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## Vascular Plant Species Diversity in Low Elevation Coniferous Forests of the Western Olympic Peninsula: A Legacy of Land Use

### Abstract

Timber management practices affect spatial patterns of seral stages and understory plant species diversity. We quantified diversity patterns in understory vascular plant species, including exotic plant species, across four broad age classes of low-elevation coniferous forests of the western Olympic Peninsula, Washington, USA—regeneration (age 0-19 years), young (20-79 years), mature (80-199 years) and late-seral ( $\geq 200$  years). Species richness varied significantly with age class: highest in newly regenerating stands, lowest in the young class, and increasing to the late-seral stage. We observed an age-class effect for total percent cover by growth form and for distribution of exotic plant species. Shrubs had highest cover in the regeneration category; forbs and subshrubs had highest cover in late-seral forest. Ferns and graminoids did not vary across age classes. Twenty percent of the species found in regeneration plots were exotic, while all species encountered in late-seral plots were native. The proportion of exotic species was intermediate in young (7%) and mature (6%) forests. On the western Olympic Peninsula the late-seral age class is the most limited in spatial extent and has the least connectivity across ownerships. Management efforts aimed at conservation of late-seral plant species at broad spatial scales will need to consider the lack of contiguity of late-seral forest and the role of ownership in its distribution.

### Introduction

Intensive timber management in the Pacific Northwest and subsequent loss and fragmentation of old forest have raised concerns about impacts on plant diversity (DeBell 1997). Silvicultural practices can affect forest biodiversity and the distribution of exotic plant species (Alaback and Herman 1988, Bailey et al. 1998, Fredericksen et al. 1999, Halpern et al. 1999, Thomas et al. 1999, Thysell and Carey 2000, Battles et al. 2001, Griffis et al. 2001). Halpern and Spies (1995) suggest that short-rotation forestry could result in local extinctions of some understory species and long-term changes in biological diversity in the Pacific Northwest. Understory plants, lichens, bryophytes, and wildlife dependent on late-seral habitat may be at particular risk (FEMAT 1993). Global proliferation of exotic plant species has been recognized as a problem because non-natives can potentially out-compete native species and affect ecosystem processes such as nutrient cycling and disturbance (D'Antonio 2000,

Simberloff 2001). The proportion of non-native species is increasing on the Olympic Peninsula; as of 1995, approximately 25% of the documented flora is non-native (Buckingham et al. 1995). In young managed forests of the western Olympic Peninsula, 50% of all germinants from the soil seed bank were exotic, ruderal forbs (Halpern et al. 1999). Occurrence of exotic plant species is typically highest in areas of high human activity and along roads, trails, and rivers. DeFerrari and Naiman (1994) found that the number of exotic plant species was 33% higher in riparian zones (where disturbance is frequent) than in adjacent uplands in the Olympic Peninsula. These species comprised almost 50% of the total understory cover in red alder (*Alnus rubra* Bong.) flats along the Hoh River (Fonda 1974).

Data characterizing understory species diversity in these coastal, low-elevation forests are limited. Previous work has described the composition and zonal distribution of species (Fonda and Bliss 1969, Franklin and Dyrness 1988, Henderson et al. 1989). Soil seed bank properties (Halpern et al. 1999) and below-ground traits of herbaceous species (Lezberg et al. 1999) have been studied in young, closed-canopy forests. Species composition and abundance have been studied over successional

<sup>1</sup>Author to whom correspondence should be addressed.  
E-mail: marnie.tyler@ecolution.us.com

<sup>2</sup>Current address: *ECOLUTION*, 1910 East Fourth Avenue, PMB 193, Olympia, WA 98506 USA

seres on the Olympic Peninsula (Lezberg 1998), on nearby Vancouver Island (Ryan et al. 1998), in the western Cascade Range of Washington and Oregon (Halpern 1988, Schoonmaker and McKee 1988, Halpern and Spies 1995), and in the Oregon Coast Range (Halpern and Spies 1995).

There is limited knowledge of the amount and spatial distribution of stand ages across the landscape and the degree of connectivity of late-seral forest ecosystems in the Pacific Northwest (but see Morrison 1990, Holthausen et al. 1995). Spies et al. (1994) compared rates of forest clearing and fragmentation across different land ownerships in the Willamette National Forest (Oregon). In a similar study, Turner et al. (1996) quantified landscape pattern of three vegetation types across different ownerships in the western Olympic Peninsula and the Appalachian Highlands and compared changes in forest clearing over time.

In this study, we characterized patterns of species diversity and distribution in coastal coniferous forests of the western Olympic Peninsula over four seral stages: regeneration (0-19 years), young (20-79 years), mature (80-199 years), and late-seral ( $\geq 200$  years) forest. We examined the relationship between age class and species diversity, constancy, and percent cover. We compared patterns of diversity, constancy, and percent cover between native and exotic plant species. Finally, we quantified the spatial extent of the four age classes and assessed the influence of land ownership on their distribution and associated patterns of plant species diversity.

This is the first analysis of species diversity of Washington's coastal forests that spans all stages of the sere. Stand-level data allow for characterization of community composition and abundance patterns at a fine resolution. Analysis at a broader spatial scale provides a coarse snapshot of diversity patterns across the western Olympic Peninsula that can assist forest planning and policy development in the context of multiple ownerships and management objectives (Tyler and Peterson 2004).

## Methods

### Study Area

The western Olympic Peninsula is located between the Pacific Ocean and the steep slopes of the Olympic Mountains in the northwest corner

of Washington State. The study area (Figure 1) is 384,687 ha in size and includes areas within the Bogachiel, Hoh, Clearwater, Queets, Quinalt and Humptulips River drainages (124°26'W, 47°18'N to 123°20'W, 47°54'N). The focus of this study is on low elevation forests; we selected 1200 m as an upper elevation bound in each drainage.

The climate is maritime, characterized by moderate, wet winters and cool, dry summers. Mean January temperature over the last 50 years was 4°C at the Clearwater weather station, and mean August temperature was 15°C (NCDC 1931-1999). Annual precipitation averages 300 cm (NCDC 1931-1999) and falls primarily as rain; areas over 700 m elevation receive precipitation primarily as snow (Henderson et al 1989). Summer fog is common at lower elevations and is important in ameliorating moisture stress during dry summer months (Franklin and Dyrness 1988).

Natural stand-replacing disturbance events include windstorms and infrequent ( $> 250$  year), high-intensity fires (Henderson et al. 1989, Agee 1993). Fires over the last 700 years have occurred primarily on southerly aspects at mid elevations and typically have covered less than 4 km<sup>2</sup> (Henderson et al. 1989). After intense fire, reestablishment of *Pseudotsuga menziesii* (Mirbel) Franco. var. *menziesii* can be slow, lasting 35 to 75 years (Huff 1995).

