American Institute of Biological Sciences

OXFORD JOURNALS
OXFORD UNIVERSITY PRESS

Conserving Biodiversity in Managed Forests
Author(s): A. J. Hansen, T. A. Spies, F. J. Swanson and J. L. Ohmann
Source: *BioScience*, Vol. 41, No. 6 (Jun., 1991), pp. 382-392
Published by: Oxford University Press on behalf of the American Institute of Biological Sciences
Stable URL: http://www.jstor.org/stable/1311745
Accessed: 11-03-2016 17:23 UTC

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

American Institute of Biological Sciences and Oxford University Press are collaborating with JSTOR to digitize, preserve and extend access to *BioScience*.

http://www.jstor.org

This content downloaded from 142.103.160.110 on Fri, 11 Mar 2016 17:23:14 UTC
All use subject to JSTOR Terms and Conditions

Conserving Biodiversity in Managed Forests

Lessons from natural forests

A. J. Hansen, T. A. Spies, F. J. Swanson, and J. L. Ohmann

Consensus is emerging among ecologists that biological diversity will not be conserved effectively in natural reserves alone (Wilcove 1989). The existing reserve network is too small, major expansion is unlikely, and barriers to migration make species in reserves especially vulnerable to global climate change (Westman 1990). Therefore, Harris (1984) recommends that the reserves be complemented with a matrix of "seminatural" lands where ecological principles are used to manage both for commodity production and conservation of species diversity. The challenge now is to design and effectively manage such multipurpose landscapes (Franklin et al. 1986, Hunter 1990).

The expanse of federal forest lands in the coastal northwest United States provides an opportunity to conserve diversity in forests that also are used for wood production. Much of this land in Washington, Oregon, and northern California west of the Cascade Mountain crest remains in unmanaged forest that includes old growth—the late stage of forest development characterized by large trees, numerous snags, and abundant woody debris (Franklin et al. 1981). Old-growth forests provide important habitat for late-seral organisms such as the spotted owl (*Strix occidental*; Gutierrez and Carey 1985). An acrimonious debate rages in the Coastal Northwest over how much of the ancient forest should be preserved and how much harvested. Concern over the continued loss of old growth has stimulated many research and conservation efforts (Franklin et al. 1981, Ruggerio et al. in press).

Natural disturbance maintains structural complexity, promoting plant and animal diversity

The results of recent studies (Ruggerio et al. in press), however, raise questions on the extent to which old growth differs in forest structure and species composition from younger natural forests. These studies suggest that we should broaden the research and conservation focus from old growth to natural forests of all ages. Moreover, to evaluate the compatibility of resource extraction and conservation of native species diversity on federal lands, comparisons of natural forests and plantations managed for wood production are necessary. These are the key questions to be addressed:

- Are plantations managed intensively for wood production more uniform in tree species, size, and spacing than are natural forests?
- Do these plantations offer less habitat diversity and support fewer species than do natural forests?
- Is the fragmentation of remaining natural forests likely to reduce biodiversity even further in natural stands?

In this article, we review patterns of disturbance and succession in natural forests in the Coastal Northwest and compare structure and composition across an age gradient of unmanaged stands. Stand and landscape patterns in managed forests are then examined and compared with those in natural forests. We draw on the results to offer guidance on the management of Coastal Northwest forests that are dedicated to both wood production and conservation of biodiversity. Finally, we suggest that the lessons learned from natural forests here may be useful in other biomes, where unmanaged forests are rare and standards for designing seminatural forests are not available.

Natural forests

Disturbance and succession in natural forests. The traditional model of forest dynamics for the Coastal Northwest (Franklin and Dyrness 1973) begins with catastrophic disturbance leading to a phase dominated by

A. J. Hansen is an assistant professor in wildlife habitat ecology in the Forest Science Department, Hatfield Marine Science Center, Oregon State University, Newport, OR 97365. T. A. Spies is a plant ecologist, F. J. Swanson is a research geologist, and J. L. Ohmann is a research forester at the USDA Forest Service Forestry Sciences Laboratory in Corvallis, OR 97331. The authors are all interested in the effects of natural disturbance and human activities on forest structure, composition, and productivity.

This content downloaded from 142.103.160.110 on Fri, 11 Mar 2016 17:23:14 UTC
All use subject to JSTOR Terms and Conditions

herbs and shrubs (0–20 years; Alaback 1982, Long 1977). Shade-intolerant conifers soon establish and the young forest stage (20–80 years) of rapid tree growth persists from canopy closure until stand maturity (Franklin et al. 1981). The mature stage (80–200 years) occurs between the time when annual growth rate reaches its maximum and the development of old-growth characteristics. In the absence of catastrophic disturbance, succession may continue for more than 750 years as shade-tolerant coniferous species replace pioneering species. According to this view of succession, structural complexity builds over time and thus is better developed in old growth than in younger seral stages.

The pattern of catastrophic disturbance by fire and windthrow frequently observed in the Northwest (Franklin and Forman 1987) lends support to this successional direction. Before human fire suppression, the mean rotation interval for stand-replacement fires was 435 years in Mount Rainier National Park (Hemstrom and Franklin 1982) and 150–276 years in the central Oregon Cascades (Morrison and Swanson 1990, Teensma 1987). Most of the natural fires were uneven in intensity. Morrison and Swanson (1990), for example, found that severely burned patches ranged from 0.2 to 100 ha, with 86% of the patches covering less than 16 ha in a study site in the Oregon Cascades.

These disturbance rates were sufficient to leave a strong imprint on landscape pattern. In Mount Rainier National Park, for example, stands less than 200 years old now cover 27% of the forest area and stands more than 600 years old cover 23% (Hemstrom and Franklin 1982). The remaining 50% is made up of stands 200–600 years old. In six national forests in Western Oregon and Washington, stands from 80 to 200 years of age comprise 32% of the natural forest (Morrison 1988). Catastrophic disturbances clearly were prevalent in natural northwest landscapes, but their variable frequencies and sizes produced a mosaic of stands of differing age and size.

However, modification of the traditional model of forest dynamics is needed to account for the influence of low-severity disturbances on forest structure. Recent studies show that events such as individual tree deaths and low-intensity fires occur in northwest forests at least as frequently as catastrophic events (Morrison and Swanson 1990, Spies et al. in press). Teensma (1987), for example, found a mean fire-return interval in the west central Cascades of Oregon of 166 years for partial or total stand-replacement fires and 114 years for all fires, including low-severity fires. Low- to moderate-severity events strongly influence forest structure by changing canopy trees into snags and downed logs (Spies et al. 1990). They also create canopy openings and/or bare soils and provide opportunities for suppressed trees and early successional herbs and shrubs (Miles and Swanson 1986), enhancing structural and species diversity within all natural forest stages (Morrison and Swanson 1990, Spies et al. 1988).

Refinement of the traditional model of forest dynamics is also necessitated because even severe disturbances do not destroy all remnants of the previous stand (Franklin et al. 1985). On a study site in the Oregon Cascades, for example, mortality of canopy trees was less than 70% in 57–69% of the area burned from 1800 to 1900 (Morrison and Swanson 1990). Trees, snags, and logs surviving a serious disturbance are incorporated into the subsequent stand, which thereby retains structural complexity (Figure 1). Trees dying before or during a catastrophic disturbance, for example, are the primary source of coarse woody debris in regenerating stands for the first hundred years or more (Spies et al. 1988). Because large trees and woody debris best survive disturbance, old growth is likely to contribute a greater structural legacy (Franklin et al. 1985) to post-disturbance stands than are young or mature forests.

