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PLANT SPECIES DIVERSITY IN NATURAL AND MANAGED FORESTS OF THE PACIFIC NORTHWEST[1,2]

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Abstract. With the exception of the tropics, nowhere has the relationship between resource management and conservation of biological diversity been more controversial than in the Pacific Northwest region of the United States. Widespread loss and fragmentation of old-growth ecosystems have stimulated critical review and revision of existing forest management policies. However, studies of the consequences of forest management for plant species diversity are sorely lacking. We present data from permanent-plot and chronosequence studies in managed and unmanaged forests of western Oregon and Washington to describe the early responses of understory communities to forest harvest, and to suggest how post-harvest practices that alter natural successional processes may influence long-term patterns of diversity and species occurrence.

Permanent-plot studies of early succession in old-growth *Pseudotsuga* forests suggest that changes in understory diversity are fairly short-lived following clear-cut logging and slash burning. Populations of most vascular plant species recover to original levels prior to canopy closure. However, diversity may remain depressed for more than two decades on severely burned sites, and some species may experience local extinction. Evidence of the effects of post-harvest practices on vascular plant diversity is limited by an absence of community-level studies in older, managed forests.

Chronosequence studies of natural forest stands indicate that, following canopy closure, vascular plant species diversity tends to increase with time, peaking in old growth. Few understory species are restricted to, or absent from, any stage of stand development (i.e., young, mature, or old growth). However, many species differ significantly in their abundance among stages. A majority of these showed greatest abundance in old growth. Changes in levels of resources (increased shade), changes in the spatial variability of resources and environments (increased horizontal and vertical heterogeneity), and species' sensitivity to fire and slow rates of reestablishment/growth may drive these trends during natural stand development.

Silvicultural prescriptions that maintain or foster spatial and temporal diversity of resources and environments will be most effective in maintaining plant species diversity. Practices associated with intensive, short-rotation plantation forestry, that preclude or delay the development of old-growth attributes, may result in long-term loss of diversity. Ultimately, it may be necessary to manage some stands on long rotations (150–300 yr) to maintain understory species that require long periods to recover from disturbance.

Key words: disturbance; diversity; forest management; forest structure; logging; old growth; overstory; Pseudotsuga menziesii; *species heterogeneity; species richness; succession; understory.*

INTRODUCTION

The correlates and causes of species diversity have long intrigued naturalists and ecologists (e.g., Darwin 1859, Clements 1916, Hutchinson 1959, Huston 1979, May 1988). Countless studies have considered patterns of diversity at spatial scales ranging from metre-square plots to latitudinal gradients, and at temporal scales ranging from seasonal changes to geologic or evolutionary time. Numerous conceptual models have been developed that offer mechanistic explanations for the pattern and maintenance of diversity (e.g., MacArthur and Wilson 1963, Grubb 1977, Connell 1978, Huston 1979, Menge and Sutherland 1987).

In recent years, motivated in large part by widespread loss of species and natural habitats, ecological research has focused increasingly on the consequences of exploitive and long-term management activities for species diversity. Consideration of biological diversity has also guided the design, implementation, and critique of existing policy on natural resource management (Harris 1984, Salwasser 1990, Westman 1990, Lubchenco et al. 1991, Kessler et al. 1992). With the exception of the humid tropics, nowhere has the rela-

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[1] Manuscript received 2 March 1994; accepted 18 June 1994; final version received 5 August 1994.

[2] For reprints of this 67-page group of papers on plant diversity in managed forests, see footnote 1, page 911.

tionship between natural resource use and conservation of biodiversity been more controversial than in the Pacific Northwest region of the United States (Swanson and Franklin 1992, 1993, Lippke and Oliver 1993). Stimulated by societal and scientific concern over the loss and fragmentation of old-growth ecosystems, USDA (United States Department of Agriculture) Forest Service management practices and policies—both explicit and perceived—are undergoing critical review (Forest Ecosystem Management Assessment Team 1993, Thomas et al. 1993).

Knowledge from recent ecological studies of natural and managed systems has helped to assess and redesign forest management policies in the Pacific Northwest (Franklin et al. 1981, Harris 1984, Spies et al. 1988, Spies and Franklin 1991, Swanson and Franklin 1992). However, research that focuses on the consequences of management activities for biological diversity has been biased heavily toward the needs and responses of wildlife (e.g., Ruggiero et al. 1991, Orians 1992:papers therein, Hansen et al. 1993, McComb et al. 1993). Despite a long history of silvicultural research in the region, community-oriented studies that consider plant species diversity are rare (but see Long 1977, Halpern 1987, Schoonmaker and McKee 1988, Halpern et al. 1992*b*). Given that the understory layer directly or indirectly supports much of the floristic and faunistic diversity of Pacific Northwest forests, and given the scale and intensity with which we have manipulated these systems, it is surprising that little ecological research has explicitly addressed the effects of management on plant species diversity.

Our objective in this paper is to fill, in part, this broad gap in understanding through a synthesis of community-level research in managed and unmanaged forests of the region. Using permanent-plot and chronosequence studies of logged and natural forests in western Oregon and Washington, we describe some of the early responses of vegetation to clear-cutting and slash burning, and suggest how post-harvest practices that alter or circumvent natural successional processes influence long-term patterns of vascular-plant species diversity. We consider two broad classes of management effects: (1) initial effects of disturbances (e.g., clear-cut logging, slash burning, and physical soil disturbance) on existing plant populations, and (2) longer-term effects of management activities (e.g., control of competing vegetation, planting, thinning, or rotation length) on recovering plant populations. To illustrate some of the early effects of forest harvest on plant species diversity, we present data from three long-term, permanent-plot studies of succession in and adjacent to the Andrews Experimental Forest, Oregon. Empirical evidence for the longer-term effects of post-harvest practices is limited by a lack of community-based studies in older, managed stands (>50 yr). We approach the problem indirectly instead, by examining trends in a chronosequence of natural stands representing young, mature, and old-growth forests of western Oregon and southwestern Washington. We describe changes in species diversity and occurrence through natural stand development; propose a set of successional mechanisms to explain these trends; and, based on species' life histories and presence in natural stands, identify a set of conditions that appear critical in maintaining plant species diversity within managed-forest landscapes. We conclude with a discussion of priorities for future research.

Ecological and Historical Setting

We limit our discussion to the low- to mid-elevation, *Pseudotsuga menziesii*-dominated forests that characterize much of the region west of the Cascade crest in Oregon and Washington. Prior to the turn of the century these forests encompassed an area of $>11.3 \times 10^6$ ha (Harris 1984), occupying a broad set of landforms and environments from British Columbia to the coastal and Klamath Mountains of northern California. Most stands originated after catastrophic wildfire of varying size (Hemstrom and Franklin 1982, Agee 1991), although periodic, low-intensity underburns were also common in places (Teensma 1987, Morrison and Swanson 1990). Prior to human suppression of fire, natural fire return intervals ranged from <50 yr along the crest of the Coast Range in southern Oregon to as many as 750 yr in moist, coastal forests of the northern Oregon Coast Range, the Olympics, and the Washington Cascades (Agee 1991). Windstorms, in the form of large catastrophic events and smaller chronic disturbances (Ruth and Yoder 1953, Lynott and Cramer 1966), and, to a lesser extent, pathogens (Childs 1970, Gedney 1981), also initiated and shaped the development of these forests.

Typically, young and mature forests in this region are dominated by *Pseudotsuga,* and occasionally by *Tsuga heterophylla* or *Alnus rubra.* Within 200 yr, stands begin to exhibit many of the compositional and structural characteristics associated with old growth (Franklin et al. 1981, Spies et al. 1988, Spies and Franklin 1991): codominance of *Tsuga* in the overstory, presence of large numbers of snags, accumulations of downed woody debris, and a vertically and horizontally complex structure created by a multi-tiered canopy. Forest structure, productivity, and understory composition vary among environments, but appear closely related to available moisture (Dyrness et al. 1974, Zobel et al. 1976, Hemstrom et al. 1987). Repeatedly within the latitudinal range of these forests, drier, less productive sites are dominated by an understory of the low shrub *Gaultheria shallon,* and moister, more productive sites, by the fern *Polystichum munitum.*

Within less than a century, natural-disturbance regimes have been severely altered by human activities. Wildfire, windstorms, and insect outbreaks of varying size, frequency, and intensity have been replaced by short-rotation timber harvest and prescribed burning—

TABLE 1. Characteristics of sites and plots, and histories of disturbance and management, on Watersheds 1, 3, and 10, H. J. Andrews Experimental Forest, Oregon, USA.

	Watershed 1	Watershed 3	Watershed 10
	Site and plot characteristics		
Area of watershed (ha)	96	101	10
Area harvested (ha)	96	25*	10
Minimum elevation (m)	442	480	430
Maximum elevation (m)	1013	1082	670
Mean slope (%)	63	53	45
Aspect†	WNW	NW	NW
Number of plots	129	59	30
Area of plot (m^2)	4	4	16‡
	Disturbance and management history		
Harvest	1962–1966	1962–1963	1975
Slash burn	1967	1963	···
Aerial seeding§	1967, 1968 (10 ha)‖	···	···
Planting¶	1969, 1971 (40 ha)	1964	1976–1977, 1978 (5 ha)

* Comprised of three patch cuts of 5.3, 8.1, and 11.3 ha.
† N = north, W = west.
‡ Sixteen 1 × 1 m subplots per plot.
§ Aerial seeding of *Pseudotsuga menziesii.*
‖ Area reseeded or replanted.
¶ 2- and 3-yr-old *Pseudotsuga menziesii* seedlings.

disturbances that are more frequent and less variable in size and intensity. In addition to early losses on private lands beginning in the mid-1800s, the area of old-growth forests on all forms of land ownership in Washington, Oregon, and California has declined by >50% since the 1930s and 1940s (Bolsinger and Waddell 1993). On federal lands the decline of old growth (which commenced after World War II) has been especially rapid since the 1970s. For example, on the Willamette National Forest, Oregon, which contains some of our study sites, 13% of coniferous forests (mostly natural stands with dominant trees >150 yr old) were clear-cut between 1972 and 1988 (Spies et al. 1994). During the same period, the portion of the landscape occupied by coniferous forest beyond the influence of clear-cut boundaries (assuming a 100-m edge effect) declined from ≈60 to 45%.

Much of the pattern in today's forested landscape reflects 40–50 yr of harvest with the "staggered setting" approach. On federal lands, units of 15 ha or more were dispersed in space and time to produce a mosaic of even-aged, structurally uniform stands (Franklin and Forman 1987). Slash was typically broadcast burned to reduce fuel loadings (lowering the probability of subsequent fire) and to control competition from surviving understory plants. Subsequent management activities have further altered natural rates and patterns of stand development. Practices varied depending on the historical period during which stands were harvested, ownership (private, state, or federal), site conditions, and characteristics of the seral vegetation. Initially, reforestation was left (often unsuccessfully) to natural seeding from adjacent stands. Currently, state and federal regulations, designed to ensure adequate restocking of harvested units, require hand-planting of nursery-grown stock. Often a single species such as *Pseudotsuga menziesii* is planted. Natural successional processes have also been reshaped by other management activities that include application of herbicides and fertilizers, and periodic thinning or pruning of young stands.

Within the last 5 yr, largely in response to social and biological concerns (primarily the production of snags for cavity-nesting birds), forest managers have begun to experiment with new silvicultural systems that include retention of live trees in various amounts and patterns, ranging from a few scattered individuals to stand densities approximating those of a shelterwood (Franklin 1989, Gillis 1990, Hopwood and Island 1991). The ecological, economic, and social consequences of this shift in philosophy and approach are not clear.

METHODS

Experimental watersheds

Physical characteristics, vegetation, and disturbance/management histories.—Early effects of forest harvest on species diversity and occurrence were studied in permanent plots on three experimental watersheds in and adjacent to the H. J. Andrews Experimental Forest, Oregon (44° N, 122°30′ W). Watersheds 1, 3, and 10 (hereafter WS1, WS3, and WS10) typify the steep, heavily dissected terrain of the western Cascade Range. Elevations range from 430–1082 m and slopes average >50% (Table 1). The soil characteristics, hydrology, and climate of the watersheds have been described previously (Rothacher et al. 1967, Dyrness 1969, Bierlmaier and McKee 1989).

