maser, C., R. F. Tarrant, J. M. Trappe, and J. F. Franklin. 1988. From the forest to the sea: a story of fallen trees. USDA Forest Service General Technical Report PNW-GTR-229. Pacific Northwest Research Station, Portland, Oregon.
- McComb, W. C., T. A. Spies, and W. H. Emmingham. 1993. Douglas-fir forests: managing for timber and mature-forest habitat. *Journal of Forestry* 91:31-42.
- Norse, E. A. 1990. *Ancient Forests of the Pacific Northwest*. Island Press, Washington D.C., USA.
- Ohlson, M., L. Söderström, G. Hörnberg, O. Zackrisson, and J. Hermansson. 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. *Biological Conservation* 81:221-231.
- Owenby, J. R., and D. S. Ezell. 1992. Monthly Station Normals of Temperature, Precipitation, and Heating and Cooling Degree Days 1961-1990 Oregon. *Climatography of the United States* 81. U.S. Department of Commerce, NOAA, National Climatic Data Center, Ashville, North Carolina.
- Peck, J. E., S. A. Acker, and W. A. McKee. 1995. Autecology of mosses in coniferous forests in the central western Cascades of Oregon. *Northwest Science* 69:184-190.
- Rambo, T. R., and P. S. Muir. 1998a. Forest floor bryophytes of *Pseudotsuga menziesii*-*Tsuga heterophylla* stands in Oregon: influences of substrate and overstory. *Bryologist* 101:116-130.
- Rambo, T. R., and P. S. Muir. 1998b. Bryophyte species associations with coarse woody debris and stand ages in Oregon. *Bryologist* 101:366-376.
- Schofield, W. B. 1976. Bryophytes of British Columbia III: habitat and distributional information for selected mosses. *Syesis* 9:317-354.
- Schofield, W. B. 1992. *Some Common Mosses of British Columbia*. Royal British Columbia Museum, Victoria, B.C., Canada
- Slack, N. G. 1977. Species diversity and community structure in bryophytes: New York State studies. *New York State Museum Bulletin* 428.
- Söderström, L. 1987. Dispersal as a limiting factor for distribution among epixylic bryophytes. *Symposia Biologia Hungarica* 35:475-483.
- Söderström, L. 1988a. The occurrence of epixylic bryophytes and lichen species in an old natural and a managed forest stand in northeast Sweden. *Biological Conservation* 45:169-178.
- Söderström, L. 1988b. Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in Northern Sweden. *Nordic Journal of Botany* 8:89-97.
- Söderström, L. 1993. Substrate preference in some forest bryophytes: a quantitative study. *Linbergia* 18:98-103.
- Spies, T. A., and J. F. Franklin. 1988. Old growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. *Natural Areas Journal* 8:190-201.
- Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69:1689-1702.
- Spies, T. A., J. F. Franklin, and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Canadian Journal of Forest Research* 20:649-658.
- SPSS. 1994. *SPSS for Windows, Ver. 6.1*. SPSS, Inc.
- Stotler, R., and B. Crandall-Stotler. 1977. A checklist of the liverworts and hornworts of North America. *Bryologist* 80:405-428.
- Thomas, J. W., and H. Salwasser. 1989. Bringing conservation biology into a position of influence in natural resource management. *Conservation Biology* 3:123-127.
- 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*. 1994-589-111/00001. U.S. Government Printing Office, Washington D.C.
- Wilcove, D. S. 1989. Protecting biodiversity in multiple-use lands: lessons from the U.S. Forest Service. *Trends in Ecology and Evolution* 4:385-388.

Received 24 January 2000

Accepted for publication 27 March 2001