### Vegetation

Forest vegetation patterns are shaped by gradients in temperature and moisture (Henderson et al. 1989). The following descriptions of vegetation are derived from Fonda (1974), Franklin and Dyrness (1988), and Henderson et al. (1989). Nomenclature follows Buckingham et al. (1995). Low elevation forests (below 200 m) along the coast and up west-facing river valleys are dominated by stands of *Picea sitchensis* (Bong.) Carr. and *Tsuga heterophylla* (Raf.) Sarg. *Alnus rubra* dominates riparian zones, with *P. sitchensis*, *Acer macrophyllum* Pursh and *Populus balsamifera* spp. *trichocarpa* T. & G. assuming dominance on the first terrace above river flats. The second and third terraces are dominated by *P. sitchensis* and *T. heterophylla*, with *T. heterophylla* assuming greater abundance on the older (third) terrace. Higher along the valley walls, *T. heterophylla*, *Pseudotsuga menziesii*, and *Thuja plicata* Donn. become the dominant woody species. Abundance

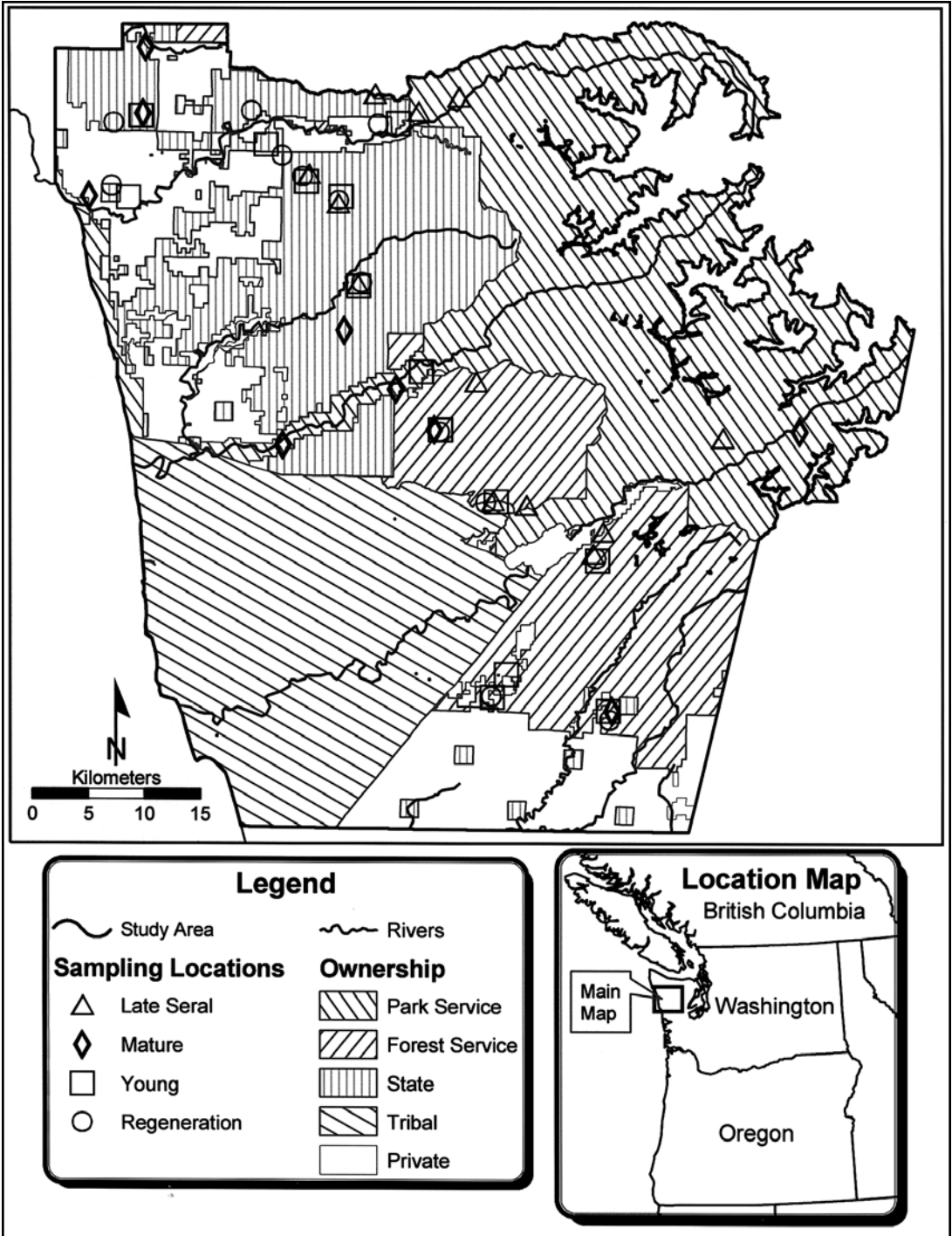


Figure 1. The study area, land ownership, and location of study sites.

of *P. menziesii* is greater on south-facing slopes and at lower elevations. Above 600 m, *Abies amabilis* (Dougl.) Forbes becomes more prevalent, replacing *P. menziesii*.

#### History of Ownership and Land Use

Current ownership includes a mix of federal, tribal, state and private lands (Figure 1): Olympic National Park (27%); Olympic National Forest (16%); Quinault Indian Nation and Hoh Tribe (21% combined); Washington Department of Natural Resources (19%); and private holdings, primarily large timber companies (17%). Virtually all lands outside Olympic National Park are currently managed for timber production or have been in the recent past. Until the early 1940s, late-seral forests on federal lands remained relatively undisturbed; by 1988 however, late-seral forests in Olympic National Forest had decreased by 76% (Morrison 1990). Timber harvest volumes reported to Washington Department of Natural Resources reached their highest values for all owners combined in the early 1970s (Larsen and Nguyen 2001). Timber harvest on federal lands virtually ceased as a result of the Interagency Scientific Committee report (Thomas et al. 1990) and implementation of the Northwest Forest Plan (USDA and USDI 1994). Washington Department of Natural Resources lands continue to be logged, although at a much slower rate than during the 1970s. Harvest on tribal and private lands has also decreased, but to a lesser extent than on public ownerships. In addition to the disturbance from logging operations themselves, 4,192 km of primary and secondary roads also open the area to human activity (Tyler 2002).