Sample plots lie within the *Tsuga heterophylla* Zone (Franklin and Dyrness 1973). Prior to harvest, stands were dominated by mature (≈120 yr old) and old-

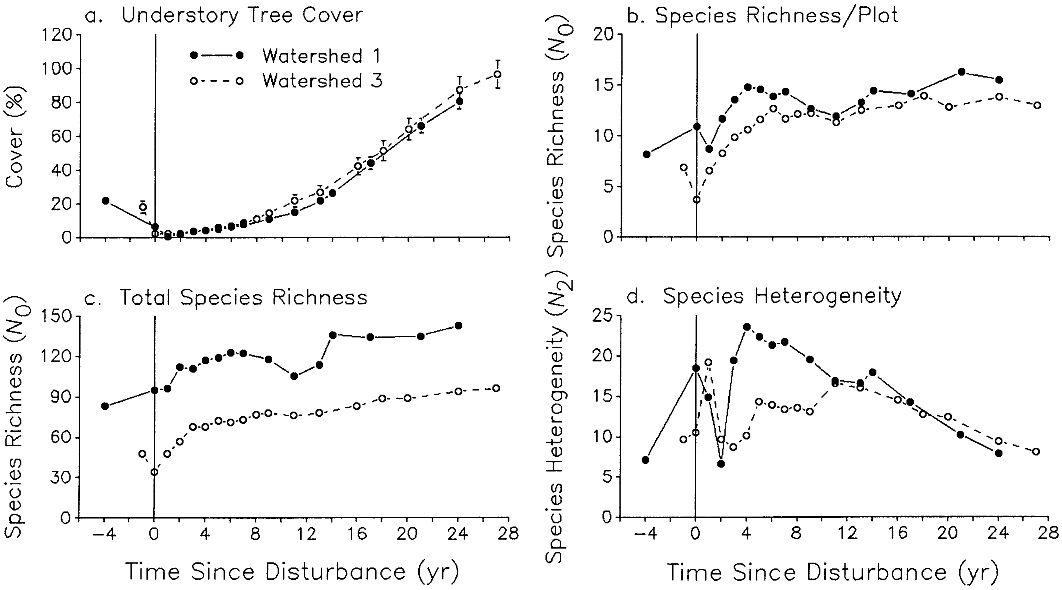

FIG. 1. Trends in plant species diversity on Watersheds 1 (WS1) and 3 (WS3), H. J. Andrews Experimental Forest, Oregon, USA. (a) Understory tree cover (mean ± 1 SE), (b) mean species richness per plot, (c) total species richness per watershed, and (d) species heterogeneity per watershed. Preharvest samples occur at times "−4" (WS1) and "−1" (WS3); times "0" and "1" represent the post-logging and first post-burning sampling dates, respectively, on both sites.

growth (>430 yr old) *Pseudotsuga menziesii,* with *Tsuga heterophylla* in a range of size and age classes. Common subcanopy and understory tree species included the conifers *Taxus brevifolia* and *Thuja plicata,* and the hardwoods *Acer macrophyllum, Alnus rubra, Castanopsis chrysophylla,* and *Cornus nuttallii.* Forest understories dominated by ferns (*Polystichum munitum*), low shrubs (*Berberis nervosa* and *Gaultheria shallon*), and/or tall shrubs (e.g., *Acer circinatum, Corylus cornuta,* and *Rhododendron macrophyllum*) represent a set of relatively dry to mesic plant communities typical of sites of similar elevation and topography in the region (Dyrness et al. 1974, Hemstrom et al. 1987). (Nomenclature follows Hitchcock and Cronquist [1973].)

Histories of logging, burning, and artificial regeneration differ among watersheds (Table 1). All 96 ha of WS1 were clear-cut logged over a period of 4 yr, between fall 1962 and spring 1966; slash was burned in fall 1966. In WS3 three smaller areas totaling 25 ha were harvested during winter 1962–1963; slash was burned in fall 1963. WS10 (10.2 ha) was harvested in fall 1975. Woody material >20 cm in diameter or >2.4 m in length was removed, so that large slash was disposed of without burning.

Attempts to seed and plant portions of the watersheds (particularly WS1 and WS10) were unsuccessful. Poor germination and/or survival of *Pseudotsuga menziesii* necessitated repeated planting (Table 1), although survival again was poor. Consequently, the resulting stands contain a large component of natural regeneration.

Field sampling.—Permanently staked sample plots were established prior to the harvest of each experimental watershed (in 1962 on WS1 and WS3; in 1973 on WS10). Sampling methods on WS1 and WS3 were identical. A total of 192, 2 × 2 m understory plots were established systematically (with a random start) along a series of evenly spaced transects (6 on WS1, 10 on WS3). Plots were sampled prior to and after logging, after burning, annually through 1972 (WS3) or 1973 (WS1), and every 2–4 yr thereafter (see Fig. 1). Within each plot, visual estimates of the percentage of canopy cover were made for all vascular plant species (including trees <6 m tall) and for mosses and lichens as groups. To assess the effects of variation in logging and burning disturbance within WS1 and WS3, sample plots were examined immediately after slash burning and were assigned to one of four soil disturbance classes (undisturbed, disturbed but unburned, lightly burned, heavily burned) representing a gradient in disturbance intensity (Dyrness 1973, Halpern 1988, 1989). Analyses in this paper are based on the 188 plots (129 on WS1, 59 on WS3) that were sampled continuously through 1990.

Prior to harvest of WS10, 36 m permanent plots each 10 × 15 m were placed randomly among four habitat types in proportion to the area encompassed by each type (Hawk 1979). Because we only present the results of presence/absence analyses for WS10, we do not describe details of the sampling design (see Hawk 1979). Plots were sampled prior to harvest (1973), annually between 1975 and 1983, and again in 1985, 1989, and 1993. Analyses are based on the 30 plots that were sampled consistently through 1989.

Analyses.—To trace the geographic source of the post-harvest vegetation, species were classified as native or exotic based on descriptions from regional floras (Hitchcock et al. 1969, Hitchcock and Cronquist 1973). To characterize the successional origins of the post-harvest flora, all species were classified as "residual" or "invading." Residuals were defined as species characteristic of the undisturbed forest, based on pre-harvest samples and knowledge of undisturbed vegetation of the area. Invaders were defined as species absent from the aboveground vegetation of the undisturbed forest or locally restricted to disturbed microsites in intact forest (Dyrness 1973, Halpern 1989, Halpern and Franklin 1990).

We examine trends in diversity at two spatial scales—the plot and watershed levels—and with two indices (Hill 1973): species richness (N_0), the mean number of species per sample; and species heterogeneity (N_2), the reciprocal of Simpson's index ($1/\Sigma\, p_i^2$), where p_i represents the proportional abundance of the ith species in the sample. N_2 integrates the number and relative abundance of species (reducing the weight of rare species). Sharing the same units as species richness, heterogeneity is often expressed as the number of equally common species required to produce the same heterogeneity as that in the observed sample (Peet 1974). All calculations were made with the program PRHILL (B. Smith, *unpublished* FORTRAN *program*).

To compare trends in diversity among disturbance classes within WS1 and WS3, data were standardized in two ways. First, because estimates of diversity are sensitive to the area or number of plots sampled, we compare mean, plot-level values of richness and heterogeneity. Second, to control for natural differences in diversity among disturbance classes prior to harvest, we present mean changes in diversity relative to pre-disturbance conditions, rather than absolute values of diversity. For each sampling date, differences in diversity among all pairs of disturbance classes were tested with the Tukey-Kramer procedure (if variances were homogeneous) or the Games and Howell method (if variances were heterogeneous) (Sokal and Rohlf 1981).

Natural forest stands

Physical characteristics and vegetation.—Our data on species diversity and occurrence in natural forests are from a chronosequence of stands (Table 2) sampled in three physiographic provinces in Washington and Oregon: the southern Washington Cascade Range, the Oregon Cascade Range, and the southern half of the Oregon Coast Range. All are mountainous landscapes characterized by steep and highly dissected slopes. The geology, soils, and climate of these provinces have been described earlier (Franklin and Dyrness 1973 and references therein).

Most of the sample plots lie within the *Tsuga heterophylla* Zone and the lower portion of the *Abies amabilis* Zone (Franklin and Dyrness 1973). Additional stands in the southern Oregon Cascade Range lie within the northern fringes of the Mixed Conifer Zone, and in the Coast Range, within the eastern margin of the *Picea sitchensis* Zone (Franklin and Dyrness 1973). *Tsuga heterophylla* and *Abies amabilis* are the climax species on most sites, although *Pseudotsuga* may be climax on drier, upper slopes and ridge tops (Means 1982). Forest understory communities represent a common set of mesic to dry-mesic plant associations, many dominated by *Rhododendron macrophyllum, Gaultheria shallon,* and/or *Berberis nervosa* (for a complete list of communities see Spies [1991]).

Field sampling.—A chronosequence of 196 *Pseudotsuga*-dominated stands was sampled in 1983 and 1984 (Table 2). All forests originated after stand-replacing wildfires. Preliminary analyses of understory vegetation data indicated that young and mature stands included a broader range of environments than did old-growth stands. To minimize this variation among age classes, detrended correspondence analysis (or DCA; Hill 1979, Gauch 1982) and knowledge of individual site conditions were used to identify and delete "outliers"—i.e., stands within an age-class that differed markedly from the range of conditions within the other two age classes (Spies 1991, Spies and Franklin 1991). This subjective elimination of samples produced a final set of 177 stands for analysis.

Stands of 4–20 ha were sampled with 3–5 circular plots spaced 100 or 150 m apart. Each plot consisted of a set of nested, circular subplots of 0.1, 0.05, and 0.02 ha. Within the 0.1-ha plot, trees >50 cm in diameter at breast height (dbh) were recorded by species and measured for diameter and height. Similar data were recorded for trees 5–50 cm dbh within the smaller, 0.05-ha plot. The percentage cover of tall shrubs and understory trees (i.e., individuals <8 m tall) was also estimated on the 0.05-ha plot. The percentage cover of low-growing woody plants, herbs, mosses, and lichens was estimated in the 0.02-ha plots. Cover of fallen, epiphytic foliose lichens (i.e., *Lobaria oregana* and *L. pulmonaria*) was also estimated in the 0.02-ha plots as a measure of their presence in the canopy (McCune 1993*a*). All species occurring in the 0.05-ha plots were recorded and used in presence/absence analyses. All vascular-plant taxa and a subset of the ground-layer mosses and lichens were keyed to species (or to genus).

Stand ages were determined in two ways. For young and mature stands, ages were obtained from increment cores of up to four dominant *Pseudotsuga menziesii* per plot (5–20 per stand) taken at breast height. Depending on site conditions, 5–7 yr were added to the annual ring counts to adjust for growth to breast height. Ages of plots were then averaged to produce stand-level estimates. For old-growth stands, ages were obtained from counts of stumps in adjacent clear-cuts, along roads or trails, or occasionally from increment cores of dominant trees. Ages of stands within Mount Rainier National Park were obtained from Hemstrom (1979).

TABLE 2. Mean and range of age and site characteristics for young (Y), mature (M), and old-growth (OG) forest stands in the three physiographic provinces.

	Washington Cascade Range					
Age class	Y		M		OG	
N*	11		9		25	
	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
Stand age (yr)	65	42–75	130	80–190	425	210–900
Aspect†	1.2	0.3–2.0	1.1	0.1–2.0	0.9	0.0–2.0
Slope (%)	40	13–66	45	19–73	35	9–80
Elevation (m)	709	472–1167	747	483–1124	730	378–1049
Latitude (deg)	46.3	45.8–46.9	46.2	45.1–46.8	46.2	45.8–46.9
Topographic position‡	2.9	2–4	2.8	2–4	2.2	1–4

Analyses.—Patterns of plant species diversity were examined separately for overstory trees (>5 cm dbh) based on basal area, and for understory vegetation based on cover. One quarter of the stands were sampled with fewer than five plots; thus, a subset of 144 stands was used to compare trends among age classes. Stands were selected so that the mean number of plots per stand or area was equal among age classes within a province. We examine diversity trends using the same measures of Hill (1973), N_0 and N_2, described (above) for the experimental watersheds.

Comparisons of species frequency and abundance data among age classes were conducted for taxa present in at least five stands within a province. In addition, within each province, stands were stratified by ecological zone (Spies 1991) based on preliminary analyses of the elevational and geographical distributions of samples and species. If a species was absent from all stands within a zone, none of the stands from that zone were used in the age-class analysis for that species. Consequently, sample sizes for these tests differ among species. Stratification limited the analysis of age-class relationships to zones within which a species could occur based on its elevational and latitudinal range. Reducing the number of zero values for species increased the power of the statistical tests. Chi-square analyses were used to test for age-class effects in the constancy (frequency of occurrence) of species. Kruskal-Wallis nonparametric analyses were used to test for differences in species abundance (as measured by cover or basal area). All analyses were conducted using SAS (SAS Institute 1987).

RESULTS

Experimental watersheds

Species persistence through logging and burning.—Clear-cut logging significantly reduced the diversity of forest understory species. On Watershed (WS)3 and WS10, 29 and 24%, respectively, of original understory taxa were absent one growing season after harvest. On WS1, ostensibly greater persistence of species through logging (i.e., only 8% loss of species) was an artifact of the timing of post-harvest sampling. Because WS1 was clear-cut over a period of 4 yr (1962–1966), a majority (87%) of sample plots experienced one or more growing seasons prior to post-logging sampling (1966), providing a longer period for species to reestablish (Halpern 1987). Broadcast burning further reduced species numbers on WS1 (i.e., 18% loss of taxa), but not on WS3.

Recovery of species diversity.—Initial declines in species diversity were short-lived (Fig. 1). For example, on WS1 and WS3, both mean plot (Fig. 1b) and watershed (Fig. 1c) richness exceeded pre-harvest values within 2 yr after burning. Thereafter, richness increased continuously with time (Fig. 1b and c), despite partial closure of the tree canopy (Fig. 1a). Longer term trends varied with spatial scale. After 4–6 yr, watershed-level richness rose more steeply and continuously (Fig. 1c) than did plot-level richness (Fig. 1b), as, increasingly, new colonists were relatively uncommon, establishing in a small portion of plots.

Trends in species diversity were also dependent on the measure of diversity. Heterogeneity (N_2) peaked and declined several times prior to canopy closure on WS1 and WS3 (Fig. 1d). In contrast to long-term trends in richness, heterogeneity returned to old-growth levels by final sampling.

Origins of the post-disturbance flora.—Exotic species contributed minimally in cover and number to the post-harvest vegetation (Fig. 2). For all but one sampling date, native taxa comprised >95% of total plant cover and >90% of all species. The minor peak in exotic plant cover in year 2 (11 and 17% of total cover on WS1 and WS3, respectively) coincided with maximal abundance of *Senecio sylvaticus,* a winter annual of European origin (Halpern 1989).