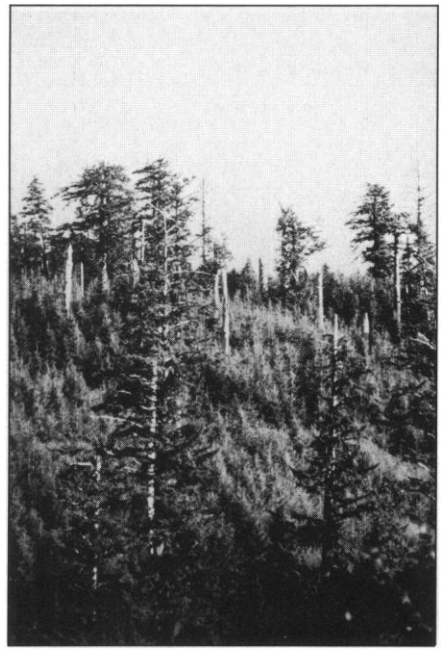


Figure 1. Old-growth trees and snags often persist through natural disturbances in Coastal Northwest forests, creating complex structural patterns and diverse habitats even in young natural stands. This hillslope experienced a wildfire 30–40 years ago. Photo by Andrew Hansen.

Thus both low- and high-severity disturbances are important agents of forest development in northwest forests. Because these disturbances influence all natural seral stages and because structural elements persist through disturbances, it is reasonable to hypothesize that young and old natural stands have structural similarities and that many types of organisms occupy the full forest sere.

Stand structure across natural forest seres. The most comprehensive effort to quantify vegetation patterns across age classes in natural forest in the Coastal Northwest has been that of the USDA Forest Service's Old-Growth Wildlife Habitat Research Program (OGWHRP; Ruggiero et al. in press). As part of this program, Spies and Franklin (in press) sampled 196 natural young (40–80 years), mature (80–200 years), and old-growth (more than 200 years) Douglas fir stands in western Oregon and Washington. (It is important to note that the study avoided young and mature stands composed of two or more widely separated age classes of Douglas fir trees. Consequently, the results are not representative of all young and mature natural stands across the region, many of which arose after patchy fires that left large live trees.)

The study showed that several measures of forest structure—abundance of large trees, variation in tree size, and abundance of understory plants—were positively associated with forest age (Table 1). Coarse woody debris,

This content downloaded from 142.103.160.110 on Fri, 11 Mar 2016 17:23:14 UTC
All use subject to JSTOR Terms and Conditions

Table 1. Comparison of natural, young, mature, and old-growth forests in western Oregon and Washington (n = 196). Data are means unless otherwise noted. All values are significantly different ($p < .05$) except those followed by the same letter.—indicates that data are not available.

Characteristic	Age class		
	Young (40–80 yrs)	Mature (80–200 yrs)	Old growth (>200 yrs)
Tree size*			
Density of Douglas fir >100 cm dbh† (number/ha)	0.5	2.5	19
Standard deviation of tree dbh (cm)	12	22	32
Canopy and understory structure*			
Density of subcanopy tree saplings (number/ha)	14	11	53
% cover deciduous shrubs	6.8	8.9	12
% cover herbs	2.5	5.1	6.4
Coefficient of variation of herb cover	81	80	75
% area occupied by gaps‡	—	18	13
Snags§			
Snag volume (m^3/ha)	175a	101	221a
Snag density (number/ha)	171	121	60
Density of snags >50 cm dbh and >15 m tall (number/ha)	2.8b	2.5b	6.4
Logs§			
Log volume (m^3/ha)	248c	148	313c
Log density (number/ha)	600	447d	415d
Density of logs >60 cm dbh (number/ha)	53ef	28e	59f

*From Spies and Franklin (in press).
†dbh = diameter at breast height
‡From Spies et al. (1990).
§From Spies et al. (1988).

however, was generally most abundant in young and old forest stages. Snag density was negatively associated with stand age, and snag volume was not significantly different between young and old-growth stands. Similarly, log density was highest in young stands, whereas log volume did not differ significantly between young and old-growth samples. Large snags were more prevalent in old stands, but large logs were not.

These results indicate that old-growth Douglas fir forests exhibit several structural features that distinguish them from younger natural stands. It is important, however, that many of the youngest forests contain an abundance of snags and fallen trees equivalent to, or higher than, those in old-growth forests, evidence of the structural legacy from the pre-disturbance condition. The presence of structural features such as snags and fallen trees promotes biological diversity. The similarities found between old and young forests in tree size and canopy structure may have been greater if regenerating stands with remnant live trees had been included in this study.

Native plant and vertebrate diversity. Forest structure underlies habitat factors such as microclimate, food abundance, and cover that affect organism fitness (Cody 1985). Hence strong correlations often exist between animal community composition and forest structure (Urban and Smith 1989). Several studies, most associated with OGWHRP (Ruggiero et al. in press), have determined the composition of vascular plant, fungi, amphibian, reptile, small-mammal, and bird communities in natural Douglas fir forests in the Coastal Northwest.

Contrary to earlier thinking, these studies showed relatively few strong differences in plant and animal communities among unmanaged young (25–80 years), mature (80–200 years), and old-growth (more than 200 years) forests (Table 2). In general, species richness was not significantly different among these forest stages. Diversity, a more sensitive measure of community composition, was quantified for vascular plants and was generally highest in old growth (Spies in press; not shown in Table 2). Total abundances of taxonomic groups sometimes differed among forest age classes. For example, fungi were most abundant in mature stands (Luoma 1988), small mammals in the Oregon Cascades reach peak levels in young and mature stands (Anthony et al. 1987), and birds wintering in the Washington Cascades were most abundant in old growth (Manuwal and Huff 1987).

Community overlap, the proportion of species not showing significant differences in abundance among forest stages, ranged from 56% for trees in the Washington Cascades (Spies in press) and herpetofauna in northwest California (Welsh and Lind 1988) to 91% for understory plants in Oregon (Spies in press). Less community overlap was found by Nelson (1988). Most species that did differ were most abundant in old growth, but several species reached peak levels in young or mature stands. Relatively few species used old growth exclusively. In summarizing the OGWHRP results, Carey (1989) concluded that nine species plus two groups (*Myotis* bats and cavity-nesting birds) were either dependent on or closely associated with old growth.

Nelson's (1988) work on cavity-nesting birds in the Oregon Coast Range differs from most other OGWHRP studies in finding that species richness and individual species abundances were often highest in old growth (Table 2). A possible explanation is that populations of cavity-nesting birds in young and mature stands in the Oregon Coast Range may be limited by the lower snag abundance in all age classes there compared with that in the Cascades (Spies et al. 1988).

These findings on species composition in natural forests must be interpreted with caution. Organism abundance, the sole measure used in these studies, may be a poor indicator of habitat preference (Van Horne 1983). A species may be abundant in habitats that confer relatively low fitness if immigration rates are high enough.