#### Site Selection

We sampled four age classes of forest: regeneration (age 0-19 years), young (20-79 years), mature (80-199 years), and late-seral (>200 years). We selected age classes to parallel Oliver's general model for stand development (1981). The regeneration class corresponds to Oliver's "stand initiation phase" dominated by shrubs and saplings. Young stands characterize the "stem exclusion phase" (post canopy closure) and consist of young, dense forest with very low understory light levels. In mature stands, stem density has declined and canopy gaps result in increased light to the forest floor with concomitant increases in understory abundance and tree regeneration. Late-seral stands coincide

with those characteristics of old-growth forest: large trees (> 100 cm diameter), complex, multi-storied canopy structure, large standing dead trees (> 60 cm in diameter and > 15 m in height), and large downed logs (> 50 metric tons per hectare) (Franklin and Spies 1983).

To select potential sampling locations (stands) we mapped each age class using 1997 LANDSAT Thematic Mapper images and stand origination data from state (Washington Department of Natural Resources) and federal (Olympic National Forest) landowners. We used land ownership, elevation, and proximity to other potential sites to screen for potential stands. We attempted to sample comparable numbers of stands in each class ( $n = 9$  to 14) and to distribute stands across the study area as evenly as possible. Large tracts of late-seral forest are extremely rare in areas where timber management occurs. Outside federal ownerships these stands are small and their accessibility is limited. Thus most late-seral stands sampled were within Olympic National Park; stands representing other classes were distributed across Washington Department of Natural Resources and Olympic National Forest lands. Within a drainage, we attempted where possible to "block" on geographical and environmental differences by selecting groups of stands to include regeneration, young, and mature stands in close proximity. When several such groups were available, we chose a group at random. Although including private and tribal lands in the sampling would have broadened the scope of analysis, we did not have access to those lands. Thus, we sampled only public lands (Olympic National Park, Olympic National Forest, and Washington Department of Natural Resources). To maximize the number of stands relative to available time and financial resources, we restricted sites to those with road accessibility; all stands were located within 4 km of a road.

#### Data Collection

We sampled the 48 selected stands between June and October of 1998 and 1999. We sampled three plots within each stand. We established circular plots of 0.01 ha in the young and regeneration classes, and 0.05 ha plots in the mature and late-seral classes where tree stem densities are much lower. Within each plot, we counted all trees  $\geq 1.4$  m tall by species. We measured canopy cover at plot center with four readings (one in each cardinal bearing) using a moosehorn densiometer.

We measured canopy height of codominant trees using a clinometer. We recorded slope, aspect, elevation, and spatial reference coordinates. We cored two to three dominant or co-dominant trees to confirm stand age. We established a single 1-m<sup>2</sup> quadrat 10 m from the plot center at a randomly selected bearing. Within the quadrat, we visually estimated the percent cover of each herbaceous and shrub species.

## Statistical Analyses

### Stand Structure and Environment

We generated stand-level means from the three plots for the variables of stem density, canopy height, slope, elevation, canopy cover, and aspect (expressed as the cosine of the angle, as a measure of southness [-1] and northness [+1]). For each of these variables, we used analysis of variance (ANOVA) to test for differences among age classes. Where we detected a significant effect of age class ( $P = 0.05$ ), we compared means with Tukey-Kramer multiple comparison tests (Zar 1996).

### Species Diversity

We used two indices to compare patterns of species diversity: species richness (the total number of species present) and the reciprocal of Simpson's diversity index, which incorporates the relative abundance of species (cover in this case) and is equivalent to  $(1/D)$ , or  $1/(\sum p_i^2)$ , where  $p_i$  is the proportional cover of species  $i$ . We calculated these statistics at two scales: 1 m<sup>2</sup> (one quadrat per plot) and 3 m<sup>2</sup> (three quadrats per stand). Thus for species richness at the 1-m<sup>2</sup> scale, we tallied the number of species in each quadrat and calculated the mean of the three quadrats in each stand (resulting in the mean number of species per m<sup>2</sup>). At the 3-m<sup>2</sup> scale, we tallied the number of unique species across the three quadrats in each stand. We took similar steps to generate averages for the reciprocal of Simpson's diversity index.

We tested for age-class effects on species richness and the reciprocal of Simpson's diversity index at both spatial scales using ANOVA. Where we detected a significant effect of age class, we compared means with a Tukey-Kramer multiple comparison tests. We log-transformed richness data at the 3-m<sup>2</sup> scale to achieve a normal distribution of residuals. Finally, we used dominance-diversity

curves (Whittaker 1975) to compare the richness and distribution of abundance of species among age classes.

We also grouped species by origin (native versus exotic) based on Buckingham et al. (1995) and calculated species richness for each group at the 1-m<sup>2</sup> scale. Members of the genus *Poa* (which could not be identified to species) were not included in this analysis because both native and exotic plant species occur in the study area. We tested for age-class effects on species richness of native and exotic plant species at 1 m<sup>2</sup> using ANOVA; where we detected a significant age class effect, we compared means using a Tukey-Kramer multiple comparison test.

### Plant Abundance

We tested for age-class effects on plant abundance by growth form and origin, followed by individual tests by species. We used ANOVA to compare total understory plant cover (sum of individual species), cover of major growth forms (shrubs, forbs and sub-shrubs, ferns, and graminoids), and total cover of natives and exotics among age classes. To test for total understory plant cover, we summed the cover of all species in each 1-m<sup>2</sup> quadrat and calculated a mean for each stand. We used the same approach for growth forms and plant origins. We calculated constancy (the proportion of stands in which a species occurred) for each species in each age class. We used multiway contingency tables (4 x 2) to test whether species constancy was independent of age class (Manly 1991). Entries in the two columns for each of the four age classes were constancy and N minus constancy for the cells representing presence and absence, respectively. We tested the  $P$ -values for the Chi-squared statistics from each individual species for significance at  $P = 0.05$  by a Monte Carlo procedure in which we generated a binomial random variable for each cell, with the mean for "presence" cells equal to the mean constancy across all age classes and the mean for "absence" cells equal to N minus mean constancy. We generated Monte Carlo  $P$ -values from Chi-squared tests for each of 1000 randomizations. The true  $P$ -value from the data was set equal to its rank among the 1000 Monte Carlo  $P$ -values, divided by 1000. We attempted to test all 67 species, however, several species occurred at very low constancies and thus the reference distribution contained many null

values. In these cases, we could not compute a test statistic. As a result, we tested only 17 species. We also tested these 17 species for an effect on cover using separate ANOVAs ( $P = 0.05$ ), followed by Tukey-Kramer multiple comparison tests as appropriate. We used the statistical package S-Plus (MathSoft, v4.0, 1997) for all analyses.