Early recovery of diversity following logging and burning (Fig. 1) reflected two underlying successional processes: rapid colonization by ruderal, non-forest species (invaders) and gradual reestablishment or recovery of characteristic understory taxa (residuals) (Fig. 3). On WS1 and WS3, invasion was most common during the first two growing seasons after burning, although new species continued to appear through final sampling (Fig. 3e and f). At the watershed scale, invading species were as common or were more numerous than residuals (WS3, Fig. 3e and f). However, many

TABLE 2. Continued.

Oregon Cascade Range						Oregon Coast Range					
Y		M		OG		Y		M		OG	
11		22		30		6		8		22	
$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
60	30–79	115	84–180	395	195–750	55	40–70	100	80–120	315	130–525
1.1	0.1–1.9	0.7	0.0–1.8	0.9	0.1–1.4	0.9	0.1–1.4	1.0	0.4–1.7	0.9	0.1–1.9
37	8–71	44	3–90	40	2–92	40	16–70	53	26–75	50	19–85
844	474–1428	808	326–1478	808	437–1284	302	86–473	487	260–1022	403	153–909
44.2	42.8–45.5	43.9	42.9–45.4	44.1	42.8–45.6	43.6	43.2–44.3	43.9	43.0–44.5	43.8	43.1–44.5
2.5	2–4	2.7	1–4	2.6	1–4	3.3	2–4	3.3	2–4	2.8	2–4

* Number of stands sampled.

† Cosine transformation: northeast (45°) = 2.0, southwest (225°) = 0.0.

‡ 1 = valley bottom, 2 = bottom third of slope, 3 = middle third of slope, 4 = upper third of slope.

of these invaders occupied relatively few plots. As illustrated by plot-level trends in cover (Fig. 3a and b) and richness (Fig. 3c and d), residual forest taxa regained dominance within 5–10 yr after burning.

Because heterogeneity indices incorporate the proportional abundances of species, the individual patterns of invaders and residuals (Fig. 3g and h) cannot be summed to yield community-level trends (Fig. 1d). Nevertheless, their separate dynamics illustrate the differential effects of disturbance on two important functional groups. Among invaders, multiple peaks and troughs in heterogeneity followed logging and burning (Fig. 3g and h), coinciding with rapid changes in the abundance of annuals (e.g., *Senecio sylvaticus* and *Epilobium paniculatum*) and relatively short-lived perennials (e.g., *Epilobium angustifolium*) (Halpern 1989). Among residuals, logging and burning enhanced species heterogeneity (Fig. 3g and h) by reducing the dominance of characteristic understory shrubs (e.g., *Acer circinatum, Rhododendron macrophyllum, Berberis nervosa,* and *Gaultheria shallon*) while releasing other subordinate ground-layer species (e.g., *Linnaea borealis, Rubus ursinus, Whipplea modesta,* and *Hieracium albiflorum*). Subsequent, longer term declines in residual species heterogeneity (Fig. 3g and h) coincided with recovery of dominance (through resprouting and clonal spread) of the principal understory species (Halpern 1989).

Effects of disturbance intensity.—Variation in disturbance intensity had a profound influence on local levels and patterns of diversity. We illustrate these effects by comparing patterns of diversity among soil disturbance classes on WS1 (Fig. 4).

Early changes in species richness and heterogeneity

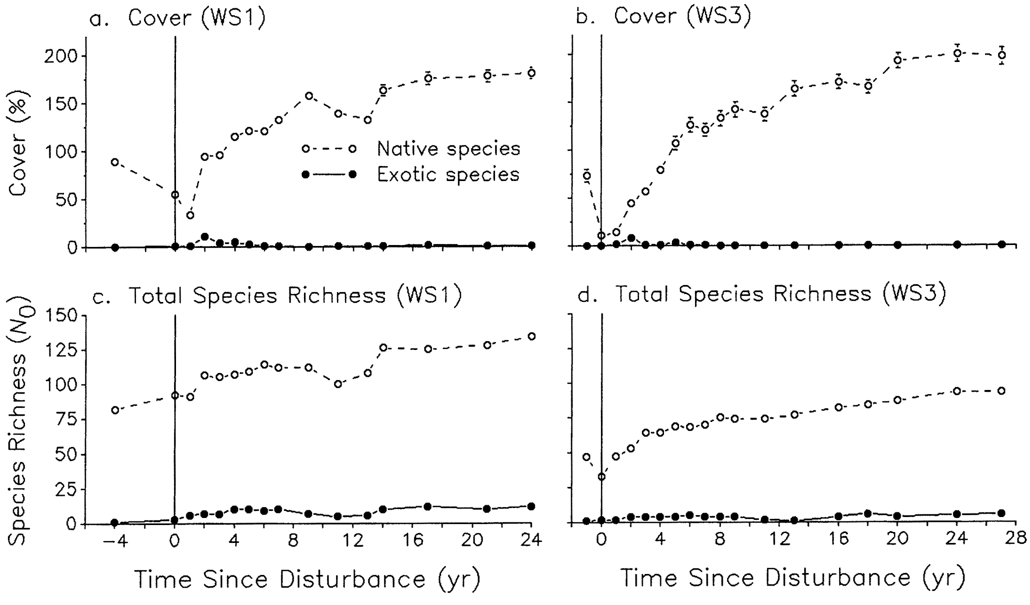

FIG. 2. Contributions of native and exotic species to (a, b) cover and (c, d) species richness per watershed on Watersheds 1 and 3, H. J. Andrews Experimental Forest, Oregon. Preharvest samples occur at times "−4" (WS1) and "−1" (WS3); times "0" and "1" represent the post-logging and first post-burning sampling dates, respectively, on both sites.

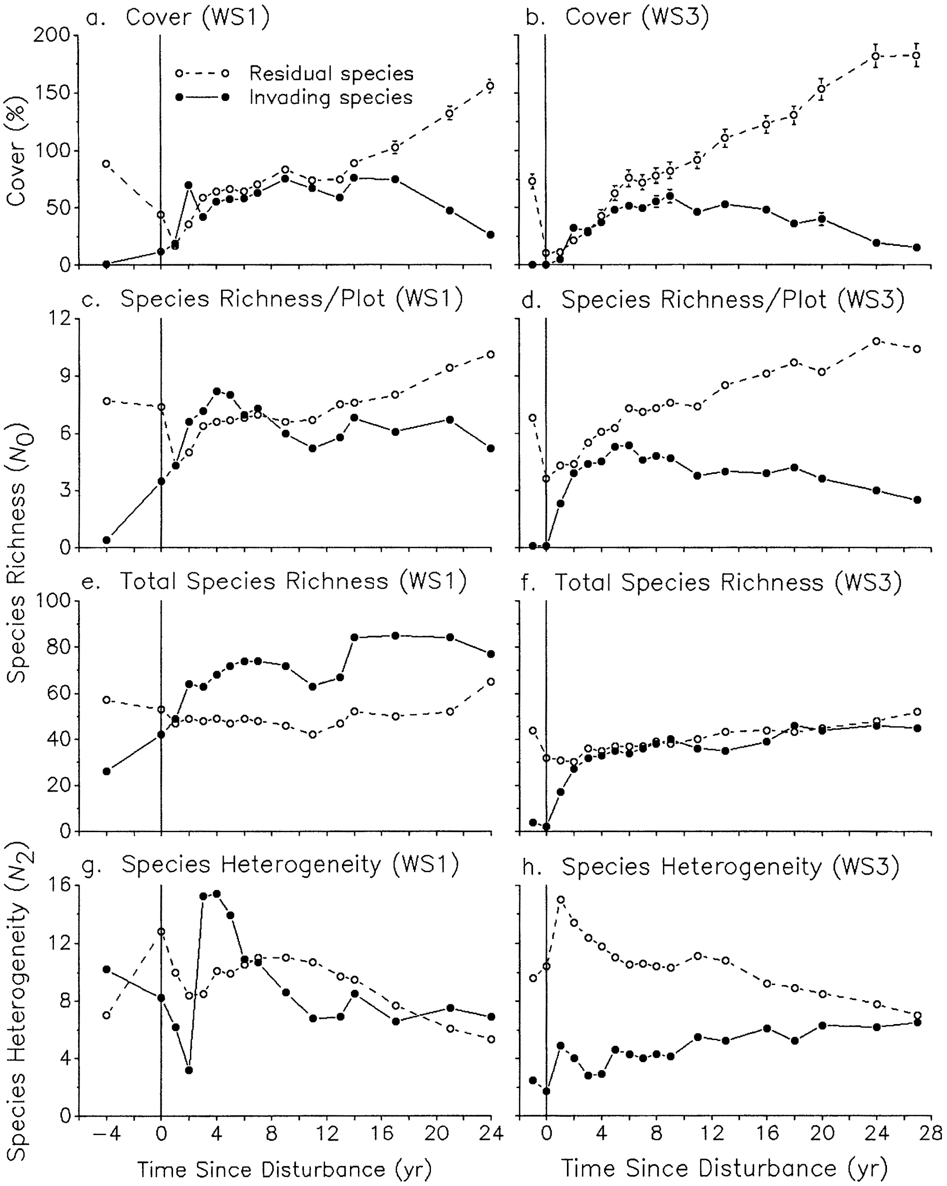

FIG. 3. Contributions of residual and invading species to (a, b) cover, (c, d) mean species richness per plot, (e, f) total species richness per watershed, and (g, h) total species heterogeneity per watershed on Watersheds 1 and 3, H. J. Andrews Experimental Forest, Oregon. Preharvest samples occur at times "−4" (WS1) and "−1" (WS3); times "0" and "1" represent the post-logging and first post-burning sampling dates, respectively, on both sites.

were correlated with disturbance intensity (Fig. 4). However, any post-logging or burning losses in total species diversity were short-lived (Fig. 4a and b). Richness and heterogeneity exceeded pre-harvest levels within 1–3 yr after burning, reflecting rapid colonization of a diverse, invading flora. Early differences in total diversity among all disturbance classes were also transient, largely limited to the first 4 yr of succession (Fig. 4a and b).

Variation in disturbance intensity had a greater and longer lasting effect on the original forest flora than on the total species pool. Both the magnitude of initial loss and the long-term recovery of diversity were proportional to disturbance intensity (Fig. 4c and d). On burned plots, residual species richness remained depressed (below original old-growth levels) for up to 20 yr after burning (Fig. 4c). Relative to richness, however, recovery of residual species heterogeneity on burned plots was less protracted (Fig. 4d), reflecting the reduced importance, or contribution of rarer taxa to this index of diversity.

Extinctions of species.—Species extinctions were observed within each of the three watersheds. Five of 57 original forest species were completely lost from

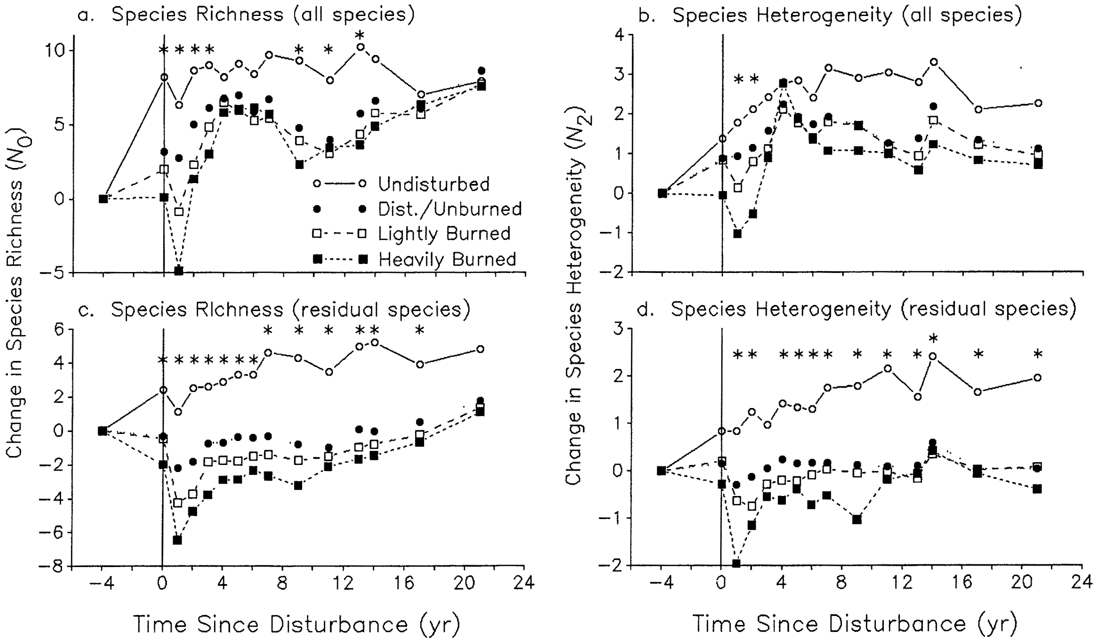

FIG. 4. Changes in species diversity among soil disturbance classes on Watershed 1, H. J. Andrews Experimental Forest, Oregon. (a) Species richness per plot for all species, (b) species heterogeneity per plot for all species, (c) residual species richness per plot, and (d) residual species heterogeneity per plot. Soil disturbance class definitions are: Undisturbed = minimal mixing of soil and litter and no evidence of fire; Disturbed but Unburned = surface litter removed or mixed with mineral soil, but little evidence of fire; Lightly Burned = litter charred by fire; Heavily Burned = litter completely consumed by intense fire. The preharvest sample is represented by time "−4" (harvested over a 4-yr period); times "0" and "1" represent the post-logging and first post-burning sampling dates, respectively. Values are expressed as the mean change in plot-level diversity (i.e., post-harvest minus pre-harvest, see *Methods*). Asterisks indicate sampling dates with significant differences in diversity between one or more pairs of disturbance classes ($P < 0.05$, Tukey-Kramer or Games and Howell procedures, see *Methods*).

the sample plots on WS1, 4 of 44 from WS3, and 7 of 55 from WS10. A greater number of species experienced local extinction, i.e., loss from plots representing one or more disturbance classes (Table 3). A total of 11 taxa were lost from at least two of the nine watershed × disturbance class categories (Table 3): the herbs *Clintonia uniflora, Corallorhiza mertensiana, Goodyera oblongifolia, Pyrola picta, Synthyris reniformis, Tiarella trifoliata* var. *unifoliata,* and *Xerophyllum tenax*; the sub-shrubs *Chimaphila menziesii* and *C. umbellata*; and the understory tree *Taxus brevifolia.* Although some of these species were uncommon in the preexisting forests, others were well distributed among plots (e.g., *Goodyera oblongifolia, Chimaphila* spp., and *Taxus brevifolia*). Eleven species were eliminated from plots representing both unburned and burned conditions (*Asarum caudatum, Chimaphila umbellata, Clintonia uniflora, Disporum smithii, Goodyera oblongifolia, Oxalis oregana, Pyrola asarifolia, P. picta, Synthyris reniformis, Tiarella trifoliata,* and *Xerophyllum tenax*). Other, less sensitive taxa were lost only from burned plots (e.g., *Achlys triphylla, Adiantum pedatum, Anemone lyallii, Disporum hookeri, Rhododendron macrophyllum, Taxus brevifolia, Thuja plicata,* and *Vaccinium membranaceum*).