This content downloaded from 142.103.160.110 on Fri, 11 Mar 2016 17:23:14 UTC
All use subject to JSTOR Terms and Conditions

To the extent that these findings reflect the habitat preferences of the organisms sampled, they suggest that there are many similarities in plant and vertebrate animal communities among closed-canopy age classes of natural forests. Although some species are strongly associated with only one of these forest stages, the majority of plant and vertebrate animal species in the region are relatively equally distributed among unmanaged young, mature, and old-growth Douglas fir forests.

A likely explanation for the similarity in species distribution is that the structural differences among these natural forest stages are insufficient to strongly influence most species of plants and animals. The natural disturbance regime and structural legacy

Table 2. Comparison of compositional characteristics of plant and vertebrate animal communities among natural young (25–80 years), mature (80–200 years), and old-growth (>200 years) Douglas fir forests in the Coastal Northwest. Most of the studies are either preliminary or final publications of the USDA Forest Service Old-Growth Wildlife Habitat Research Program (Ruggiero et al. in press). — indicates that data are not available or the variable is not applicable to the study.

Study	Location*	Number of sites	Subdivision	Number of species†	Difference in species richness‡	Difference in total abundance§	Community overlap‖	Number of species associated with each age class¶		
								Young	Mature	Old-growth
Vascular plants										
Spies (in press)	W	45	Overstory	9	NS	—	56%	0	1	3
			Understory	126	NS	—	86%	5	4	6
	OC	63	Overstory	16	NS	—	81%	0	1	2
			Understory	173	NS	—	91%	5	7	5
	OCR	36	Overstory	9	O>M	—	78%	0	1	4
			Understory	98	NS	—	91%	1	0	8
Fungi										
Luoma (1988)¶	OC	10	—	47	—	M>O>Y#	—	7#	3#	8#
Amphibians and reptiles										
Raphael (1984)**	C	46	Amphibians	12	NS	M>O>Y	—	—	—	—
			Reptiles	15	Y>O	—	—	—	—	—
Bury and Corn (1988)	W, OC	30	—	18 (5)	NS	—	80%	0	0	1
Welsh and Lind (1988)	SO, C	42	—	25 (9)	NS	O>Y	56%	0	0	4
Small mammals										
Raphael (1984)**	C	46	—	29	NS	—	—	—	—	—
Anthony et al. (1987)††	OC	12	—	16 (5)	NS	Y+M>O	60%	1	0	1
Taylor et al. (1988)	C	47	—	23 (5)	—	—	80%	0	0	1
Corn et al. (1988)	W, OC	30	—	27 (9)	NS	NS	89%	1	0	0
Birds										
Raphael (1984)**	C	46	Winter	94	NS	NS	—	—	—	—
	C		Spring		NS	NS	—	—	—	—
Anthony et al. (1984)††	OC	12	Winter	19 (7)	NS	—	86%	1	0	0
			Summer	39 (21)	NS	—	71%	2	1	3
Manuwal and Huff (1987)	W	16	Winter	15 (13)	NS	O>Y	69%	0	1	3
			Spring	46 (45)	NS	NS	65%	7	2	6
Nelson 1988††	OCR	47	1985	16 (8)	O>Y	—	38%	0	0	5
			1986	15 (8)	O>Y	—	25%	0	0	6

*W, Southern Washington Cascades; OC, Oregon Cascades; OCR, Oregon Coast Range; C, Northwest California; SO, Southwest Oregon.
†Number of species used in analyses of richness and total abundance, with the number used to calculate community overlap in parentheses if different.
‡All relationships are significant at p = .05 unless noted as not significant (NS). O, old-growth stands; M, mature stands; Y, young stands.
§Proportion of species that do not differ significantly in abundance between forest age classes. Species occurring too infrequently to allow statistical analyses are omitted.
‖Only species differing significantly in abundance among forest age classes are included.
¶Fruiting bodies of hypogeous ectomycorrhizal fungi were studied.
#Statistical significance not determined.
**Age classes are: young (50–150 years); mature (150–250 years); old-growth (>250 years).
††R. B. Anthony, G. A. Green, E. D. Forsman, S. K. Nelson, 1984, unpublished report. USDA Forest Service, Olympia, WA. The young forest sites originated after clearcutting.
‡‡Five of the 18 young and mature sites resulted from clearcutting.

This content downloaded from 142.103.160.110 on Fri, 11 Mar 2016 17:23:14 UTC
All use subject to JSTOR Terms and Conditions

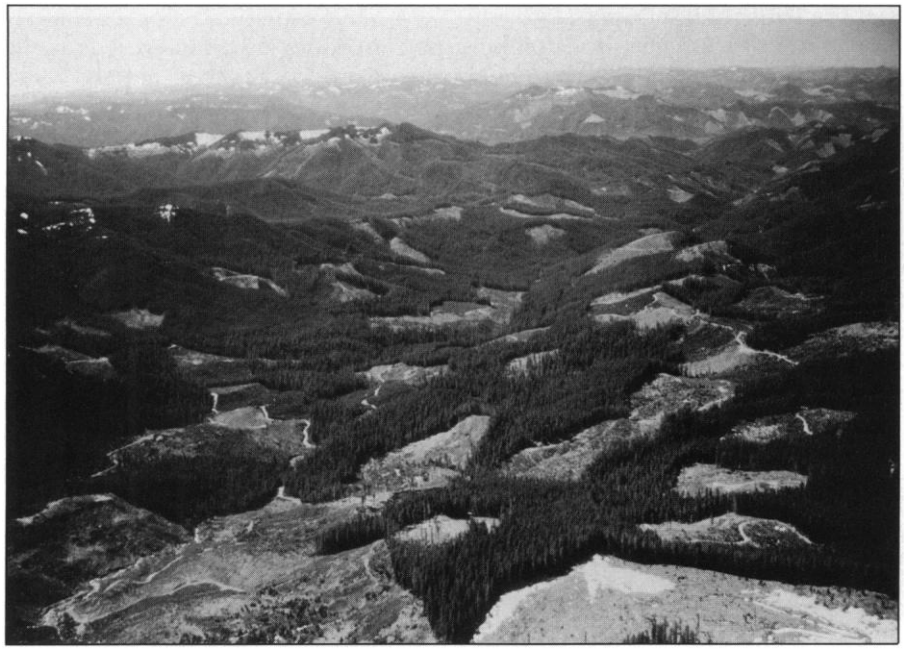


Figure 2. The staggered-setting harvest design, typical on federal lands in Coastal Northwest forests, strongly influences landscape patterning. Photo by Al Levno.

in all closed-canopy age classes of natural forest apparently provide the resources and habitats required by many species. The important conclusion is that the canopy structures, snag densities, and levels of fallen trees found in unmanaged young, mature, and old-growth stands appear to make all three of these seral stages suitable habitat for most species of forest plants and vertebrate animals.

One stage of development in natural Douglas-fir forests appears to be distinctive in structure and composition from those mentioned so far. It is the herb/shrub stage (0–20 years) that follows severe natural disturbance. Studies of clear-cuts indicate that plant and animal diversity is as high before canopy closure as at any time thereafter (Long 1977, Schoonmaker and McKey 1988). High diversity occurs especially when snags and downed logs are present (Marcot 1985) and thus is likely to be even more pronounced in naturally disturbed patches than in clear-cut patches. Many of the species that appear after natural disturbance or clearcutting specialize in early successional habitats, and a few are rarely found in closed-canopy forests (Gashwiler 1970, Long 1977). Thus the early successional herb/shrub seral stage has a structure and composition that differs substantially from all older forest stages, a fact that should be considered in forest management.