### Spatial Distribution of Age Classes

The age-class map used to identify potential field sites proved to have classification errors due to outdated stand origination data (resulting in the unbalanced number of stands among age classes). We deemed it desirable to have a consistent data source for the age-class spatial analysis. We thus developed a second age classification after field sampling had been completed. By this time, more current and comprehensive data sources were available in the form of the Interagency Vegetation Mapping Project (IVMP, USDI and USDA, 2001a) “continuous quadratic mean diameter” data layer. This layer depicts mean diameter of dominant and codominant trees. The data were derived from a supervised classification of 1996 Thematic Mapper imagery (25-m resolution). This classification process used field data collected by the USDI Bureau of Land Management (Current Vegetation Survey) and USDA Forest Service (Forest Inventory Analysis) to model, test and assess accuracy (USDI, and USDA 2001b). We compared the IVMP quadratic mean diameter values with 144 plots of known age as determined by tree cores collected

between 1998 and 2000. We used linear regression to identify relationships between diameter and age and thus select minimum diameter thresholds for the mature and late-seral age classes; we initially combined the regeneration and young classes into one class. We then used change detection techniques (Lunetta and Elvidge, 1998) to separate the regeneration and young classes, and to update the map to 1998. After mapping all age classes, we quantified the spatial extent of each age class across each ownership and across the study area as a whole. We used ARC/INFO (v. 7.1, ESRI) for change detection analyses and map production, and ERDAS IMAGINE software (v. 8.5, ERDAS, Inc.) for all other analyses.

## Results

### Stand Structure and Environment

Elevation, slope, and aspect were similar among age classes (Table 1). Although mean elevation and slope were highest in the late-seral class, the differences were not significant.

### Species Diversity

There were 67 herbaceous and shrub taxa in the 48 quadrats. These included 9 graminoids, 6 ferns, 38 forbs and sub-shrubs, and 14 shrubs. Of the total pool of species, 11 were exotic (excluding *Poa*). We found 40 species in the regeneration class, 31 in the young class, and 32 and 36 in the mature and late seral classes respectively.

TABLE 1. Characteristics of each forest age class. Stand-level means were generated from three plots. A mean for each age category was then derived from the stand-level means.

Age category	n	Age (yr)	Stem Density (stems/ha)	Canopy height (m)	Canopy openness (%)	Elevation (m)	Slope (%)	Aspect <sup>a</sup>
Regeneration								
mean	13	10	2,568	5	85	258	12	-0.3
range	2–15	0–11,774	0–12	3–100	120–538	0–33	-1.0–0.9	
Young								
mean	14	39	2,864	21	12	238	12	-0.6
range	25–70	200–20,097	7–33	3–27	98–520	0–46	-1.0–0.9	
Mature								
mean	9	131	510	42	23	216	18	-0.4
range	80–195	140–1,905	26–60	6–65	79–479	0–67	-1.0–1.0	
Late seral								
mean	12	>200	652	50	19	379	22	-0.2
range	N/A	140–2,105	25–83	6–51	145–874	0–71	-1.0–0.8	

<sup>a</sup> Aspect was expressed as the cosine of the angle for a measure of “southness” (-1) or “northness” (+1).

TABLE 2. Species richness and the reciprocal of Simpson's diversity index for each age category at the scale of 1 m<sup>2</sup> (quadrat) and 3 m<sup>2</sup> (stand). *P*-values are derived from ANOVA tests (*P* = 0.05). Tukey refers to the Tukey-Kramer multiple comparison test; categories with the same letter are not significantly different.

Age category	<i>n</i>	1 m <sup>2</sup>						3 m <sup>2</sup>					
		Species Richness			Reciprocal of Simpson's Index			Species Richness			Reciprocal of Simpson's Index		
		mean	SE	Tukey	mean	SE	Tukey	mean	SE	Tukey	mean	SE	Tukey
Regeneration	13	5.6	0.4	a	2.2	0.2	a	9.8	0.5	a	2.8	0.3	a
Young	14	3.5	0.3	b	1.9	0.2	a	6.6	0.4	b	2.6	0.3	a
Mature	9	3.7	0.4	ab	2.1	0.3	a	7.9	0.6	ab	3.8	0.6	a
Late seral	12	5.1	0.4	ab	2.6	0.3	a	9.2	0.4	ab	3.8	0.4	a
<i>P</i>		0.02			NS			0.03			NS		

Species richness was significantly greater in regeneration than young stands. Mature and late seral stands had intermediate levels of richness. We found no significant relationship between age class and the reciprocal of Simpson's diversity index at either scale (Table 2).

Dominance-diversity curves revealed comparable patterns among age classes, except for young stands, which supported relatively few species and

a stronger pattern of dominance than older age classes (Figure 2).

Richness of native species was significantly greater in late-seral than in young stands, and richness of exotics was significantly greater in regeneration than in late-seral stands (Figure 3). Eight (20%) of the 40 species observed in the regeneration class were exotic, of which two — *Cytisus scoparius* (L.) Link and *Hypochaeris*

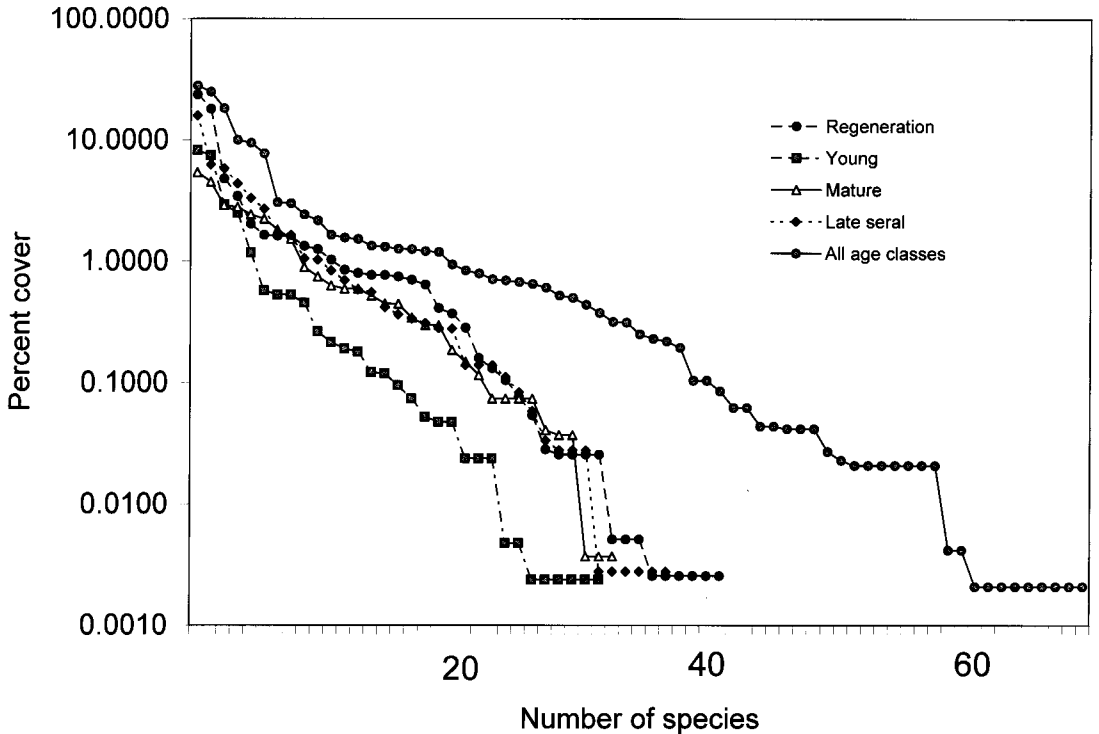


Figure 2. Dominance-diversity curves depicting the relationship between richness and abundance (as measured by percent cover). Species are arranged in order from the most to least dominant.