Natural forest stands

Trends in species diversity among age-classes.—Age-class-related trends in diversity varied greatly among physiographic provinces, although the general pattern was of peaks early and late in succession. Richness of overstory trees (i.e., >5 cm dbh) differed significantly among age classes only in the Oregon Coast Range (Fig. 5e), where old-growth stands had the greatest number of species, and mature stands the fewest. Heterogeneity of overstory species showed an age-class effect in the two Cascade Range provinces (Fig. 5b and d), where old-growth stands were most diverse.

Differences in richness of understory species were marginally significant in the Oregon Coast Range (Fig. 6e), where species number increased with mean stand age. Heterogeneity of understory species showed an age-class effect in the Washington Cascade (Fig. 6b) and Oregon Coast (Fig. 6f) ranges, with greatest diversity in old-growth stands.

Occurrence and abundance of species among age-classes.—Within each physiographic province, few overstory tree species were restricted to, or completely absent from, an age class (Table 4). Moreover, few species showed significant age-class effects for total basal area (but see *Abies amabilis, Taxus brevifolia,*

TABLE 3. Local extinctions of old-growth forest species on Watersheds 1 and 3 (by soil disturbance class) and on Watershed 10, H. J. Andrews Experimental Forest, Oregon, USA.

	Watershed 1				Watershed 3				Watershed 10
Soil disturbance class*	U	DU	LB	HB	U	DU	LB	HB	All plots
N:†	10	40	70	9	10	20	22	7	30
Trees									
Castanopsis chrysophylla	a‡	···	···	a	a	···	···	E	···
Libocedrus decurrens	a	a	a	a	a	a	a	a	E
Pinus lambertiana	a	a	E	a	a	a	a	a	···
Taxus brevifolia	···	···	···	E	···	···	···	E	···
Thuja plicata	···	···	···	E	···	···	···	···	···
Tall shrubs									
Rhododendron macrophyllum	···	···	···	E	···	···	···	···	···
Vaccinium membranaceum	···	a	E	···	a	a	a	a	···
Sub-shrubs									
Chimaphila menziesii	···	···	···	E	···	···	···	a	E
C. umbellata	E	···	E	E	···	···	···	···	···
Herbs and Ferns									
Achlys triphylla	···	···	···	a	a	···	E	a	···
Adiantum pedatum	a	···	···	a	a	a	E	a	a
Anemone lyallii	a	a	···	E	a	a	a	a	···
Asarum caudatum	a	a	···	a	E	···	a	a	···
Athyrium filix-femina	a	···	a	a	a	E	a	a	a
Clintonia uniflora	a	E	···	a	a	a	a	E	···
Corallorhiza maculata	a	a	a	a	a	a	a	a	E
C. mertensiana	a	a	E	a	a	a	a	a	E
Disporum hookeri	···	···	a	E	a	a	a	a	···
D. smithii	a	a	a	a	E	a	a	a	···
Goodyera oblongifolia	···	E	E	E	E	···	E	a	···
Listera cordata	a	a	E	a	a	a	a	a	a
Oxalis oregana	a	···	···	a	···	E	a	a	···
Polypodium glychyrriza	a	a	a	a	a	a	a	a	E
Pyrola asarifolia	E	a	a	a	···	a	···	a	···
P. picta	E	···	E	E	a	a	a	a	E
Smilacina racemosa	a	···	···	a	···	E	a	a	···
Synthyris reniformis	···	···	···	E	E	···	E	a	···
Tiarella trifoliata var. *trifoliata*	a	E	a	a	a	a	a	a	···
T. trifoliata var. *unifoliata*	E	···	E	E	···	···	···	···	E
Xerophyllum tenax	a	···	···	E	E	···	···	a	···
Total extinctions (%)§	12.9	4.2	12.7	46.2	15.6	7.5	13.3	13.6	12.7

* Soil disturbance class codes: U = Undisturbed, DU = Disturbed but Unburned, LB = Lightly Burned, HB = Heavily Burned (see Fig. 4 for definitions). Plots on WS10 were not burned.

† Number of plots sampled.

‡ Species extinction/persistence codes: a = species absent from pre-harvest plots, E = species eliminated (as of 1990 on WS1 and WS3, as of 1989 on WS10), ··· = species survived or reestablished during the study period.

§ Proportion of original forest species eliminated from each disturbance class (WS1, WS3) or watershed (WS10).

Tsuga heterophylla, Acer macrophyllum, and *Alnus rubra,* Table 4). *Taxus* was the only species for which basal area differed significantly ($P < 0.05$) among age classes in all provinces. Its basal area was up to 75 times greater in old growth than in younger age-classes in the Cascade provinces; no overstory individuals were found in stands of <200 yr in the Oregon Coast Range.

As with the overstory stratum, few understory species were either restricted to or absent from an age class. More commonly, species were present in >25% of stands of two or more age classes. Among the total pool of understory taxa (129, 171, and 98 species in the Washington Cascades, Oregon Cascades, and Oregon Coast Range, respectively), 11–16% of species showed significant differences ($P < 0.05$) in constancy among age classes. Of these, most species attained maximal constancy in old growth: in the Cascade Ranges, *Chimaphila umbellata, Coptis laciniata, Gaultheria ovatifolia, Tiarella trifoliata* var. *unifoliata,* and *Vaccinium membranaceum,* and in the Oregon Coast Range, *Achlys triphylla, Adenocaulon bicolor, Disporum hookeri, Linnaea borealis, Synthyris reniformis,* and *Tsuga heterophylla* (Table 5). Two taxa, *Taxus brevifolia* and *Lobaria* spp., exhibited peak constancy in old growth across all provinces (Table 5).

Percentage canopy cover of understory species differed significantly ($P < 0.05$) among age classes to a greater extent than did constancy. Age-class effects were found for 11% (Oregon Coast Range), 19% (Washington Cascades), and 21% (Oregon Cascades) of understory species. Of these, maximal cover in old

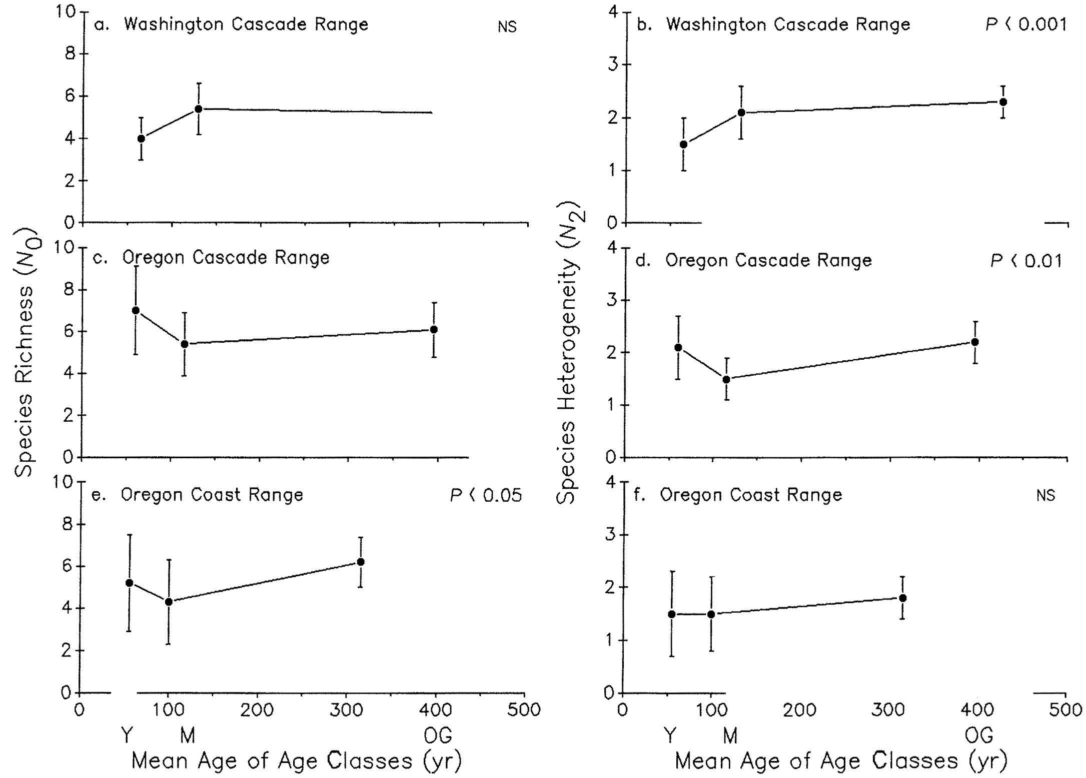

FIG. 5. Mean species richness and species heterogeneity of forest overstory taxa among young (Y), mature (M), and old-growth (OG) age classes for the three physiographic provinces in Oregon and Washington. Values represent stand-level means (see *Methods*). Vertical bars are Scheffé's 95% confidence intervals. Significant age-class effects from ANOVA are indicated by *P* values; NS = nonsignificant.

growth occurred for 7–9% of taxa in each province (Table 6).

Seven taxa displayed peak development in old growth in two or more provinces (*Achlys triphylla, Chimaphila umbellata, Goodyera oblongifolia, Linnaea borealis, Lobaria* spp., *Taxus brevifolia,* and *Tsuga heterophylla*). Ratios of mean cover in old growth to cover in mature or young stands were very high (>25) for *Abies amabilis, Achlys triphylla, Coptis laciniata, Corallorhiza mertensiana, Tiarella trifoliata,* and *Vaccinium membranaceum* in the Cascade Ranges; for *Goodyera oblongifolia, Synthyris reniformis,* and *Tsuga heterophylla* in the Oregon Coast Range; and for *Lobaria* spp. and *Taxus brevifolia* in all three provinces (Table 6).

DISCUSSION

As a simple measure of the number and/or distribution of abundance of species, diversity has long been used to characterize the taxonomic structure of communities (e.g., Simpson 1949, Margalef 1958). Despite the potential ambiguity of indices that consider rare and common taxa equally (richness) or that weight species relative to their abundances (heterogeneity), diversity remains an invaluable ecological tool and metric with which to simplify, characterize, and compare the complexity of species assemblages (Christensen and Peet 1984, Magurran 1988).

However, use of an exclusively index-based approach to examine the effects of forest management on biological diversity affords a relatively narrow view of an ecologically complex problem. Moreover, the results of simple numerical analyses can be misleading. By nature, diversity indices are not sensitive to the ecological attributes of individual species. For example, the relative contributions of "specialists"—taxa with narrow geographical, successional, or environmental ranges—will be overlooked. Consequently, we have considered not only species' numbers, but species' functional or successional roles (e.g., invaders vs. residuals, exotics vs. natives) and individual identities. In doing so, the dramatic increase in diversity (richness) induced by logging and burning is clearly separable into two distinct patterns: temporary decline in the number of residual forest species, and rapid accumulation of native, ruderal, non-forest herbs. Additionally, by examining the temporal patterns of occurrence and abundance of individual taxa, we are able to identify the morphological and life-history traits of species that confer resistance or susceptibility to forest management practices.