Managed forest

Across much of the Coastal Northwest, natural disturbance has largely been supplanted by human activities, such as timber harvesting and reforestation. Forest management practices across the region vary substantially with ownership, management objectives, and other factors. Intensive management of plantations for wood production typically involves some or all of the following: clearcutting all trees and snags; prescribed burning and/or use of herbicides to control competing vegetation; replanting with a single species; periodic thinning to maintain vigorous, evenly spaced crop trees; and harvesting at 50–100 year intervals (Franklin et al. 1986). At the landscape level, cutting units on federal lands are generally staggered in space and harvested at a constant rate, thus maintaining a uniform mosaic of stand sizes and ages (Franklin and Forman 1987). Natural disturbances such as fire and insect outbreak are often suppressed in managed forests, and landscape patterns are largely shaped by timber management activities.

Current data do not allow rigorous comparison of disturbance regimes in plantations managed intensively for wood production and natural forests in the region. Management practices probably differ from natural disturbances both in mean range and variance; management activities are likely to be more frequent and intense and less variable. Within plantations, the management regime is likely to reduce structural legacy and produce managed plantations that are relatively uniform in tree species, size, and spacing. To the extent that these management strategies are successful, managed plantations will lack the multilayered canopy, diverse tree sizes, and abundant snags and fallen trees that exist in natural forests.

Timber management regimes may also produce differing landscape patterns than do natural disturbances. The uniform size and spacing of harvest units under the staggered-setting design used on federal lands contrasts with the more variable mosaic typical of natural landscapes (Figure 2). Also, the edges of harvest units are probably straighter, more abrupt, and of higher contrast than the edges of naturally disturbed patches (Franklin and Forman 1987). A possible consequence of the staggered-setting design is increased fragmentation of the natural forest matrix and a reduction of natural forest interior habitats. Hence processes and organisms associated with sharp, high-contrast forest edges may be favored over those dependent on natural forest interiors.

Habitat patterns in managed forests. Nature may not entirely concede to silvicultural plans. Environmental gradients and uncontrolled natural disturbance may enhance habitat heterogeneity in managed forest landscapes. Moreover, forest landscapes encompass diverse ownerships with various management objectives and practices. These factors may produce considerable variation within and among stands, even in areas where intensive forest management prevails. We are aware of no studies in the Coastal Northwest that rigorously compare within-stand structure of managed and natural forests of similar age.

However, some insights on large tree and large snag abundances within natural and managed stands

This content downloaded from 142.103.160.110 on Fri, 11 Mar 2016 17:23:14 UTC
All use subject to JSTOR Terms and Conditions

can be gained from the continuing work of the Forest Inventory and Analysis Project of the USDA Forest Service (Ohmann 1990). Project participants have evaluated more than 900 permanent plots on nonfederal forest lands in western Oregon. We analyzed data from north of latitude 43° N by comparing the densities of large trees and large snags in 220 plots that showed either no evidence of harvest or evidence of being clear-cut at least once. The large tree and large snag size classes in this study were identical to those used in the Old Growth Definition Task Group (1986) definition of old growth. Sites were stratified by age class, and sites with stands less than 40 years old were excluded because unharvested plots were few in number and limited in spatial distribution.

Large trees and large snags (more than 50.8 cm diameter at 1.37 m and more than 4.6 m tall) were each three to five times more dense in the unharvested plots than in clear-cut plots for the 40–79 and 80–200 year age classes. The differences were statistically significant (Wilcoxon rank sums, $p < .05$). But these data should be viewed with caution because assessment of cutting history in the field may have been inaccurate, the mean age of samples in the 80–200-year age class was higher in the unharvested plots (121 years) than in the clear-cut plots (98 years), and logging practices used before 1950 differ from those of today. To the extent that these limitations do not strongly influence the results, the data indicate that clear-cutting substantially reduces structural complexity. Furthermore, the large trees and large snags that remained in the clear-cut plots are a legacy from the preharvest condition, and they will not be replenished under current practices for maximal wood production.

The continued loss of coarse woody debris under successive cycles of clear-cutting was modeled by Spies and Cline (1988). They predicted that snag and log abundances would be 30% of the preharvest level at the end of the first 100-year rotation and 6% after the second.

The influence of timber management on forest patterns at the landscape level was studied by Ripple et al. (in press). They mapped natural and managed forest at 15 sites (1750 ha each) on National Forest lands in the west Cascades of Oregon for the years 1972 and 1987. Individual cutting units averaged 19.5 ha in 1972 and 16.2 ha in 1987 and were dispersed regularly over the sites. The proportion of the area in clear-cuts was 9.5% in 1972 and 18.2% in 1987, a twofold increase. The area of natural forest interior decreased by 18% during this period (assuming an edge width of 100 m). These data verify that natural stands on some public lands are being fragmented substantially by timber harvest, even where cutting units make up less than 20% of the landscape.

Fragmentation of natural forest is much more acute outside of the national forests. Only 6% of nonfederal forest lands in western Oregon remain in large sawtimber or old-growth forest (Ohmann et al. 1988). For comparison, more than 50% of the federal lands studied by Rosenberg and Raphael (1986) and Lehmkuhl and colleagues (in press) contained later seral stages.

Animal communities in managed stands. Current data also are insufficient for direct comparison of animal and plant assemblages in natural and managed Douglas-fir forests of similar age. The best available information comes from an ongoing study in the Oregon Coast Range of breeding birds, small mammals, and amphibians in closed-canopy, Douglas fir plantation (25–30 years) and natural mature forest (90–140 years).[1] First-year results showed that species richness for the three taxonomic groups combined was slightly higher in natural forest than in managed forest, but the difference was not statistically significant. Total abundance of birds was 50% higher, and amphibians 130% higher, in natural forests than in plantations. Both differences were statistically significant. Total mammal abundance did not differ significantly between the two habitats. Among all three groups, 11 species reached significantly higher abundances in the forest, whereas only 2 species were most abundant in the plantation. The proportion of species not differing significantly between the two habitats was 41%.

The extent to which these findings are due to dissimilarity in stand age rather than to management history is not known. However, the animal com-

[1]A. J. Hansen and J. R. Peterson, 1989, unpublished data. Hatfield Marine Science Center, Oregon State University, Newport, OR.

Figure 3. The varied thrush (*Ixoreus naevius*) appears to be associated with forest interior habitats and may be sensitive to forest fragmentation. Photo by Donald Waite.

This content downloaded from 142.103.160.110 on Fri, 11 Mar 2016 17:23:14 UTC
All use subject to JSTOR Terms and Conditions

munities in these two stand types were generally less alike than those in young natural forest and old growth (Table 2), suggesting that the results are not due to differences in stand age alone.