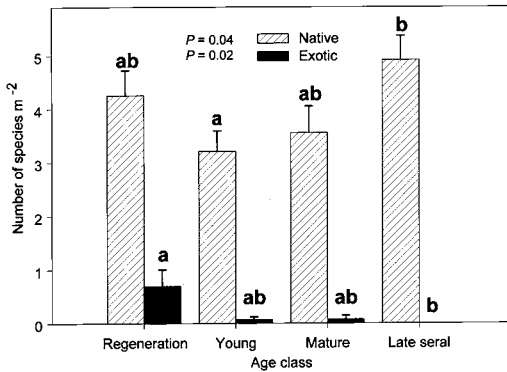


Figure 3. Age-class effects on native and exotic species richness (mean number of species per m<sup>2</sup>). *P*-values were derived from ANOVA tests ( $n = 9-14$ ). Error bars reflect 1 standard error of the mean. Plants of the same type (native or exotic) with the same letter over their bar did not have significantly different richness among stand age classes based on Tukey-Kramer tests ( $P = 0.05$ ).

*radicata* L.—are considered noxious weeds in Washington State (Rice 1998). All species encountered in late-seral stands were native to the region. An intermediate proportion of exotic species were found in young (7%) and mature (6%) stands.

### Plant Abundance

Total understory plant cover in regeneration stands was significantly greater than that in young and mature stands ( $P < 0.001$ , Figure 4). Tests for age-class effects by growth form revealed significant differences among classes for shrubs, and forbs and sub-shrubs, but not for ferns or graminoids (Figure 4). Cover of shrubs was significantly higher in the regeneration stands than in older age classes. Cover of forbs and sub-shrubs was greatest in late-seral stands, but comparable among younger age classes. Total cover of native and exotic plant species also differed among age classes

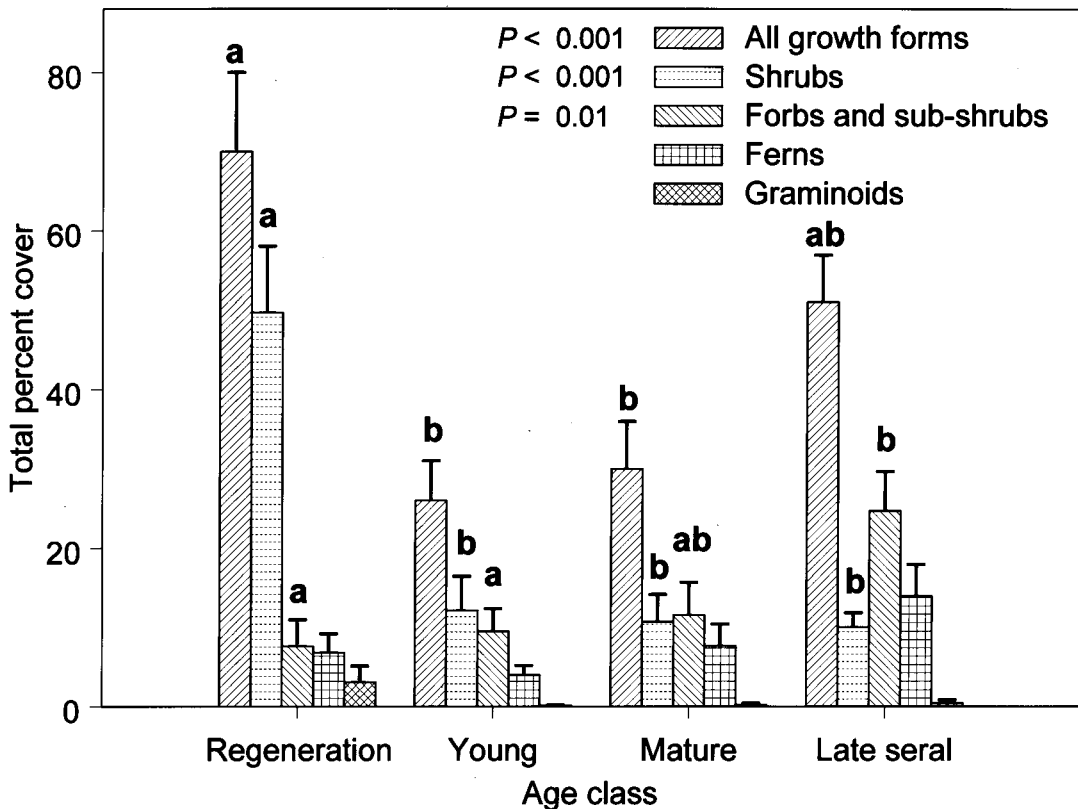


Figure 4. Age-class effects on total percent cover by growth form. Error bars reflect 1 standard error of the mean. Growth forms with the same letter over their bar did not have significantly different percent cover among age classes based on Tukey-Kramer tests ( $P = 0.05$ ). Multiple comparison tests were not conducted for ferns or graminoids because ANOVA results were not significant.

( $P = 0.004$  and  $P = 0.03$ , respectively; Figure 5). Cover of native species was significantly lower in young and mature stands than in regeneration

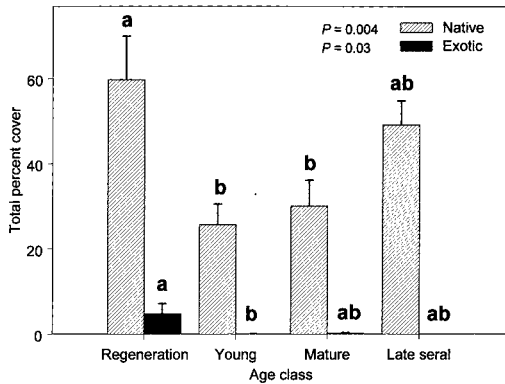


Figure 5. Age-class effects on native and exotic species percent cover. Error bars reflect 1 standard error of the mean. Plants of the same type (native or exotic) with the same letter over their bar did not have significantly different percent cover among age classes based on Tukey-Kramer tests ( $P = 0.05$ ). *Poa* species were not included in this analysis. Both native and exotic *Poa* species can be found in the study area and members of this genus were not identified to species.

and late-seral stands. Cover of exotic plant species was significantly greater in regeneration than in young stands.