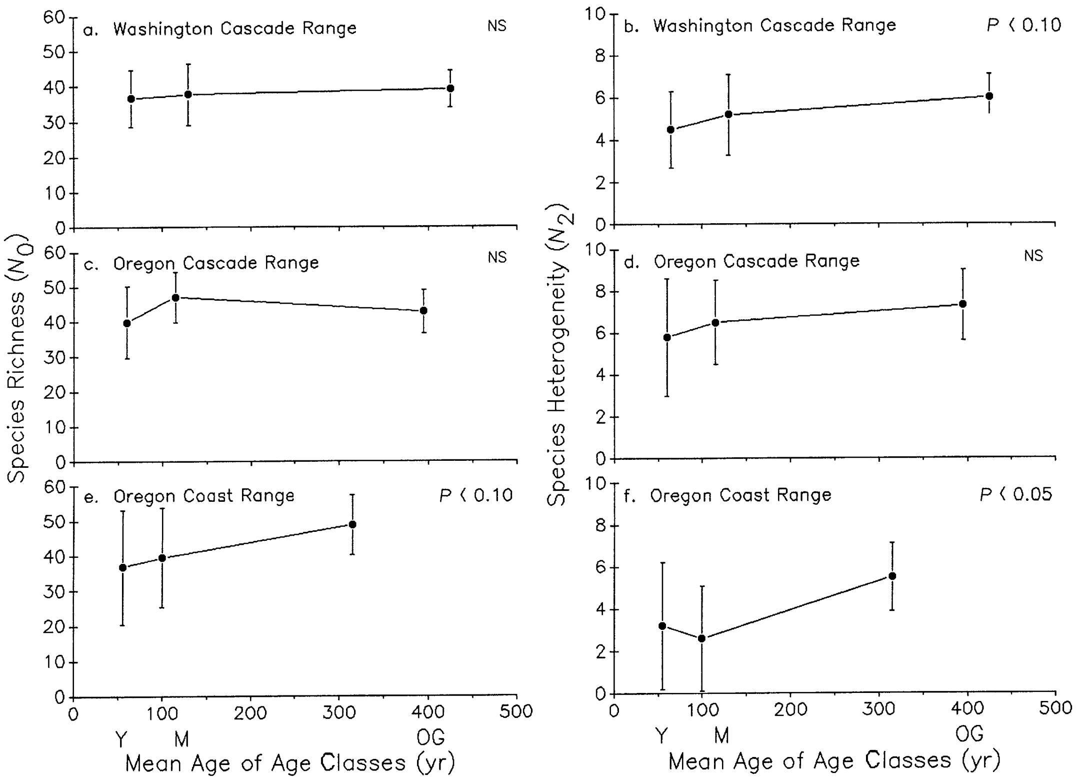

FIG. 6. Mean species richness and species heterogeneity of forest understory taxa among young (Y), mature (M), and old-growth (OG) age-classes for the three physiographic provinces in Oregon and Washington. Values represent stand-level means (see *Methods*). Vertical bars are Scheffé's 95% confidence intervals. Significant age-class effects from ANOVA are indicated by P values.

Temporal trends in diversity

Attempts to generalize about the spatial and temporal nature of diversity have led to numerous conceptual models (Whittaker 1965, Pielou 1966, Odum 1969, Connell 1978, Huston 1979, Menge and Sutherland 1987) supported by contrasting empirical results. For forest ecosystems, various temporal trends in diversity have been observed during succession, including increases (e.g., Monk 1967, Nicholson and Monk 1974, Clebsch and Busing 1989), decreases (e.g., Habeck 1968, Whittaker 1969, Loucks 1970, Reiners et al. 1971), and one or more peaks with time (e.g., AuClair and Goff 1971, Shafi and Yarranton 1973, Schoonmaker and McKee 1988, Clebsch and Busing 1989). These results suggest that relationships between diversity and succession are complex, and ultimately may be system-specific.

Of the handful of successional studies that explicitly address diversity in forests of the Pacific Northwest (Long 1977, Halpern 1987, Schoonmaker and McKee 1988, Spies 1991, Halpern et al. 1992*b*), none have considered all stages of stand development. Moreover, interpolation or comparison of diversity patterns among studies are problematic due to differences in sampling design (permanent plot vs. chronosequence), number or area of plots, indices used to express diversity, or origin of the sere (natural disturbance vs. forest harvest). With these caveats, we generalize qualitatively about long-term trends in plant species diversity in *Pseudotsuga*-dominated forests. Our studies support a general model formulated by Franklin (1982) (motivated by patterns described in Harris et al. 1982): diversity increases to a peak at some point prior to closure of the tree canopy, declines to its lowest values under canopy closure, and increases again as canopies of young and mature stands reopen. At finer temporal resolution, however, patterns are more complex. Annual sampling of the experimental watersheds illustrates that species heterogeneity may peak several times prior to canopy closure, reflecting rapid changes in the composition and dominance of annual and perennial colonists (Halpern 1988, 1989). Schoonmaker and McKee (1988) observed similar fluctuations in diversity within a chronosequence of 2- to 40-yr-old, post-harvest stands.

Our combined studies of managed and natural stands also suggest a strong dependence of temporal trends in diversity on the spatial scale of consideration and on the measure of diversity. For example, on Watershed (WS)1 and WS3 richness peaked sooner for individual plots (4 m^2), than for entire watersheds (25–100 ha). On the same sites, diversity as expressed by species

TABLE 4. Mean basal area (in square metres per hectare) of tree species >5 cm dbh in young (Y), mature (M), and old-growth (OG) stands in the three physiographic provinces.

	Washington Cascade Range				Oregon Cascade Range				Oregon Coast Range			
	Y	M	OG	*P*	Y	M	OG	*P*	Y	M	OG	*P*
Conifers												
Abies amabilis	0.4	0.2	5.4	***	<0.1	0.1	0.9		0.0	0.0	0.0	
A. concolor	0.0	0.0	0.0		9.8	11.8	3.3		0.0	0.0	0.0	
A. grandis	<0.1	<0.1	<0.1		0.4	1.2	0.5		<0.1	0.0	1.6	
A. procera	<0.1	0.3	0.4		0.0	0.0	0.0		0.0	0.0	0.0	
Libocedrus decurrens	0.0	0.0	0.0		0.5	3.2	2.0		0.0	0.1	1.7	
Pinus lambertiana	0.0	0.0	0.0		0.4	1.4	2.0		0.0	0.0	0.0	
P. monticola	0.0	<0.1	0.1		0.1	<0.1	<0.1		0.0	0.0	0.0	
Pseudotsuga menziesii	38.5	36.0	31.3		28.6	48.8	47.8	***	36.4	47.1	49.8	
Taxus brevifolia	<0.1	<0.1	0.7	***	0.2	0.1	0.7	**	0.0	0.0	0.4	
Thuja plicata	1.0	4.4	6.3		2.1	1.3	7.4		<0.1	2.8	2.9	
Tsuga heterophylla	7.4	15.0	24.0	***	7.9	1.5	14.0	***	4.2	6.1	9.9	
Hardwoods												
Acer macrophyllum	0.1	0.2	<0.1	**	0.7	0.5	<0.1	*	0.5	0.4	1.6	
Alnus rubra	<0.1	0.3	0.0		0.6	0.3	0.0	*	1.6	2.1	0.1	
Arbutus menziesii	0.0	0.0	0.0		<0.1	0.2	0.1		2.2	0.1	0.4	
Castanopsis chrysophylla	0.0	0.0	0.0		1.0	0.3	0.3		0.4	0.2	0.2	
Cornus nuttallii	<0.1	0.2	<0.1		0.3	0.1	0.1		0.2	0.1	0.4	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; P values from Kruskal-Wallis test for age-class effect.

heterogeneity declined more rapidly than did species richness. Similarly, for most comparisons among natural forest age-classes, significant differences were found for one, but not for both, indices of diversity.

To interpret the ecological mechanisms by which forest management practices may alter these natural trajectories of diversity, we find it useful to consider two broad classes of effects: initial effects of disturbance on forest understory populations, and longer term effects of management activities on recovering plant populations.

Initial effects on diversity: responses to forest harvest and slash burning

Despite dramatic loss of plant cover in response to clear-cut logging and slash burning of the experimental watersheds (Halpern 1989, Halpern and Franklin 1990), loss of diversity was a short-lived phenomenon. Within 2 yr after burning, species richness exceeded old-growth levels. Most additional taxa were native, ruderal herbs. Longer term trends on WS1 indicate that these non-forest species may comprise more than half of the post-harvest flora, and that new species may continue to colonize harvested sites for more than 20 yr. Although exotic species can play a prominent floristic role in clear-cuts of the region (Isaac 1940, DeFerrari and Naiman 1994), they contributed minimally in number and cover on our sites. It is likely that their presence is largely determined by proximity to source populations, and thus by the spatial distribution, density, age, and composition of adjacent clear-cut or disturbed sites. WS1 and WS3 have remained fairly well buffered by old-growth and young, closed-canopy stands. The minor peak in exotic-species abundance in year 2 was attributable to *Senecio sylvaticus,* a European annual that has become a ubiquitous member of the regional flora. The causes and consequences of its ephemeral dominance in these systems are the subject of ongoing field experiments (Halpern et al. 1992*a,* M. Geyer *unpublished data*).

A comparison of early changes in diversity on WS1 and WS3 illustrates the importance of timing of multiple disturbance events (i.e., logging and slash burning) on the resulting richness of the invading flora. At both the plot and site levels, invaders were far more common after burning on WS1 than on WS3 (Fig. 3c–f), favored by the protracted harvest during which local populations established and spread prior to burning.

The initial survival and early recovery of residual-species diversity suggest that, at larger spatial scales (stand or watershed), old-growth understories are largely tolerant of disturbances associated with clear-cut logging and broadcast burning, a conclusion supported by earlier species- and community-level analyses (Halpern 1988, 1989, Halpern and Franklin 1990). In fact, comparable survival of species through logging and burning on WS3 suggests that the effects of canopy removal or physical soil disturbance are potentially as severe as those of fire. Floristically, 70–90% of understory taxa survived logging and burning; of the 10–30% of species that initially disappeared, most eventually recolonized or reemerged. This community-level resilience reflects a successional process driven by vegetative recovery. The regenerative structures (e.g., tubers, roots, rhizomes) of most plants are buried deeply enough to ensure survival, although species with aboveground perennating structures (e.g., *Linnaea borealis* and *Whipplea modesta*) are sensitive to burning and survive only in unburned microsites (Dyrness 1973, Halpern 1989). Disturbance tolerance and rapid resprouting and/or clonal expansion of initially dom-

TABLE 5. Constancy (percentage frequency of occurrence among stands) of species showing a significant age-class effect ($P < 0.05$, Chi-square test). Only species with greater constancy in old-growth (OG) than in mature (M) or young (Y) stands are shown.

	Washington Cascade Range				Oregon Cascade Range				Oregon Coast Range			
	Y	M	OG	*P*	Y	M	OG	*P*	Y	M	OG	*P*
Trees												
Abies amabilis	62	60	90	*	...	...	...		...	...	...	
Taxus brevifolia	46	70	90	**	61	44	79	**	0	0	55	**
Tsuga heterophylla	...	...	...		...	...	...		33	78	91	**
Tall shrubs												
Vaccinium membranaceum	15	50	80	***	...	...	...		...	...	...	
Acer circinatum	...	...	...		...	...	...		50	56	91	*
Low shrubs and Sub-shrubs												
Gaultheria ovatifolia	8	20	43	*	...	...	...		...	...	...	
Cornus canadensis	54	60	87	*	56	28	58	*	...	...	...	
Chimaphila umbellata	...	...	...		50	64	84	*	...	...	...	
Linnaea borealis	...	...	...		89	80	98	*	17	56	74	*
Berberis nervosa	...	...	...		...	...	...		67	78	100	*
Herbs, Ferns, and Fern allies												
Lycopodium clavatum	0	10	30	*	...	...	...		...	...	...	
Tiarella trifoliata var. *unifoliata*	39	70	80	*	...	...	...		...	...	...	
Achlys triphylla	77	100	100	**	...	...	...		17	67	78	**
Coptis laciniata	...	...	...		20	46	62	*	...	...	...	
Adenocaulon bicolor	...	...	...		...	...	...		33	57	86	*
Disporum hookeri	...	...	...		...	...	...		50	67	91	*
Synthyris reniformis	...	...	...		...	...	...		0	14	64	**
Lichens												
Lobaria spp.	23	30	80	***	39	64	91	***	27	33	87	***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; P values from Chi-square test for age-class effect.

inant forest shrubs (e.g., *Berberis nervosa, Gaultheria shallon, Acer circinatum,* and *Rhododendron macrophyllum*) drive the gradual decline in species heterogeneity observed prior to canopy closure. Long (1977) attributed a similar decline in species diversity to competitive exclusion by *Gaultheria shallon.*

Patterns of residual species survival and recovery at smaller spatial scales—among plots representing different soil disturbance classes—illustrate a strong relationship between disturbance intensity and diversity. On burned sites on WS1, richness and heterogeneity of forest species remained depressed relative to old-growth levels for 20 yr after burning. This potential loss of, or long-term depression of, diversity naturally leads to the question: Are there forest understory species that are eliminated by clear-cut logging and/or slash burning? Successional observations of up to 27 yr—to the point where tree canopies begin to close—suggest that there are species susceptible to these types of disturbances. Some taxa (e.g., *Chimaphila umbellata, Goodyera oblongifolia, Pyrola* spp.) appear as sensitive to removal of the tree canopy as to fire. However, there is a clear threshold effect: relatively few taxa are eliminated by physical soil disturbance or light burning, and many more, by intense fire. Loss of some species (e.g., *Xerophyllum tenax*) is difficult to explain because they are typically less sensitive to disturbance. Although local extinctions may reflect species' rarity in the preexisting forest (e.g., *Corallorhiza* spp. and *Listera cordata*), some taxa were common understory plants (e.g., *Goodyera oblongifolia, Chimaphila* spp., and *Taxus brevifolia*). Other authors have commented on the relative susceptibility of some of these species to fire (McLean 1968, Volland and Dell 1981, McCune 1982, Crane et al. 1983, Crawford 1983). Schoonmaker and McKee (1988) compared the flora of a 40-yr chronosequence of post-harvest stands with adjacent old growth and reported extirpation of only two forest species (*Corallorhiza mertensiana* and *Pterospora andromedea*). Their inferences about local extinctions, however, are limited by a lack of site-specific, pre-harvest data.