Inferences on the similarities of animal communities in natural and managed forests can be drawn based on the microhabitat requirements of various groups of organisms. Many animals in Douglas fir forests are strongly associated with habitat features that are best developed in natural forest, such as large trees, snags, and downed logs. The diversity and density of cavity-nesting birds, for example, are positively correlated with the abundance of snags, especially tall and/or large-diameter snags (Nelson 1988, Zarnowitz and Manuwal 1985). Schreiber (1987) found that cavity-nesters comprised approximately 30% of the bird species in clear-cuts with some snags remaining in the Oregon Coast Range. Six of these species did not breed in clear-cuts with insufficient snag levels. Similarly, several species of birds, mammals, and amphibians are associated with large live trees and downed logs (Ruggiero et al. in press). These data make a strong case for the hypothesis that animal species diversity and abundance are considerably lower in intensively managed plantations than in natural forests.

Animal responses to landscape patterns. The landscape patterns unique to managed forests may also exert strong influence on animal communities (Hansen et al. in press). The few landscape-level studies done thus far in the Coastal Northwest have focused on distribution of seral stages and forest fragmentation.

The current 50- to 100-year harvest intervals in the region raise concern that viable populations of species requiring late successional habitats will be lost from managed landscapes (Harris 1984). This concern appears to be justified; Forsman (1989) found that spotted owl densities were extremely low in the northern Oregon Coast Range where young managed forests predominate. Densities there were 5–18 times lower than in landscapes composed of natural mature and old-growth forest.

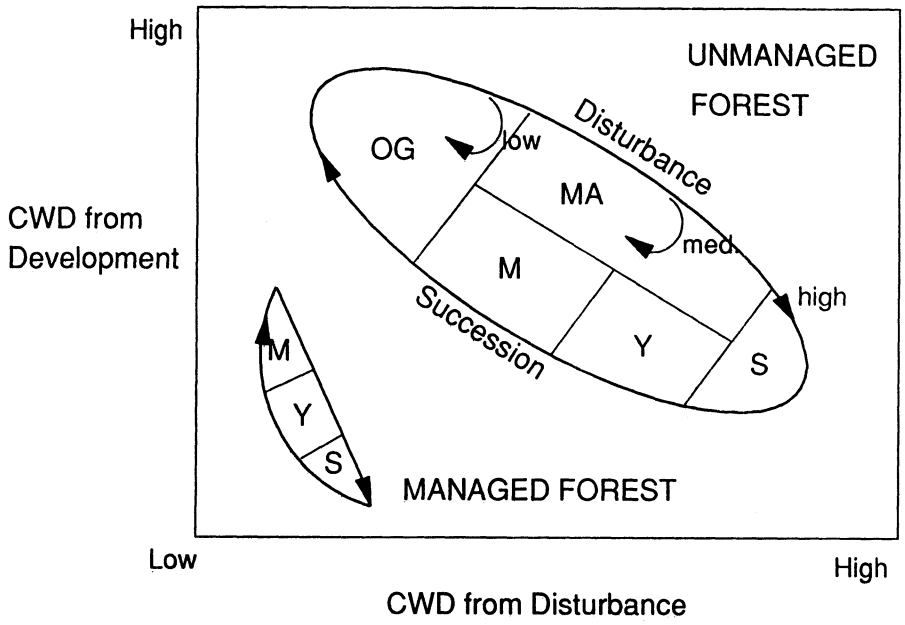


Figure 4. Conceptual model of the dynamics of coarse woody debris (CWD) in unmanaged forest and in plantations managed intensively for fiber production. In both natural forest and plantations, CWD resulting from forest development (via establishment, growth, and senescence) increases during succession, whereas CWD produced by previous disturbance decays. This trend is reversed as disturbances such as fire convert living biomass to CWD and reduce the CWD resulting from development. Disturbances of high severity produce more CWD than low-severity disturbances. Total CWD is lower in managed than in unmanaged forests because harvest truncates structural development well before large amounts of CWD can accumulate and because most snags and fallen trees are removed from harvest sites, unlike in the case of naturally disturbed patches, where most CWD remains at the site. The domains of the shrub (S), young (Y), mature (M), old-growth (OG), and mixed-age (MA) seral stages are depicted.

The effects of fragmentation of natural Northwest forests on wildlife diversity are not yet clear. Ongoing studies of natural forest/clear-cut edges by Hansen et al.[2] indicate that some bird species in the Oregon Coast range do specialize on interior habitats (Figure 3). Of the species sampled, 11% were more abundant in forest interior than near the forest edge, and 22% had higher densities in clear-cut interiors than at clear-cut edges. Total bird density was significantly higher in forest and clear-cut interiors than at the stand edges. These findings suggest that some animal species in the region are responsive to patch size, with some probably sensitive to fragmentation of natural forests.

Similarly, Rosenburg and Raphael (1986) found that relative abundances of several animal species in northwest California were related to natural forest area and isolation of natural forest patches. The relative abundances of 18% of bird, 9% of herpetile, and none of the mammal species were positively correlated with stand area. Animals in these stands were also influenced by proximity to clear-cuts; the abundances of 14% of species were positively and 12% negatively correlated with area of surrounding clear-cuts. Species richness within natural stands was not significantly related to degree of fragmentation of the surrounding landscape. Presumably, the loss of species sensitive to fragmentation was offset by gains in species benefiting by adjacency to clear-cuts. Lehmkuhl et al. (in press) reported similar results for the southern Washington Cascades. Both studies were on lands less than 50% cut over and the authors predicted that animal species richness will eventually fall as fragmentation continues and organisms that depend on natural forest decline.

Altering the forest cycle

In summary, existing data, although certainly not conclusive, suggest that

[2]See footnote 1.

This content downloaded from 142.103.160.110 on Fri, 11 Mar 2016 17:23:14 UTC
All use subject to JSTOR Terms and Conditions

forests managed intensively for wood production differ from natural forests in structure and species composition. Our analysis of USDA Forest Service inventory data found that large trees and large snags were more abundant in natural forests than in managed stands. We speculate that natural stands of all ages often have greater structural complexity than managed plantations (Figure 4). The period between catastrophic disturbances is often long enough in natural forests to allow development of large trees, snags, and fallen trees typical of old growth. Furthermore, some of these large structures survive catastrophic events and enhance the structural richness of naturally regenerating stands.

It is the cycle of structural development through plant growth, and the retention of structural complexity via legacy, that characterizes natural forests in the Coastal Northwest. Intensive wood production practices may alter this cycle both by truncating succession before large structures develop and by removing most existing structures during harvest. Planting and thinning may further promote uniformity in tree species, size, and spacing.

Managed forests of federal lands are also relatively uniform at the landscape level. Stand size, shape, and dispersion are probably less variable in managed than in unmanaged forest (Ripple et al. in press), which results in a greater number of sharp, high-contrast edges and increasing fragmentation of natural forest.

Not surprisingly, some vertebrates respond strongly to these forest changes. Some animals may be more abundant in managed forests, but several species appear to be substantially less abundant there than in natural forests.[3] This outcome is predictable based on the strong affinities many species have for habitat features typical of natural forests. The studies reviewed here suggest that the availability of microhabitat features in managed plantations is below the levels required by many vertebrate species, whereas natural closed-canopy stands of all ages exceed this threshold level. Thus species requiring these habitat features are likely to be lost in managed forests but persist in natural forests. No native species, on the other hand, are known to depend on closed-canopy managed forest. Some animals in natural forests are at risk if the stands are fragmented by timber harvest (Lehmkuhl et al. in press, Rosenburg and Raphael 1986).