Three of 17 species (all native) significantly differed in constancy among age-classes (Table 3). Significant age-class effects on cover were found for 5 of the 17 species tested (Table 3). *Rubus spectabilis* Pursh and *Gaultheria shallon* Pursh had significantly higher cover in regeneration than in older age classes. *Tiarella trifoliata* L. and *Oxalis oregana* Nutt. had significantly greater percent cover in the late-seral class. *Vaccinium alaskense* Howell also had greatest percent cover in the late-seral class and showed a significant difference between the late-seral and young class.

### Spatial Distribution of Age Classes

Visual assessment of the age-class distribution across the study area shows a forest landscape highly fragmented in the mature and late-seral classes (Figure 6). Large contiguous areas of late-seral forest are found exclusively in the Olympic National Park. Tribal, state and private lands are comprised predominantly of young and regenerat-

TABLE 3. Species tested for an age-class effect for constancy (Con) and cover (Cov). Because many species occurred at low constancies over the study area as a whole, a test statistic for constancy could be computed for only 17 of the 67 species observed in the study area. Those species tested for constancy were also tested for an age-class effect for cover ( $P = 0.05$ ). t = trace occurrence (< 1% in a single plot over the entire age category).

Species	Regeneration		Young		Mature		Late seral		Con (%)	
	Con (%)	Cov (%)	Con (%)	Cov (%)	Con (%)	Cov (%)	Con (%)	Cov (%)	Monte Carlo	P
<i>Athyrium filix-femina</i> var. <i>cyclosorum</i>	23	0.05	21	0.12	22	0.52	42	0.31	NS	NS
<i>Blechnum spicant</i>	85	4.77	71	1.17	67	2.23	75	4.36	NS	NS
<i>Claytonia sibirica</i> var. <i>sibirica</i>	15	0.01	29	0.18	22	2.41	8	0.03	NS	NS
<i>Cornus unalascenkensis</i>	15	0.03	7	0.02	0	0.00	17	0.36	NS	NS
<i>Dryopteris expansa</i>	8	t	29	0.21	22	0.45	42	0.34	NS	NS
<i>Gaultheria shallon</i>	62	23.54	43	7.43	56	1.81	33	1.64	NS	0.01
<i>Maianthemum dilatatum</i>	46	0.37	21	0.26	11	0.18	58	0.84	NS	NS
<i>Menziesia ferruginea</i>	15	0.77	21	0.45	22	0.04	17	0.28	NS	NS
<i>Oxalis oregana</i>	62	3.42	64	8.17	67	5.38	75	15.83	NS	0.03
<i>Polystichum munitum</i>	54	0.70	64	2.48	67	4.48	50	6.25	NS	NS
<i>Pteridium aquilinum</i> var. <i>pubescens</i>	23	1.26	0	0.00	0	0.00	33	2.69	0.04	NS
<i>Rubus pedatus</i>	23	0.16	7	0.05	11	0.59	67	3.31	0.002	NS
<i>Rubus spectabilis</i> var. <i>spectabilis</i>	85	17.98	57	2.93	56	0.34	33	1.06	NS	<0.001
<i>Tiarella trifoliata</i>	15	0.01	36	0.53	44	0.74	75	1.70	0.02	0.05
<i>Vaccinium alaskense</i>	54	1.60	29	0.53	67	2.89	75	5.78	NS	0.03
<i>Vaccinium parvifolium</i>	31	1.33	14	0.07	44	1.51	33	0.56	NS	NS