Longer term changes in diversity: patterns and mechanisms in natural forests

Empirically, our understanding of the longer term effects of forest management practices on plant species diversity is limited by an absence of community-based studies in older, managed stands. Nonetheless, to judge the magnitude of these effects, and to identify the causal mechanisms, it is critical to understand how plant species diversity and occurrence vary under natural disturbance regimes. Our interpretation of these patterns as a simple consequence of succession must be qualified, however. To characterize the relationship between age and diversity in natural forest stands, we have used space as a surrogate for time. Given the limitations of this basic assumption and the geographic

TABLE 6. Ratios of mean species cover in old-growth to cover in mature and young stands (OG/M and OG/Y, respectively) for species showing an age-class effect. Only species with greater cover in old-growth than in mature and young stands are listed.

	Washington Cascade Range			Oregon Cascade Range			Oregon Coast Range		
	OG/M	OG/Y	*P*	OG/M	OG/Y	*P*	OG/M	OG/Y	*P*
Trees									
Abies amabilis	20.0	33.3	***	···	···		···	···	
Taxus brevifolia	16.7	25.0	***	50.0	10.0	***	>100.0	>100.0	**
Tsuga heterophylla	···	···		3.0	1.9	**	4.0	50.0	**
Tall shrubs									
Vaccinium alaskaense	10.0	20.0	**	···	···		···	···	
V. membranaceum	11.1	33.3	***	···	···		···	···	
V. parvifolium	4.2	2.7	**	···	···		···	···	
Low shrubs and Sub-shrubs									
Cornus canadensis	2.8	4.2	***	···	···		···	···	
Chimaphila umbellata	2.1	9.1	***	1.1	4.2	*	···	···	
Linnaea borealis	2.0	3.3	***	2.9	2.4	***	16.7	14.3	**
Berberis nervosa	···	···		···	···		5.6	5.6	**
Herbs, Ferns, and Fern allies									
Clintonia uniflora	7.7	7.1	*	···	···		···	···	
Corallorhiza mertensiana	7.7	>100.0	*	···	···		···	···	
Goodyera oblongifolia	1.2	9.1	*	1.3	7.1	**	>100.0	2.9	*
Coptis laciniata	···	···		3.6	33.3	**	···	···	
Pyrola asarifolia	···	···		9.1	3.2	*	···	···	
Tiarella trifoliata var. *trifoliata*	···	···		>100.0	>100.0	*	···	···	
T. trifoliata var. *unifoliata*	···	···		10.0	100.0	**	···	···	
Vancouveria hexandra	···	···		1.6	11.1	**	···	···	
Achlys triphylla	···	···		1.3	25.0	***	2.5	12.5	*
Synthyris reniformis	···	···		···	···		>100.0	100.0	*
Lichens									
Lobaria spp.	100.0	50.0	***	2.6	50.0	***	33.3	111.1	***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; P values from Chi-square test for age-class effect.

breadth of our sampling, it is likely that to some extent our results have been confounded by variation in site history and environment. Several features of the sampling design and analysis were chosen to reduce these sources of variation. First, differences in site history were reduced by limiting sampling to forests that originated after stand-replacing fires. (This restriction, however, inhibits our ability to generalize to young and mature forests composed of two or more age classes, whose origin reflects multiple, lower severity fires.) Second, variation in site environment was controlled by maintaining similar levels and ranges of site characteristics among age classes (Spies 1991, Spies and Franklin 1991). Finally, analyses of individual species' distributions among age classes were limited to those elevational and latitudinal zones within which species occurred (see *Methods*). Although attempts have been made to reduce the confounding effects of site history and environment, inferences about natural changes in diversity and species' occurrence still should be made with caution.

Temporal trends in overstory diversity were neither strong nor consistent among provinces. Nonetheless, they suggested greater diversity early and late in succession. The peak in diversity in younger stands (particularly in the two more southern provinces) reflects persistence of early successional hardwoods (e.g., *Alnus, Castanopsis,* and *Arbutus*) through canopy closure and subsequent loss as stands mature. Increased diversity in old growth reflects recruitment of shade-tolerant conifers (*Abies, Taxus, Thuja,* and *Tsuga*) into the overstory stratum. Despite these numerical trends in diversity, few species were restricted to, or absent from, an age class, and few showed significant age-class effects for basal area. *Taxus brevifolia* was the principal exception. Sensitive to fire (Stickney 1980, McCune 1982, Crawford 1983), as observed on our experimental watersheds, and slow growing (Daoust et al. 1992), it may take centuries for suppressed individuals of *Taxus* to emerge from the understory. Maximum size and population densities are found in old-growth stands that have been free of low- and moderate-intensity ground fires for centuries. *Taxus* shows similar old-growth dependence in mixed coniferous forest of the Rocky Mountains in Montana (McCune and Allen 1985). The continuous presence of most other tree taxa through succession is a consequence of three general phenomena. First, individuals of most species can establish fairly early in succession, although shade-tolerant taxa (e.g., *Thuja*) may not reestablish for one or more centuries under particular environmental or historical conditions (Klopsch 1985).

Second, with the exception of shade-intolerant hardwoods (e.g., *Alnus*), longevities of ≈300–1000 yr or more for most trees (Franklin and Dyrness 1973) ensure their long-term presence in these forests. Finally, shorter lived, but moderately shade-tolerant hardwoods (*Acer* and *Cornus*) can persist under canopy gaps in mature and old-growth stands.

As with the overstory, diversity of understory species increased gradually with time. However, the increase may be stronger than indicated by this study. The wide range of ages (≈130–900 yr) represented by the old-growth age-class may obscure a steeper increase, followed by a decline, as more open, *Pseudotsuga*-dominated stands are replaced by denser forests dominated by shade-tolerant *Tsuga.* The suggestion of a steeper rise is supported by patterns in the Coast Range. Here, where understory richness and heterogeneity showed the strongest increase with age, old-growth stands were ≈100 yr younger, and basal area of *Tsuga* was 40–70% lower than in the Cascade Range. Likewise, in *Thuja–Tsuga* forests of Montana, Habeck (1968) found lower species richness in stands dominated by *Tsuga* than in younger stands containing both early and late-successional tree species. Berg and Clement (1992) also report marked increases in herb and shrub diversity between mature (80 yr) and old-growth (>180 yr) stands in southwestern Washington.

A majority of understory species did not show a strong association with a particular successional stage. Moreover, the sheer number of individual statistical tests (398) necessitates caution in making inferences about species with significant results. Given a significance level of $P < 0.05$, we would expect 5% of the tests to yield significant results purely by chance. However, 10–20% of understory species differed significantly in abundance among age classes within a province, with a majority of these most abundant in old growth. For many, differences were greater for cover than for frequency, suggesting that species are not strongly restricted to a particular successional stage, but differ in their abundance within each stage. This broad temporal distribution of species may stem, in part, from the scattered occurrence in younger stands of ecological conditions characteristic of old growth: gaps, deeply shaded microsites, and accumulations of coarse woody debris—legacies of the previous forest (Spies et al. 1988, Hansen et al. 1991).

Many of the understory species that showed maximal development in old growth were also identified as sensitive to disturbance on the experimental watersheds (e.g., *Achlys triphylla, Chimaphila umbellata, Clintonia uniflora, Corallorhiza mertensiana, Cornus canadensis, Disporum* spp., *Goodyera oblongifolia, Pyrola asarifolia, P. picta, Synthyris reniformis, Taxus brevifolia,* and *Tiarella trifoliata*). Furthermore, a subset of these (e.g., *Cornus canadensis, Goodyera oblongifolia, Pyrola asarifolia, Tiarella trifoliata,* and *Taxus brevifolia*) have been associated with late-successional, coniferous forests elsewhere: in the western Cascade Range of Oregon (Stewart 1988), in Mount Rainier National Park (Moir et al. 1979), in the Rocky Mountains of Montana (Habeck 1968, Antos and Shearer 1980, McCune and Allen 1985) and in southeast Alaska (Alaback 1982). On the other hand, some species associated with mature or old-growth forests in our region (e.g., *Adenocaulon bicolor, Vaccinium membranaceum,* and *V. parvifolium*), have different successional affinities elsewhere (Habeck 1968, Alaback 1982).

Assuming that these patterns of diversity and species association are a natural consequence of succession, we propose three mechanisms to explain the greater diversity and the close association of some species with old growth. First, levels of resources, particularly light, change as forests assume old-growth characteristics. Although gaps in the overstory canopy are more common in old-growth than in mature stands, *Tsuga heterophylla* can become a prominent component of older stands. Light intensities beneath these *Tsuga* canopies are lower than under young or mature forests dominated by *Pseudotsuga* (Spies et al. 1990). The suite of herbs and sub-shrubs that characterize these deeply shaded microsites (e.g., *Clintonia biflora, Cornus canadensis, Synthyris reniformis,* and *Tiarella trifoliata*) appear to exhibit a strategy of stress tolerance (sensu Grime 1977). However, the affinity of these species for old growth may simply stem from a physiological requirement for the relatively cool, moist conditions found during the otherwise warm, dry summers. Buffered by dense, multi-layered canopies, humidity as well as air and soil temperature fluctuate minimally (Chen 1991). Levels of soil moisture may also be greater, a consequence of the large accumulations of coarse woody debris on the forest floor (Spies and Franklin 1991).

On the other hand, the effects of resource limitation may operate indirectly, through changes in the competitive abilities of potentially dominant understory plants. In younger forests with more uniform, open conditions, aggressive, less shade-tolerant taxa such as *Gaultheria shallon* can form dense monocultures that exclude these smaller, less robust herbs and sub-shrubs (Long and Turner 1975, Long 1977). In contrast, under lower levels of light, shade-tolerant herbs are competitively superior. This switch in composition is consistent with predictions of the "resource-ratio" hypothesis (Tilman 1985), i.e., that species' replacements during succession reflect changes in the abilities of species to capture resources as levels of resources change.

A second mechanism that may explain the greater diversity of plant species in old-growth than in younger stands is an increase in the spatial heterogeneity of resources and environments. It has been hypothesized that the degree of spatial variation in available habitats (e.g., the "niche diversification" hypothesis of Connell [1978]) or in resource availability (Tilman 1982), may control species diversity. Empirical support comes from a variety of terrestrial ecosystems (Williams et al. 1969, Shafi and Yarranton 1973, Collins and Barber 1985). The gradual transition from mature to old-growth *Pseudotsuga* forest is accompanied by an increase in vertical and horizontal complexity. Both the height and number of canopy layers increase, and the diameter distributions of trees become more variable (Spies and Franklin 1991). Relatively uniform stands dominated by *Pseudotsuga* are gradually replaced by a mosaic of old-growth *Pseudotsuga,* dense patches of *Tsuga,* and canopy gaps; these overlie large accumulations of woody debris and tip-up mounds. The complexity of forest structure creates a shifting mosaic of resources and environments that potentially support a greater diversity of species, or species that, morphologically or physiologically, can capitalize on the spatial variability. *Linnaea borealis,* for example, can take advantage of this resource heterogeneity. It can persist with low abundance under deep shade, but can spread rapidly by stolons to occupy newly formed gaps (Antos and Zobel 1984, Halpern 1989).

The most conspicuous response to an increase in the vertical diversity and complexity of forest canopies with stand age was the strong association of the epiphytic lichens, *Lobaria* spp., with old growth. Although only a small portion of the cryptogamic flora was sampled in our studies, given the dramatic differences in *Lobaria* presence and abundance among age classes, we hypothesize that the taxonomic diversity of arboreal bryophytes and lichens and other vascular epiphytes in *Pseudotsuga* forests show similar responses with stand age. Many species of bryophytes and lichens are dependent on old trees and old-growth forests elsewhere in North America and Europe (Rose 1976, Söderström 1988, Broad 1989, Lesica et al. 1991, Laaka 1992, McCune 1993*b*). Their absence in younger stands reflects, in part, a combination of narrow substrate and microclimatic requirements, limited dispersal, and slow growth (citations in Forest Ecosystem Management Assessment Team 1993).

The final mechanism contributing to increased diversity with stand age and to the strong association of some species with old growth, may be species' sensitivity to fire and slow rates of reestablishment and growth. For example, *Taxus brevifolia* is typically killed by fires of light to moderate severity (Stickney 1980, McCune 1982, Crawford 1983, Halpern 1989); its subsequent establishment depends on seed dispersed from off site. Coupled with an inherently slow growth rate, it may take centuries for population densities to recover or for individuals to reenter lower canopy layers. Many species associated with natural, old-growth stands also appear sensitive to fire, as suggested by their extirpation from burned plots on our experimental watersheds (e.g., *Achlys triphylla, Chimaphila umbellata, Corallorhiza mertensiana, Disporum hookeri, Goodyera oblongifolia, Pyrola asarifolia, Synthyris reniformis, Taxus brevifolia, Tiarella trifoliata,* and *Vaccinium membranaceum*). Yet the occurrence of these species in old growth does not imply that these stands have been free of fire since their inception. Rather, they have experienced periodic, localized, low- to moderate-intensity disturbance (e.g., ground fire, single tree or group windthrow), a pattern confirmed by stand- and landscape-level reconstructions of disturbance history (Stewart 1986*a, b,* Teensma 1987, Morrison and Swanson 1990). However, the patchy nature of these events offers greater probability for survival of individuals within relatively undisturbed microsites.