Guidelines for multiple-use lands

The objectives of forest managers differ substantially among ownerships and geographic locations. The conservation of biological diversity is a high priority in some settings and a low priority in others. Even where consideration of biodiversity is mandated by law (e.g., US national forests), there is uncertainty over difficult questions such as what constitutes a minimal viable population size and what proportion of a species range should be maintained in suitable habitats (Wilcove 1989). We now explore the implications of our findings for those lands used both for wood production and conservation of biodiversity. Drawing on knowledge from natural forests, we offer a few general guidelines on ways to maintain biodiversity in such multiple-use lands.

Studies in unmanaged forests teach us that natural disturbance maintains structural complexity within stands and that this complexity promotes plant and animal diversity. Intensive

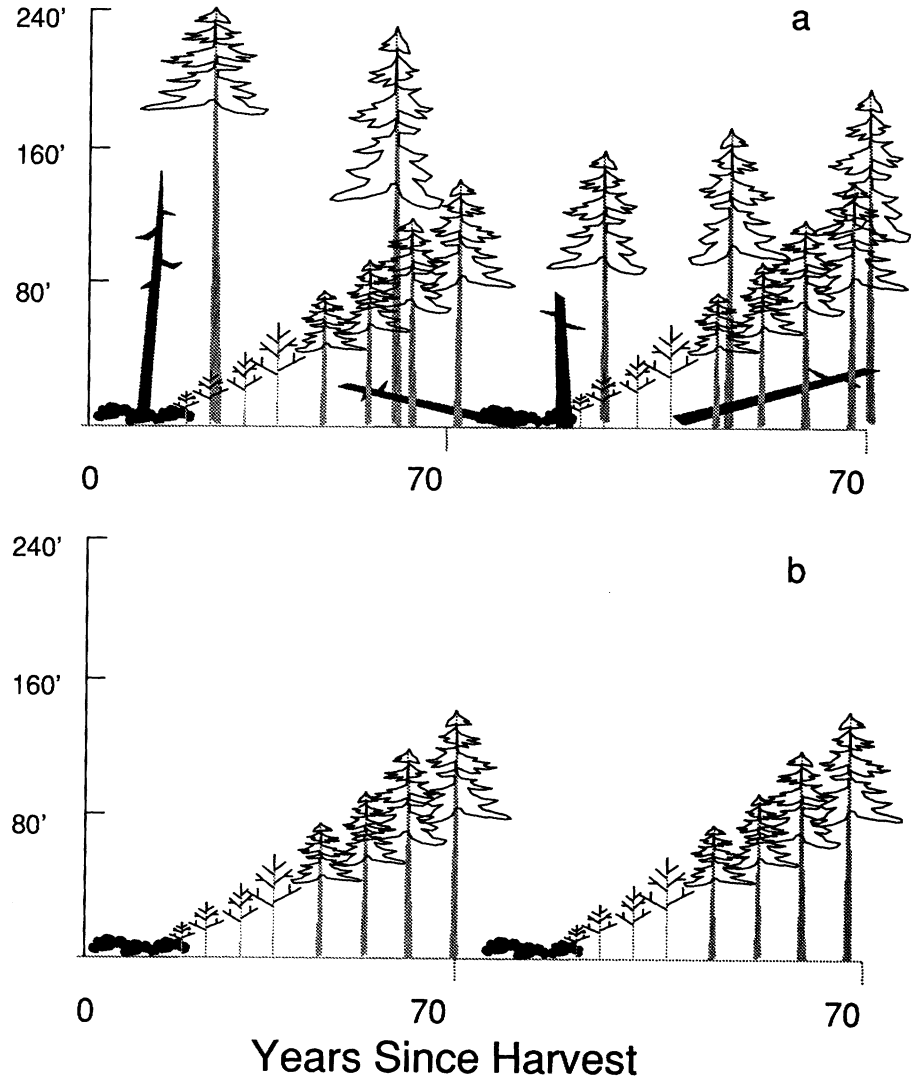


Figure 5. Comparison of idealized development in stands designed for (**a**) both structural diversity and wood production and (**b**) maximum wood production. Traditional management practices for maximizing wood production in Coastal Northwest forests create plantations that are relatively simple in structure and habitat diversity. Practices that better mimic natural forest patterns are being developed for lands dedicated to both wood production and the maintenance of biological diversity.

[3]See footnote 1.

This content downloaded from 142.103.160.110 on Fri, 11 Mar 2016 17:23:14 UTC
All use subject to JSTOR Terms and Conditions

Figure 6. A timber harvest unit in the Willamette National Forest, Oregon, designed to mimic the rich structural patterns typical of natural forests. Although many fallen trees were retained in this unit, log removal had not been completed when this picture was taken. Photo by Andrew Hansen.

timber management appears to constrain the contribution of structural elements from older to younger stands. Where maintenance of diversity is a goal, ways must be found to enrich forest structure within managed stands (Figure 5). Techniques for developing structurally diverse, mixed-species stands are mentioned in silviculture texts (Smith 1986), but they have not been widely adopted in management.

Attention to structural complexity is a core concept of the "new forestry" now being advocated in the Coastal Northwest (Franklin 1989, Gillis 1990). Many federal land managers are currently leaving live trees, snags, and fallen trees in clear-cuts to serve as habitat (Figure 6). Much more work is needed to adapt silvicultural techniques that extend the structural domain of managed plantations to resemble that in natural forests (Figure 1). This goal involves both retaining structural legacy from the preharvest stand and producing new large trees, snags, and fallen trees over the course of forest development.

Another lesson from natural forests is that old growth is only one of the common natural seral stages, and each stage provides important and/or critical habitats to some plants and animals. Retaining these species in managed forests may require that a full suite of seral stages be provided across the landscape. Current practices on federal lands both reduce the duration of the herb/shrub stage and remove mature and old-growth stages and are thus likely to reduce native species diversity. Research is needed on the temporal and spatial patterning of seral stages that is required by native species.

Finally, comparisons between natural and managed forests teach us that native species diversity is influenced by the size, distribution, edge characteristics, and dispersion of stands across landscapes. Knowledge of the relationships between the demography of individual species and spatial patterning of habitats is meager at present. Nonetheless, some federal land managers in the Northwest are beginning to experiment with harvest patterns designed to minimize forest fragmentation (Franklin 1989). Such landscape-scale experiments can provide information to help guide forest management.

Some federal agencies are continuing to develop coordinated research and management programs to conserve species diversity on public forest lands (Wilcove 1989). We suggest that additional work is needed on the stand- and landscape-level habitat requirements of native species in various types of private and public managed and unmanaged forests. This research should include both descriptive studies of existing landscapes with diverse structural configurations and manipulative studies that evaluate traditional and new forest-management strategies. Information on tree growth, long-term site productivity, plant and animal communities, and implementation costs under different management systems should be collected simultaneously.

These data can be used to classify organisms into groups (guilds) that use similar habitats and to map habitat suitability for each guild within a planning area. Alternative management scenarios can then be evaluated with regard to their potential effects both on plant and animal communities and on the productivity of other resources. With such information, managers would be able to choose silvicultural strategies that optimize commodity and conservation objectives. This approach is now being used for conservation of spotted owls on federal lands in the northwest.