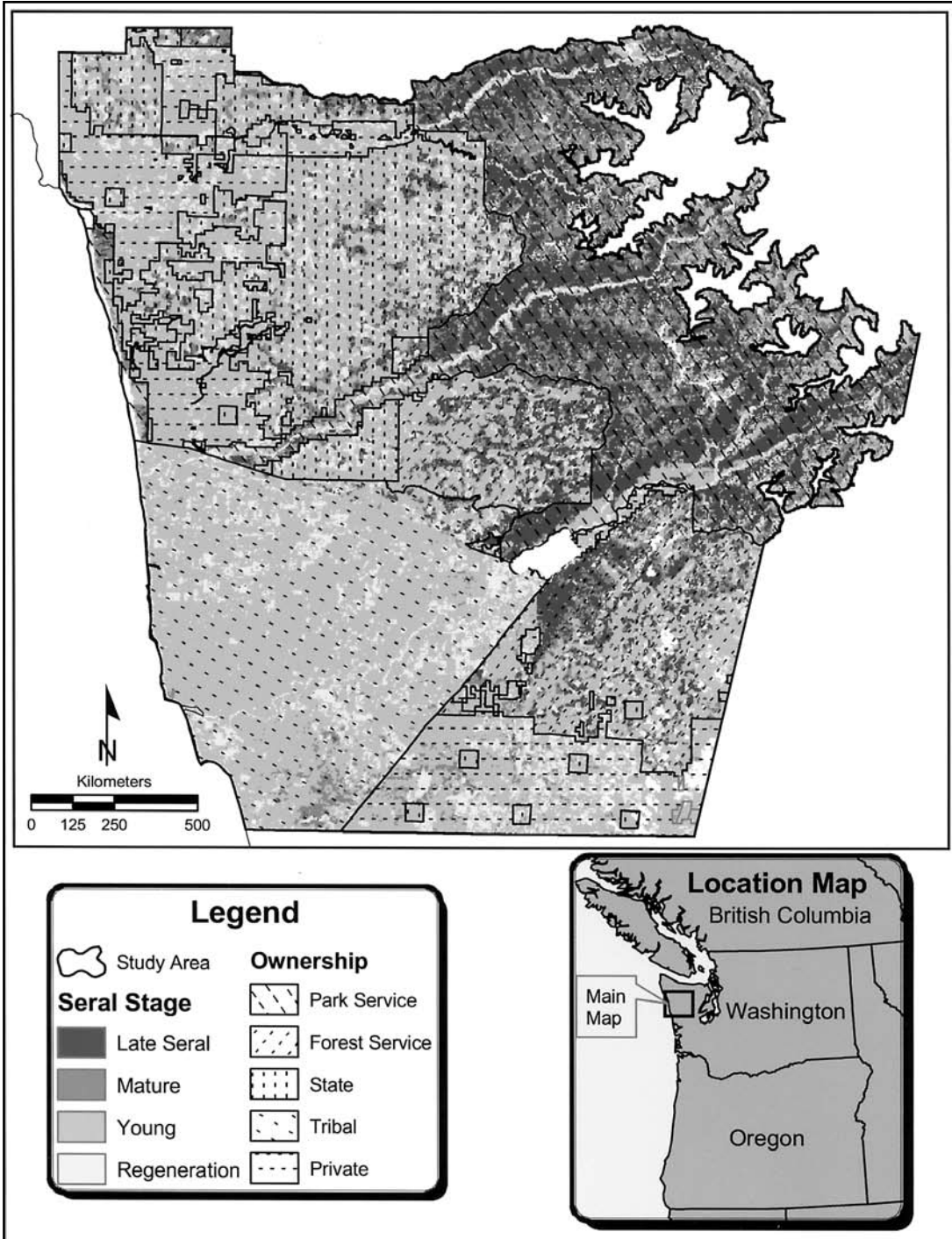


Figure 6. Spatial distribution of age classes and ownerships.

TABLE 4. Percentage distribution of age classes within the Olympic National Park, Olympic National Forest, tribal ownerships of the Quinault Indian Nation and Hoh River Indian Tribe, Washington Department of Natural Resources, and private holdings.<sup>a</sup>

Age category	Olympic National Park	Olympic National Forest	Tribal	Washington Department of Natural Resources	Private	All owners outside Olympic National Park
Regeneration	6	8	15	15	19	14
Young	22	44	77	67	73	65
Mature	28	24	7	11	7	13
Late seral	44	24	1	7	1	8

<sup>a</sup> Generated from the land distributions depicted in Figure 6.

ing forests (Table 4). Approximately 58% of the study area is in the young forest class with low species diversity. This is in contrast to the 23% this class occupies within Olympic National Park (Table 4). Late-seral forest, having the highest native species diversity, occupies only 8% of the landscape outside Olympic National Park, but 44% within the park (Table 4).

## Discussion

### Species Diversity

The trends in species richness with stand age observed in this study are consistent with previous studies in the Pacific Northwest (Long 1977, Alaback 1982, Schoonmaker and McKee 1988, Halpern 1989, Spies 1991, Halpern and Spies 1995). Rapid increases in diversity, including invasion of exotic plant species, take place during early stand recovery. However, canopy closure within these highly productive forests can occur within 20 years, resulting in extremely low levels of light (Tyler 2002) and concomitant loss of many plant species. Species numbers rise thereafter, as light becomes more available on the forest floor. Although species richness in late-seral stands is comparable to that of regeneration stands, exotics are completely absent in the former and comprise 20% of the flora in the latter.

We did not detect significant differences for the reciprocal of Simpson's diversity index (which emphasizes dominant species) at either the 1-m<sup>2</sup> or 3-m<sup>2</sup> scales, however the temporal trend of increasing diversity (Table 2) matches that observed by Spies (1991) in the Washington Cascades. It is reasonable that species richness, which gives equal weight to rare and common species, showed

a significant age-class effect, while the reciprocal of Simpson's diversity index did not. The significant difference detected for species richness reflects differences between the regeneration and young class: the former had more species that occurred with low cover; the latter had the fewest species, but these occurred with more similar cover. This difference between the regeneration and young classes is also evident in the dominance-diversity curves.

### Plant Abundance

Our observations of age-class effects for cover and constancy are similar to observations reported by Spies (1991) for other Pacific Northwest forests. Results must be interpreted with some caution, because of the possibility of Type I error inherent with multiple tests (Zar 1996). At a significance level of  $P < 0.05$ , 5% of the tests could be expected to be significant simply by chance (e.g. one test out of 17). In this study, three of the 17 species tested (18%) had an age-class effect on constancy, and five of the 17 (29%) had an age-class effect on cover.

Species most abundant in late-seral stands, *Tiarella trifoliata*, *Rubus pedatus* J.E. Smith, *Oxalis oregana*, and *Vaccinium alaskense*, were present in regeneration, young, and mature stands but with lower cover. In contrast, those species that were most abundant in the regeneration class (e.g. *Digitalis purpurea* L., *Hypochaeris radicata*, *Rubus lacianatus* Willd., and *Anaphalis margaritacea* (L.) B. & H.) had little or no representation in the other classes, however, these species could not be tested for constancy and therefore were not tested for age-class effects in cover. Several of these species are exotic, which as a group tend to be

associated with recently disturbed areas, including clearcuts (DeFerrari and Naiman 1994).

Patterns of species cover in this study are consistent with the results of other studies, with a few exceptions. For example, as we observed, *Tiarella trifoliata* reaches greatest cover in late-seral forests of Montana (Habeck 1968), the western Cascades of Washington (Moir et al. 1979, Spies 1991) and the Oregon Cascades (Spies 1991). Percent cover patterns for *Rubus spectabilis* in southeastern Alaska (Alaback 1984) are similar to those of the Olympic Peninsula, reaching highest abundance in the regeneration class, lowest levels in the mature class, and increasing somewhat in the late-seral class. *Vaccinium alaskense* reaches greatest percent cover in late-seral forests of the Washington Cascades (Spies 1991) and the Olympic Peninsula, while in Alaska, this species is most abundant in regenerating stands (Alaback 1984).

*Pteridium aquilinum* (L.) Kuhn. is most frequently found in young stands of the Washington and Oregon Cascades and Oregon Coast Range (Halpern and Spies 1995). However, on the Olympic Peninsula, constancy was highest in late-seral forests, followed by regenerating stands; *P. aquilinum* did not appear in quadrats sampled in young or mature stands, however we did observe this species in these age classes. We suspect that we would observe *P. aquilinum* had we used larger quadrats or increased the number of plots sampled. Different patterns between the studies may also be due to variation in climate and soils among geographic regions.

### Native Versus Exotic Plant Species

The number of exotic plant species becoming established on the Olympic Peninsula is increasing. Jones (1936) reported that 40 exotic plant species had been identified on the Peninsula prior to 1900, however this had grown to 143 by 1936. Buckingham et al. (1995) identified 333 exotic plant species on the Peninsula, or roughly 25 percent of the Peninsula's flora (17% of the species found in this study were exotic). In some cases, exotics may out-compete rare species (Buckingham et al. 1995). Roadsides often are comprised entirely of exotics. Forest interiors typically do not harbor any exotics. In the Hoh River drainage, DeFerrari and Naiman (1994) found that the number and abundance of exotic plant species were negatively correlated with stand

age and canopy cover, similar to the results of this study. The type and intensity of disturbance are probably important factors in determining the presence of exotics in addition to the density of roads and degree of human presence (DeFerrari and Naiman 1994). At present, exotic plant species of the Peninsula are primarily herbaceous. However, *Cytisus scoparius* competes favorably with young conifers and eventually could pose a significant threat to regeneration of native woody species. It is possible that continued range expansion of shade tolerant exotics in western Washington (such as *Hedera helix* L., *Ilex aquifolium* L., and *Geranium robertianum* L.), or the introduction of new shade-tolerant exotics could allow exotics to proliferate in forest interiors.