Implications and recommendations for management

The effects of forest management practices on plant species diversity in the Pacific Northwest are not well understood. This lack of basic knowledge reflects the paucity of community-level studies in managed stands, and, to some extent, the diverse and complex history of manipulation in these forests. For example, managed forests include young and mature stands on federal lands that regenerated naturally after railroad logging in the early 1900s, as well as second- and third-rotation plantations in private ownership that have been burned, treated with herbicide, fertilized, planted, and/or pruned and thinned. Given the virtual absence of data from managed stands, studies of unmanaged forests offer insights into the potential effects of silvicultural practices that alter natural successional processes.

Operating at different stages of stand development, forest management effects can be grouped into two broad categories: (1) initial effects of disturbances associated with logging and site preparation, and (2) effects of subsequent activities that directly or indirectly alter rates or patterns of succession. For most understory species in these systems, the initial effects of clear-cut logging and broadcast burning are probably no more severe that those of wildfire, although it is unclear to what extent the occurrence of these two closely timed disturbance events affect species survival or recovery. Populations of most understory species are able to recover to original levels prior to canopy closure. However, epiphytic taxa that are dependent on the existence of tree canopies (*Lobaria* spp. and other cryptogams), or species that are sensitive to fire (e.g., *Chimaphila umbellata* and *Taxus brevifolia*), may require centuries to recover.

Although initial survival and early rates of recovery of forest species are closely tied to the intensity of burning, it is more likely that frequency of disturbance limits the long-term persistence of populations. Thus, conversion to a system of frequent, short-rotation harvests may ultimately reduce populations of some species. The historical practice of complete canopy removal also minimizes the probability that strictly shade-loving plants will survive disturbance; for some understory species, removal of the tree canopy is sufficient to induce local extinction. The environmental requirements of these species, rather than the direct effects of disturbance, may limit their persistence. Consequently, the use of cooler, spring burns, or elimination of burning as a tool for site preparation, may be insufficient to maintain populations of some species if overstories are completely removed during harvest. On the other hand, retention of large canopy trees in aggregates or islands may ameliorate ground-layer environments enough to provide refugia, and, thus, sources for recolonization of more disturbed microsites. Tree clumps are also critical for maintaining local populations of arboreal cryptogams. Large trees with emergent canopies and well-developed lateral branches provide the best substrates for many lichens (Forest Ecosystem Management Assessment Team 1993). Moreover, because of the limited dispersal and slow growth of most lichens, it may be necessary to retain the same trees through several rotations.

Silvicultural alternatives to clear-cutting and even-aged management have been proposed, including "retention harvest" and uneven-aged systems (Franklin 1989, 1992, Hansen et al. 1991, Forest Ecosystem Management Assessment Team 1993, McComb et al. 1993, Thomas et al. 1993). It is likely that at the stand level; group selection, "green-tree" retention, and dispersed cutting—approaches designed to create structurally diverse environments for wildlife—will create microhabitats that ensure persistence of canopy-dependent and disturbance-sensitive plant species. Leaving live canopy trees in cutting units may also maintain and promote regeneration of canopy and subcanopy species such as *Taxus,* that would otherwise recolonize seral forests more slowly. However, it is unclear to what extent altered microclimates and increased herbivory from ungulates would affect survival of remnant individuals of *Taxus* (Daoust et al. 1992).

In examining natural successional trends, we have emphasized contrasts in diversity and species association between age classes. The contrasts between managed and unmanaged stands of similar age may be more striking. For example, the traditional practice of removing most merchantable wood during clear-cut logging contrasts sharply with patterns created by natural disturbances. Wildfires and windstorms produce much of the structural complexity found on the forest floor. Logs and tip-up mounds, legacies of former stands, can persist for centuries. Model results of Spies and Cline (1988) predict that successive cycles of clear-cutting reduce log abundances to 30% and 6% of pre-harvest levels after one and two, 100-yr rotations, respectively. Coarse woody debris serves as critical rooting sites for some species (e.g., *Tsuga heterophylla*; Harmon and Franklin 1986, see also Forest Ecosystem Management Assessment Team 1993), and as structural and functional elements that increase the spatial heterogeneity of moisture and nutrients (Harmon et al. 1986); long-term reductions in coarse woody debris may therefore have significant consequences for plant species diversity during all stages of forest development. Thus, silvicultural prescriptions need to incorporate both the retention of large structural elements (live trees, snags, and logs) from previous stands, and the production of similar structures for future rotations. These legacies may be partly responsible for the long-term presence of many forest species through natural stand development.

Post-harvest practices may have greater consequences for plant species diversity than the direct effects of logging and burning. For example, the pattern, density, and composition of planting are critical variables in the maintenance of plant species diversity in managed forests. If stands are uniformly planted to high densities and not thinned, recovery of understory populations may not be possible prior to canopy closure. Likewise, if tree composition is strongly controlled to favor one species such as *Pseudotsuga,* not only will tree diversity be minimized, but understory diversity will also suffer from a horizontally and vertically simple canopy structure. In young natural forests, and in managed stands in which they have not been removed, hardwoods such as *Alnus rubra* and *Castanopsis chrysophylla* may dominate the tree canopy. In older conifer-dominated forests, they contribute significantly to the floristic and structural diversity of a relatively species-poor overstory. Additionally, hardwoods such *Acer macrophyllum* indirectly augment local plant species diversity, as they harbor diverse communities of epiphytic bryophytes (Coleman et al. 1956).

Ultimately, practices that preclude or delay the development of old-growth attributes may result in long-term loss of species diversity. Silvicultural techniques for promoting structurally diverse, mixed-species stands have been implemented successfully in Europe and have been devised locally (Smith 1986). Until now, however, uneven-aged management has not been considered an economically viable option for managing coastal *Pseudotsuga* forests. Regardless of the structural changes that can be engineered by manipulating the composition, density, and spatial patterning of the overstory, it will be necessary to manage some stands on fairly long rotations to maintain those understory species that require long periods between catastrophic events for recovery.

Relatively little is known about landscape-scale effects of management on the dynamics of plant populations in the Pacific Northwest. However, it is likely that populations of forest understory species with low dispersal will decline in landscapes where habitats are fragmented and disturbance frequency and intensity are too high to maintain local seed sources. Conversely, ruderal species, favored by frequent and intense disturbance (Grime 1977), may become even more dominant in the disturbed habitats of increasingly fragmented landscapes. The effects of landscape fragmentation on populations of old-growth plant species have been observed in highly fragmented ecosystems of eastern North America (Matlack 1994) and Great Britain (Peterkin and Game 1984). If the landscape-scale distributions of some late-successional species in the Pacific Northwest are limited by high rates of disturbance and habitat fragmentation, then retention of specific habitat structures, maintenance of larger patches of old forest, and longer rotations should enhance the mobility and population growth of these species.

Future research

With a growing sense of urgency, silviculturists and forest managers in the Pacific Northwest are designing and implementing harvesting schemes and silvicultural systems with the expressed goal of producing structurally diverse habitats for wildlife. Although consideration of plant species diversity may be implicit in these "new" approaches, the consequences of "old" practices have not been explicitly identified. Simply, species- and community-level data from managed stands—the "controls" against which to judge the relative effectiveness of alternative approaches—are not available. Consequently, there is a clear need for basic inventory and analysis to describe and interpret existing conditions and patterns in forest understories across a spectrum of public and private lands. Uni- and multivariate analytical techniques can be used to identify and tease apart complex relationships between community attributes and site characteristics (e.g., management history, site environment, canopy structure, or stand age) and to suggest causal mechanisms for these patterns. Hypotheses generated from these correlative studies can then be tested with small-scale or stand-level experiments. Chronosequence studies of unmanaged forests illustrate that understory composition and structure may continue to change for centuries after natural disturbance. Although short-term responses of plant populations to stand-level manipulations may be indicative of future trends, longer term studies must also be conducted. As a model, the DEMO (Demonstration of Ecosystem Management Options) project, a multidisciplinary experiment on two National Forests of western Washington and Oregon, will compare the long-term response of forest ecosystems to varying the amount and pattern (i.e., dispersed vs. aggregated) of retention of live trees, including the response of forest overstory and understory communities (see DeBell and Curtis 1993).

Landscape-level research that addresses the response of plant populations to the spatial scale or to the spatial patterning of forest management activities is also necessary. For example, there may be subtle but important effects on seed availability and dispersibility that cannot be discerned with stand-level studies. Modeling of population and species dynamics may be a necessary component of these studies, because of the logistic and financial constraints of landscape-scale surveys and experiments.

Finally, the dearth of information on the life histories of many forest understory plants underscores the need for further autecological research in the region. We know very little about the habitat requirements, tolerances of disturbance, responses to altered canopy and ground-layer conditions, and reproductive ecologies of many vascular and non-vascular plants in Pacific Northwest forests. Such knowledge is critical in managing for rare and sensitive taxa. Our understanding of the mechanisms by which forest management practices influence plant species, and ultimately the success of forest managers in maintaining or enhancing levels of biological diversity, hinge on the acquisition of such knowledge.

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LITERATURE CITED

Agee, J. K. 1991. Fire history of Douglas-fir forests in the Pacific Northwest. Pages 25–33 *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report **PNW-GTR-285**.

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

Antos, J. A., and R. C. Shearer. 1980. Vegetation development on disturbed grand fir sites, Swan Valley, northwestern Montana. USDA Forest Service Research Paper **INT-251**.

Antos, J. A., and D. B. Zobel. 1984. Ecological implications of belowground morphology of nine coniferous forest herbs. Botanical Gazette **145**:508–517.

AuClair, A. N., and F. G. Goff. 1971. Diversity relations of upland forests in the western Great Lakes area. American Naturalist **105**:499–528.

Berg, D. R., and N. C. Clement. 1992. Differences in diversity of vegetation between mature and old-growth forests in the Cascade Range of the Pacific Northwest, USA. Northwest Environmental Journal **8**:190–193.

Bierlmaier, F. A., and A. McKee. 1989. Climatic summaries and documentation for the primary meteorological station, H. J. Andrews Experimental Forest, 1972 to 1984. USDA Forest Service General Technical Report **PNW-GTR-242**.

Bolsinger, C. L., and K. L. Waddell. 1993. Area of old-growth forests in California, Oregon, and Washington. USDA Forest Service Resource Bulletin **PNW-RB-197**.

Broad, K. 1989. Lichens in southern woodlands. Forestry Commission Handbook Number 4. NMSO Publications, London, England.

Chen, J. 1991. Edge effects: microclimatic pattern and biological responses in old-growth Douglas-fir forests. Dissertation. University of Washington, Seattle, Washington, USA.

Childs, T. W. 1970. Laminated root rot of Douglas-fir in western Oregon and Washington. USDA Forest Service Research Paper **PNW-102**.

Christensen, N. L., and R. K. Peet. 1984. Measures of natural diversity. Pages 43–58 *in* J. L. Cooley and J. H. Cooley, editors. Natural diversity in forest ecosystems. Institute of Ecology, University of Georgia, Athens, Georgia, USA.

Clebsch, E. E. C., and R. T. Busing. 1989. Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. Ecology **70**:728–735.

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institute of Washington Publication **242**.

Coleman, B. B., W. C. Muenscher, and D. R. Charles. 1956. A distributional study of the epiphytic plants of the Olympic Peninsula, Washington. American Midland Naturalist **56**:54–87.

Collins, S. L., and S. C. Barber. 1985. Effects of disturbance on diversity in mixed-grass prairie. Vegetatio **64**:87–94.

Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. Science **199**:1302–1310.

Crane, M. F., J. R. Habeck, and W. C. Fischer. 1983. Early postfire revegetation in a western Montana Douglas-fir forest. USDA Forest Service Research Paper **INT-319**.

Crawford, R. C. 1983. Pacific yew community ecology in north-central Idaho with implications to forest land management. Dissertation. University of Idaho, Moscow, Idaho, USA.

Daoust, D., T. Atzet, F. Betlejewski, C. Bolsinger, R. Crawford, D. Doede, P. Green, J. Kitzmiller, S. Martinson, B. McComb, D. Minore, T. Spies, and R. Ward. 1992. Interim guide to conservation and management of Pacific yew. A report of the Pacific yew technical committee. USDA Forest Service, Pacific Northwest Region, Portland, Oregon, USA.

Darwin, C. 1859. On the origin of species. First edition. John Murray, London, England. (Reprinted by Watts and Company, London, England [1950] and Harvard University Press, Cambridge, Massachusetts, USA [1964]).

DeBell, D. S., and R. O. Curtis. 1993. Silviculture and new forestry in the Pacific Northwest. Journal of Forestry **91**: 25–30.

DeFerrari, C. M., and R. J. Naiman. 1994. A multi-scale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. Journal of Vegetation Science **5**:247–258.

Dyrness, C. T. 1969. Hydrologic properties of soils on three small watersheds in the western Cascades of Oregon. USDA Forest Service Research Note **PNW-11**.

———. 1973. Early stages of plant succession following logging and slash burning in the western Cascades of Oregon. Ecology **54**:57–68.

Dyrness, C. T., J. F. Franklin, and W. H. Moir. 1974. A preliminary classification of forest communities in the central portion of the western Cascades of Oregon. US/IBP, Coniferous Forest Biome Bulletin 4. Coniferous Forest Biome, College of Forest Resources, University of Washington, Seattle, Washington, USA.