"New forestry" continues to be developed and evaluated in the Northwest. It has not yet been proven effective in integrating wood production and conservation of biodiversity. Until it is clear that forests managed for wood production can be made suitable for native species, managers should consider retaining within managed forests representative tracts of all natural forest stages, not just old growth.

Restrictions on the harvest of old growth have put additional pressure on the remaining young and mature natural forests in the Coastal Northwest. The value of younger natural stands for conservation of biodiversity is often underestimated. The fact that species richness in natural forests in the region is more strongly related to elevation and latitude than to stand age (Ruggiero et al. in press) suggests that younger natural forests at low elevations in northern California and southern Oregon may support higher diversity than old-growth stands at higher elevations and latitudes.

Conservation strategies should take into account such regional gradients

This content downloaded from 142.103.160.110 on Fri, 11 Mar 2016 17:23:14 UTC
All use subject to JSTOR Terms and Conditions

when setting priorities for retention of natural stands. The locations and age distributions of natural forests on federal lands in the Northwest are currently being inventoried. This information, along with data on habitat needs of sensitive plant and animal species, can be used to determine the sizes of locations of natural forest tracts that should be reserved for species conservation.

Additionally, it is important to emphasize that under current fire-control policies, the natural postfire herb/shrub stage, rich both in structural complexity and in species, brush is probably the least common seral stage in the region. The rarity of this seral stage should be a consideration before salvage logging after wildfire or blow-down and thereby reducing the structural complexity of this important habitat type.

These guidelines for managing biodiversity do, of course, have social and economic implications. Retaining large trees in cutting units, extending rotation ages to provide later successional habitats, and removing some natural stands from the harvest base will undoubtedly reduce timber outputs. Also, adequate research on managing biodiversity will require substantial funding. These costs may be offset by social, economic, and ecological benefits associated with these strategies (Franklin 1989, Perry et al. 1989). Land managers and, ultimately, society must decide how best to optimize these costs and benefits.

Finally, we suggest that these lessons are not unique to the Pacific Northwest. They are probably also evident in other biomes where natural forests are undergoing harvest. The roles of biological legacy, stand structural richness, and landscape diversity may now be much less visible in regions where natural forests no longer remain. Undoubtedly, the influence of these factors on species diversity varies among biomes, and local research is needed. Nonetheless, it is reasonable to speculate that management strategies based on ecological relationships can help to maintain and/or revive native species biodiversity in any biome. The challenge of a new forestry that provides both commodity production and species conservation rests with forests managers and conservationists everywhere.

Acknowledgments

Helpful comments on drafts of the manuscript were made by K. Aubry, D. Hibbs, S. Hobbs, W. McComb, T. McMahon, and L. Norris. L. Melton drew Figure 5 and M. Berg typed the tables. This contribution is from the Coastal Oregon Productivity Enhancement Program, College of Forestry, Oregon State University and the National Science Foundation–sponsored Long-Term Ecological Research program at the H. J. Andrews Experimental Forest (BSR85-14325).

References cited

Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce–western hemlock forests of southeast Alaska. *Ecology* 63: 1932–1948.

Anthony, R. G., E. D. Forsman, G. A. Green, G. Wiemer, and S. K. Nelson. 1987. Small mammal populations in riparian zones of different-aged coniferous forests. *Murrelet* 68: 94–102.

Bury, R. B., and P. S. Corn. 1988. Douglas-fir forests in the Oregon and Washington Cascades: relation of the herpetofauna to stand age and moisture. Pages 11–22 in R. C. Szaro, K. E. Severson, and D. R. Patton, eds. *Proceedings of a Symposium, Management of Amphibians, Reptiles, and Small Mammals in North America.* Flagstaff, AZ, 19–21 July 1988. USDA Forest Service General Technical Report RM-166, Ft. Collins, CO.

Carey, A. B. 1989. Wildlife associated with old-growth forests in the Pacific Northwest. *Nat. Areas J.* 9: 151–162.

Cody, M. L. 1985. An introduction to habitat selection in birds. Pages 4–46 in M. L. Cody, ed. *Habitat Selection in Birds.* Academic Press, Orlando, FL.

Corn, P. S., R. B. Bury, and T. A. Spies. 1988. Douglas-fir forests in the Cascade Mountains of Oregon and Washington: is the abundance of small mammals related to stand age and moisture? Pages 340–352 in R. C. Szaro, K. E. Severson, and D. R. Patton, eds. *Proceedings of a Symposium, Management of Amphibians, Reptiles, and Small Mammals in North America.* Flagstaff, AZ, 19–21 July 1988. USDA Forest Service General Technical Report RM-166, Ft. Collins, CO.

Forsman, E. D. 1989. A survey of spotted owls in young forests in the northern coast range of Oregon. *Murrelet* 69: 65–68.

Franklin, J. 1989. Towards a new forestry. *Am. For.* November/December: 37–44.

Franklin, J. F., K. Cromack, 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, Portland, OR.

Franklin, J. F., and C. T. Dyrness. 1973. *Natural Vegetation of Oregon and Washington.* Oregon State University Press, Corvallis.

Franklin, J. F., and R. T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Lands. Ecol.* 1: 5–18.

Franklin, J. F., J. A. MacMahon, F. J. Swanson, and J. R. Sedell. 1985. Ecosystem responses to the eruption of Mount St. Helens. *Natl. Geogr. Res.* 1: 198–216.

Franklin, J. F., T. Spies, D. Perry, M. Harmon, and A. McKee. 1986. Modifying Douglas-fir management regimes for nontimber objectives. Pages 373–379 in C. D. Oliver, D. P. Hanley, and J. A. Johnson, eds. *Modifying Douglas-fir Management Regimes for Nontimber Objectives.* USDA Forest Service, Seattle, WA.

Gashwiler, J. S. 1970. Plant and mammal changes on a clearcut in west-central Oregon. *Ecology* 51: 1018–1026.

Gillis, A. M. 1990. The new forestry. *BioScience* 40: 558–562.

Gutierrez, R. J., and A. B. Carey, eds. 1985. *Ecology and Management of the Spotted Owl in the Pacific Northwest.* USDA Forest Service General Technical Report PNW-185, Portland, OR.

Hansen, A. J., D. L. Urban, and B. Marks. In press. The effects of vertebrate life history traits and landscape patterns on bird community dynamics. In F. di Castri and A. J. Hansen, eds. *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows.* Springer-Verlag, New York.

Harris, L. D. 1984. *The Fragmented Forest.* University of Chicago Press, Chicago.

Hemstrom, M. A., and J. F. Franklin. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. *Quat. Res.* 18: 32–51.

Hunter, M. L. 1990. *Wildlife, Forests and Forestry: Principles of Managing Forests for Biological Diversity.* Prentice Hall, Englewood Cliffs, NJ.

Lehmkuhl, J. F., L. F. Ruggiero, and P. A. Hall. In press. Landscape-level patterns of wildlife richness and abundance in the Pacific Northwest. In L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, eds. *Wildlife Habitat Relationships in Old-Growth Douglas-fir Forests.* USDA Forest Service General Technical Report PNW-GTR, Portland, OR.

Long, J. N. 1977. Trends in plant species diversity associated with development in a series of *Pseudotsuga menziesii/Gaultheria shallon* stands. *Northwest Sci.* 51: 119–130.

Luoma, D. L. 1988. Biomass and community structure of sporocarps formed by hypogeous ectomycorrhizal fungi within selected forest habitats of the H. J. Andrews Experimental Forest, Oregon. Ph.D. dissertation Oregon State University, Corvallis.

Manuwal, D. A., and M. H. Huff. 1987. Spring and winter bird populations in a Douglas-fir forest sere. *J. Wildl. Manage.* 51: 586–595.

Marcot, B. G. 1985. Habitat relationships of birds and young-growth Douglas-fir in northwestern California. Ph.D. dissertation, Oregon State University, Corvallis.

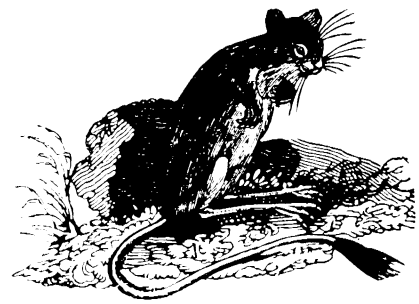
Miles, D. W. R., and F. J. Swanson. 1986. Vegetation composition on recent landslides in the Cascade Mountains of western Oregon. *Can. J. For. Res.* 16: 739–744.

Morrison, P. H. 1988. *Old Growth in the Pacific Northwest: A Status Report.* The Wilderness Society, Washington, DC.

Morrison, P. H., and F. J. Swanson. 1990. *Fire History and Pattern in a Cascade Mountain*

This content downloaded from 142.103.160.110 on Fri, 11 Mar 2016 17:23:14 UTC
All use subject to JSTOR Terms and Conditions

Landscape. USDA Forest Service General Technical Report PNW-GTR-254, Portland, OR.
Nelson, S. K. 1988. Habitat use and densities of cavity nesting birds in the Oregon coast ranges. Masters dissertation, Oregon State University, Corvallis.
Ohmann, J. L. 1990. Multiresource inventories in the Pacific Coast states—progress and future direction. Pages 529–537 in V. J. LaBau and T. Cunia, eds. *Proceedings for the Symposium on the State-of-the-Art Methodology of Forest Inventory*. USDA Forest Service General Technical Report PNW-GTR-263, Portland, OR.
Ohmann, J. L., D. Carleson, P. L. Lee, and A. L. Oakley. 1988. Status of forest-related wildlife and fish resources in Oregon. Pages 17–32 in G. J. Lettman, ed. *Assessment of Oregon's Forests*. Oregon State Department of Forestry, Salem.
Old Growth Definition Task Group. 1986. *Interim Definitions for Old-Growth Douglas-fir and Mixed-Conifer Forests in the Pacific Northwest and California*. USDA Forest Service Research Note PNW-447, Portland, OR.
Perry, D. A., M. P. Amaranthus, J. G. Borchers, S. L. Borchers, and R. E. Brainerd. 1989. Bootstrapping in ecosystems. *BioScience* 39: 230–237.
Raphael, M. G. 1984. Wildlife populations in relation to stand age and area in Douglas-fir forests of northwestern California. Pages 259–273 in W. R. Meehan, T. R. Merrell Jr., and T. A. Hanley, eds. *Fish and Wildlife Relationships in Old-Growth Forests*. American Institute of Fishery Research Biologists, Morehead City, NC.
Ripple, W. J., G. A. Bradshaw, and T. A. Spies. In press. Measuring forest fragmentation in the Cascade Range of Oregon. *Biol. Conserv.*
Rosenberg, K. V., and M. G. Raphael. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. Pages 263–272 in J. Verner, M. L. Morrision, and C. J. Ralph, eds. *Wildlife 2000*. University of Wisconsin Press, Madison.
Ruggiero, L., K. B. Aubry, A. B. Carey, and M. H. Huff. In press. Old-growth Douglas-fir forests: wildlife communities and habitat relationships. In *Old-Growth Douglas-fir Forests: Wildlife Communities and Habitat Relationships*. USDA Forest Service General Technical Report PNW-GTR, Portland, OR.
Schoonmaker, P., and A. McKee. 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. *For. Sci.* 34: 960–979.
Schreiber, B. 1987. Diurnal bird use of snags on clearcuts in central coastal Oregon. Masters dissertation, Oregon State University, Corvallis, OR.
Smith, D. M. 1986. *The Practice of Silviculture*. John Wiley & Sons, New York.
Spies, T. A. In press. Plant species diversity and occurrence in young, mature and old-growth Douglas-fir stands in western Oregon and Washington. In L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, eds. *Wildlife Habitat Relationships in Old-Growth Douglas-Fir Forests*. USDA Forest Service General Technical Report PNW-GTR, Portland, OR.
Spies, T. A., and S. P. Cline. 1988. Coarse woody debris in forests and plantations of coastal Oregon. Pages 5–23 in C. Maser, R. F. Tarrant, J. M. Trappe, and J. F. Franklin, eds. *From the Forest to the Sea: A Story of Fallen Trees*. USDA Forest Service General Technical Report PNW-GTR-229, Portland, OR.
Spies, T. A., and J. F. Franklin. In press. The structure of young, mature, and old-growth forests in Oregon and Washington. In L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, eds. *Wildlife Habitat Relationships in Old-Growth Douglas-Fir Forests*. USDA Forest Service General Technical Report PNW-GTR, Portland, OR.
Spies, T. A., J. F. Franklin, and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Can. J. For. Res.* 20: 649–658.
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.
Taylor, C. A., C. J. Ralph, and A. T. Doyle. 1988. Differences in the ability of vegetation models to predict small mammal abundance in different aged Douglas-fir forests. Pages 368–374 in R. C. Szaro, K. E. Severson, and D. R. Patton, eds. *Management of Amphibians, Reptiles, and Small Mammals in North America*. USDA Forest Service General Technical Report RM-166, Ft. Collins, CO.
Teensma, P. D. A. 1987. Fire history and fire regimes of the central western Cascades of Oregon. Ph.D. dissertation, University of Oregon, Eugene.
Urban, D. L., and T. M. Smith. 1989. Microhabitat pattern and the structure of forest bird communities. *Am. Nat.* 133: 811–829.
Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* 47: 893–901.
Welsh, H. H., and A. J. Lind. 1988. Old growth forests and the distribution of the terrestrial herpetofauna. Pages 439–455 in R. C. Szaro, K. E. Severson, and D. R. Patton, eds. *Management of Amphibians, Reptiles, and Small Mammals in North America*. USDA Forest Service General Technical Report RM-166, Ft. Collins, CO.
Westman, W. E. 1990. Managing for biodiversity. *BioScience* 40: 26–33.
Wilcove, D. S. 1989. Protecting biodiversity in multiple-use lands: lessons from the US Forest Service. *Trends Ecol. Evol.* 4: 385–388.
Zarnowitz, J. E., and D. A. Manuwal. 1985. The effects of forest management on cavity-nesting birds in northwestern Washington. *J. Wildl. Manage.* 49: 255–263.



This content downloaded from 142.103.160.110 on Fri, 11 Mar 2016 17:23:14 UTC
All use subject to JSTOR Terms and Conditions