Forest Ecosystem Management Assessment Team. 1993. Forest ecosystem management: an ecological, economic, and social assessment. Joint publication of the United States Department of Agriculture: Forest Service; United States Department of Commerce: National Oceanic and Atmospheric Administration and National Marine Fisheries Service; United States Department of the Interior: Bureau of Land Management, Fish and Wildlife Service, and National Park Service; and United States Environmental Protection Agency, Washington, D.C., USA.

Franklin, J. F. 1982. Old-growth forests in the Pacific Northwest: an ecological view. Pages 5–27 *in* Old-growth forests: a balanced perspective. University of Oregon, Bureau of Governmental Research and Service, Eugene, Oregon, USA.

———. 1989. Towards a new forestry. American Forestry **95**:37–44.

———. 1992. Scientific basis for new perspectives in forests and streams. Pages 25–72 *in* R. J. Naiman, editor. Watershed management: balancing sustainability and environment change. Springer-Verlag, New York, New York, USA.

———. 1993. Lessons from old-growth: fueling controversy and providing direction. Journal of Forestry **91**:10–13.

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-118**.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service General Technical Report **PNW-8**.

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

Gauch, H. G., Jr. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, England.

Gedney, D. R. 1981. The occurrence of laminated root rot on nonfederal timberland in northwestern Oregon. USDA Forest Service Research Note **PNW-381**.

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

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist **111**:1169–1194.

Grubb, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Reviews **52**:107–145.

Habeck, J. R. 1968. Forest succession in the Glacier Peak cedar–hemlock forests. Ecology **49**:872–880.

Halpern, C. B. 1987. Twenty-one years of secondary succession in *Pseudotsuga* forests of the western Cascade Range, Oregon. Dissertation. Oregon State University, Corvallis, Oregon, USA.

———. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology **69**: 1703--1715.

———. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology **70**:704–720.

Halpern, C. B., J. A. Antos, K. Cromack, Jr., and A. M. Olson. 1992*a*. Species' interactions and plant diversity during secondary succession. Northwest Environmental Journal **8**: 203–205.

Halpern, C. B., and J. F. Franklin. 1990. Physiognomic development of *Pseudotsuga* forests in relation to initial structure and disturbance intensity. Journal of Vegetation Science **1**:475–482.

Halpern, C. B., J. F. Franklin, and A. McKee. 1992*b*. Changes in plant species diversity after harvest of Douglas-fir forests. Northwest Environmental Journal **8**:205–207.

Hansen, A. J., S. L. Garman, B. Marks, and D. L. Urban. 1993. An approach for managing vertebrate diversity across multiple-use landscapes. Ecological Applications **3**: 481–496.

Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests. BioScience **41**:382–392.

Harmon, M. E., and J. F. Franklin. 1986. Tree seedlings on logs in *Picea–Tsuga* forests of Oregon and Washington. Ecology **70**:48–59.

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. University of Chicago Press, Chicago, Illinois, USA.

Harris, L. D., C. Maser, and A. McKee. 1982. Patterns of old-growth harvest and implications for Cascades wildlife. Transactions of the North American Wildlife and Natural Resources Conference **47**:374–392.

Hawk, G. M. 1979. Vegetation mapping and community description of a small western Cascade watershed. Northwest Science **53**:200–212.

Hemstrom, M. A. 1979. A recent disturbance history of forest ecosystems at Mount Rainier National Park. Dissertation. Oregon State University, Corvallis, Oregon, USA.

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

Hemstrom, M. A., S. E. Logan, and W. Pavlat. 1987. Plant association and management guide, Willamette National Forest. R6-Ecol-257-B-86. USDA Forest Service, Pacific Northwest Region, Portland, Oregon, USA.

Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology **54**:427–432.

———. 1979. DECORANA: a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ecology and Systematics, Cornell University, Ithaca, New York, USA.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, Washington, USA.

Hitchcock, C. L., A. Cronquist, M. Ownbey, and J. W. Thompson. 1969. Vascular plants of the Pacific Northwest. Volumes 1–5. University of Washington Press, Seattle, Washington, USA.

Hopwood, D., and L. Island. 1991. Principles and practices of new forestry. Land Management Report 71. British Columbia Ministry of Forests, Victoria, British Columbia, Canada.

Huston, M. 1979. A general hypothesis of species diversity. American Naturalist **113**:81–101.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? American Naturalist **93**:145–159.

Isaac, L. A. 1940. Vegetative succession following logging in the Douglas-fir region with special reference to fire. Journal of Forestry **38**:716–721.

Kessler, W. B., H. Salwasser, C. W. Cartwright, Jr., and J. Caplan. 1992. New perspectives for sustainable natural resource management. Ecological Applications **2**:221–225.

Klopsch, M. W. 1985. Structure of mature Douglas-fir stands in a western Oregon watershed and implications for interpretation of disturbance history and succession. Thesis. Oregon State University, Corvallis, Oregon, USA.

Laaka, S. 1992. The threatened epixylic bryophytes in old primeval forests in Finland. Biological Conservation **59**: 151–154.

Lesica, P., B. McCune, S. V. Cooper, 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.

Lippke, B., and C. D. Oliver. 1993. Managing for multiple values: a proposal for the Pacific Northwest. Journal of Forestry **91**:14–18.

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

Long, J. N., and J. Turner. 1975. Aboveground biomass of understory and overstory in an age sequence of four Douglas-fir stands. Journal of Applied Ecology **12**:179–188.

Loucks, O. L. 1970. Evolution of diversity, efficiency, and community stability. American Zoologist **10**:17–25.

Lubchenco, J., A. M. Olson, L. B. Brubaker, S. R. Carpenter, M. M. Holland, S. P. Hubbell, S. A. Levin, J. A. MacMahon, P. A. Matson, J. M. Melillo, H. A. Mooney, C. H. Peterson, H. R. Pulliam, L. A. Real, P. J. Regal, and P. G. Risser. 1991. The sustainable biosphere initiative: an ecological research agenda. Ecology **72**:371–412.

Lynott, R. E., and O. P. Cramer. 1966. Detailed analysis of the 1962 Columbus Day windstorm in Oregon and Washington. Monthly Weather Review **94**:313–339.

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution **17**:373–387.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey, USA.

Margalef, D. R. 1958. Information theory in ecology. General Systems Bulletin **3**:36–71.

Matlack, G. R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. Ecology **75**:1491–1502.

May, R. M. 1988. How many species are there on Earth? Science **241**:1441–1449.

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.

McCune, B. 1982. Site, history, and forest dynamics in the Bitterroot Canyons, Montana. Dissertation. University of Wisconsin, Madison, Wisconsin, USA.

———. 1993*a*. Epiphyte litter pickup—methods manual. Internal methods manual, Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon, USA.

———. 1993*b*. Gradients in epiphyte biomass in three *Pseudotsuga–Tsuga* forests of different ages in western Oregon and Washington. Bryologist **96**:405–411.

McCune, B., and T. F. H. Allen. 1985. Forest dynamics in the Bitterroot Canyons, Montana. Canadian Journal of Botany **63**:377–383.

McLean, A. 1968. Fire resistance of forest species as influenced by root systems. Journal of Range Management **22**: 120–122.

Means, J. E. 1982. Developmental history of dry coniferous forests in the western Oregon Cascades. Pages 142–158 *in* J. E. Means, editor. Forest succession and stand development research in the Northwest. Forestry Research Laboratory, Oregon State University, Corvallis, Oregon, USA.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist **130**:730–757.

Moir, W. H., F. D. Hobson, M. Hemstrom, and J. F. Franklin. 1979. Forest ecosystems of Mount Rainier National Park. Pages 201–208 *in* R. M. Linn, editor. Proceedings of the first conference on scientific research in the National Parks. Volume 1. United States Department of the Interior, National Park Service Transactions and Proceedings Series, Number **5**.

Monk, C. D. 1967. Tree species diversity in the eastern deciduous forests with particular reference to North Central Florida. American Naturalist **101**:173–187.

Morrison, P. H., and F. J. Swanson. 1990. Fire history and pattern in a Cascade Range landscape. USDA Forest Service General Technical Report **PNW-254**.

Nicholson, S. A., and C. D. Monk. 1974. Plant species diversity in old field succession on the Georgia Piedmont. Ecology **55**:1075–1085.

Odum, E. P. 1969. The strategy of ecosystem development. Science **164**:262–270.

Orians, G. H., editor. 1992. Biological diversity: focus on Northwestern North America. Northwest Environmental Journal **8**.

Peet, R. K. 1974. The measurement of species diversity. Annual Review of Ecology and Systematics **5**:285–307.

Peterkin, G. F., and M. Game. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. Journal of Ecology **72**:155–182.

Pielou, E. C. 1966. Species diversity and pattern diversity in the study of ecological succession. Journal of Theoretical Biology **10**:370–383.

Reiners, W. A., I. A. Worley, and D. B. Lawrence. 1971. Plant diversity in a chronosequence at Glacier Bay, Alaska. Ecology **52**:55–69.

Rose, F. 1976. Lichenological indicators of age and environmental continuity in woodlands. Pages 297–307 *in* D. H. Brown, D. L. Hawksworth, and R. H. Bailey, editors. Lichen ecology: progress and problems. Academic Press, London, England.

Rothacher, J. C., C. T. Dyrness, and R. L. Fredriksen. 1967. Hydrologic and related characteristics of three small watersheds in the Oregon Cascades. United States Forest Service Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.

Ruggiero, L. F., K. B. Aubry, A. B. Carey, and M. H. Huff, coordinators. 1991. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report **PNW-GTR-285**.

Ruth, R. H., and R. A. Yoder. 1953. Reducing wind damage in the forests of the Oregon Coast Range. USDA Forest Service Pacific Northwest Forest and Range Experiment Station, Research Paper **7**.

Salwasser, H. 1990. Gaining perspective: forestry in the future. Journal of Forestry **88**:32–38.

SAS Institute. 1987. SAS/STAT user's guide. Version 6 edition. SAS Institute, Cary, North Carolina, USA.

Schoonmaker, P., and A. McKee. 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. Forest Science **34**:960–979.

Shafi, M. I., and G. A. Yarranton. 1973. Diversity, floristic richness, and species evenness during a secondary (post-fire) succession. Ecology **54**:897–902.

Simpson, E. H. 1949. Measurement of diversity. Nature **163**: 688.

Smith, D. M. 1986. The practice of silviculture. John Wiley & Sons, New York, New York, USA.

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

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second edition. W. H. Freeman & Company, San Francisco, California, USA.

Spies, T. A. 1991. Plant species diversity and occurrence in young, mature, and old-growth Douglas-fir stands in western Oregon and Washington. Pages 111–121 *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report **PNW-GTR-285**.

Spies, T. A., and S. P. Cline. 1988. Coarse woody debris in forests and plantations of coastal Oregon. Pages 5–24 *in* C. Maser, R. F. Tarrant, J. M. Trappe, and J. F. Franklin, technical editors. From the forest to the sea: a story of fallen trees. USDA Forest Service General Technical Report **PNW-GTR-229**.

Spies, T. A., and J. F. Franklin. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 91–109 *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report **PNW-GTR-285**.

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.

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., W. J. Ripple, and G. A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecological Applications **4**:555–568.

Stewart, G. H. 1986*a*. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Oregon Cascade Range. Canadian Journal of Forest Research **16**:558–568.

———. 1986*b*. Population dynamics of a montane conifer forest, western Cascade Range, Oregon, USA. Ecology **67**: 534–544.

———. 1988. The influence of canopy cover on understory development in forests of the western Cascade Range, Oregon, USA. Vegetatio **76**:79–88.

Stickney, P. F. 1980. Data base for post-fire succession, first 6 to 9 years, in Montana larch–fir forests. USDA Forest Service General Technical Report **INT-62**.

Swanson, F. J., and J. F. Franklin. 1992. New forestry principles from ecosystem analysis of Pacific Northwest forests. Ecological Applications **2**:262–274.

Teensma, P. D. A. 1987. Fire history and fire regimes of the central western Cascades of Oregon. Dissertation. University of Oregon, Eugene, Oregon, USA.

Thomas, J. W., M. G. Raphael, R. G. Anthony, E. D. Forsman, A. G. Gunderson, R. S. Holthausen, B. G. Marcot, G. H. Reeves, J. R. Sedell, and D. M. Solis. 1993. Viability assessments and management considerations for species associated with late-successional and old-growth forests of the Pacific Northwest. A report of the scientific analysis team. USDA Forest Service, Portland, Oregon, USA.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

———. 1985. The resource-ratio hypothesis of succession. American Naturalist **125**:827–852.

Volland, L. A., and J. D. Dell. 1981. Fire effects on Pacific Northwest forest and range vegetation. R6-RM-067. USDA Forest Service Pacific Northwest Region, Range Management and Aviation and Fire Management Report, Portland, Oregon, USA.

Westman, W. E. 1990. Managing for biodiversity. BioScience **40**:26–33.

Whittaker, R. H. 1965. Dominance and diversity in land plant communities. Science **147**:250–260.

———. 1969. Evolution of diversity in plant communities. Pages 178–195 *in* G. M. Woodwell and H. H. Smith, editors. Diversity and stability in ecological systems. Brookhaven Symposium in Biology Number 22. Brookhaven National Laboratory, Associated Universities, Upton, New York, USA.

Williams, W. T., G. N. Lance, L. J. Webb, J. G. Tracy, and M. B. Dale. 1969. Studies in the numerical analysis of complex rain forest communities. III. The analysis of successional data. Journal of Ecology **57**:515–536.

Zobel, D. B., A. McKee, G. M. Hawk, and C. T. Dyrness. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. Ecological Monographs **46**: 135–156.