### Sampling Limitations

Increasing the size of quadrats, the number of quadrats per plot, including more plots, including plots in rare microhabitats, or including a walking survey of the entire stand would have increased sampling of rare species and allowed greater inference and increased statistical power in detecting differences in individual species constancy and percent cover. Our inferences about patterns of species diversity may be limited by the absence of late-seral plots in the timber-managed landscape. Because late-seral forest is uncommon outside of Olympic National Park, most late-seral stands sampled were within the park.

### Spatial Distribution of Age Classes

The distribution of late-seral forest in this study is clearly linked to ownership patterns. Turner et al. (1996) also observed a strong relationship between ownership and landscape pattern in the Olympic Peninsula and the Appalachian highlands. In both regions, forest cover on private lands was less extensive, more fragmented, and had more edge than public lands. However, landscape pattern was similar on lands actively managed for timber, regardless of ownership. Similar to this study, Turner et al. (1996) observed that the extent of forest cover was highest on federal lands, intermediate on state lands, and lowest on private lands. Differences in landscape pattern among owners can largely be attributed to socioeconomic and political factors, such as management objectives, policies and laws, market conditions, distance to market, and population density (Turner et al. 1996).

## Implications for Land Management

If biological diversity is a goal embraced by forest policy makers, forest managers should be mindful of the impact of timber management practices on the distribution of species diversity patterns. Presently, the western Olympic Peninsula is dominated by young forest characteristically low in species diversity. Outside of Olympic National Park, regeneration stands comprise the second largest age class in this landscape. This age class is high in species diversity, but also high in non-native species. Late-seral forest holds the highest native species diversity, yet comprises the smallest component of this landscape and is the most spatially disjunct. Extreme fragmentation in conjunction with short rotation harvest schedules has reduced the abundance of late-seral species on a regional scale, with potential effects on rare, endangered, and disturbance-sensitive species (Schoonmaker and McKee 1988, Spies et al. 1994).

Little is known about primary reproductive strategies of forest herbs, although few are thought to be successful long-distance dispersers (Cain et al. 2000). Species that do not disperse well by seed may be particularly disadvantaged by fragmentation and environmental stressors (Bierzychudek 1982, Jules 1998, Cain et al. 1998, 2000). This pool of diversity in late-seral forests is thus vulnerable to environmental change, particularly large-scale disturbance, and species requiring the late-seral forest environment will be at particular risk. Further research in reproductive ecology and dispersal abilities of woodland herbs would enhance our understanding of the magnitude of this risk and provide policy makers with better information in developing management plans.

Longer rotations (>200 years) and silvicultural prescriptions that create late-seral qualities, such as variable density thinning and underplanting, may be beneficial in increasing the extent and connectivity of late-seral environments. However, further research is needed to understand the risks associated with such prescriptions. Some components of federal management plans prescribe thinning as a means of simulating or accelerating late-seral conditions in young managed forests (FEMAT 1993). However, Halpern et al. (1999) suggests that the assemblage of species present in thinned stands may differ from the mature community that would have developed under a

natural trajectory, and that thinning may encourage establishment of exotic, ruderal species via the seedbank. Bailey et al. (1998) found that within 24 years after commercial thinning, both constancy and cover of exotics were significantly higher in thinned stands than in unthinned stands in western Oregon.

Adequately addressing maintenance of biological diversity for rare forest types will require coordination across ownerships. Management practices vary widely over ownerships, and understanding the ramifications of these practices on the distribution of diversity patterns should be considered at much broader spatial and temporal scales. Management efforts that address short (~50 year) timeframes and individual owners and political boundaries are unlikely to be successful or efficient in addressing large-scale ecological phenomena (Tyler and Peterson 2004). Finally, increasing our understanding of the human and market factors affecting land-use change will be critical in managing patterns of species diversity. Successful planning and management to preserve late-seral ecosystems in the face of climatic variability and other environmental stressors may rely as much on innovative social and economic incentives for stewardship as on scientific understanding of the ecology of these forests.

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## Literature Cited

- Agee, J. K. 1993. Fire ecology of the Pacific Northwest. Island Press, Washington, D.C.
- Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. *Ecology* 63:1932-1948.
- Alaback, P. B. 1984. Plant succession following logging in the Sitka spruce-western hemlock forests of southeast Alaska: Implications for management. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. PNW-173.
- Alaback, P. B., and F. R. Herman. 1988. Long-term response of understory vegetation to stand density in *Picea-Tsuga* forests. *Canadian Journal of Forest Research* 18:1522-1530.
- Bailey, J. D., C. Mayrsohn, P. S. Doescher, E. St Pierre, and J. C. Tappeiner. 1998. Understory vegetation in old and young Douglas-fir forests of western Oregon. *Forest Ecology and Management* 112:289-302.
- Battles, J. J., A. J. Shlisky, R. H. Barrett, R. C. Heald, and B. H. Allen-Diaz. 2001. The effects of forest management on plant species diversity in a Sierran conifer forest. *Forest Ecology and Management* 146:211-222.
- Bierzzychudek, P. 1982. Life histories and demography of shade-tolerant temperate forest herbs - a review. *New Phytologist* 90:757-776.
- Buckingham, N. M., E. G. Schreiner, T. N. Kaye, J. E. Burger, and E. L. Tisch. 1995. Flora of the Olympic Peninsula. Northwest Interpretive Association, Seattle, Washington.
- Cain, M. L., H. Damman, and A. Muir. 1998. Seed dispersal and the Holocene migration of woodland herbs. *Ecological Monographs* 68:325-347.
- Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany* 87:1217-1227.
- D'Antonio, C. M. 2000. Fire, plant invasions, and global change. In H. Mooney and R. Hobbs (editors), *Invasive Species in a Changing World*. Island Press, Covelo, California. pp. 65-94.
- DeBell, D. S., R. O. Curtis, C. A. Harrington, and J. C. Tappeiner. 1997. Shaping stand development through silvicultural practices. In K.A. Kohm and J.F. Franklin (editors), *Creating a Forestry for the 21st Century: The Science of Ecosystem Management*. Island Press, Washington, D.C. pp. 141-149.
- DeFerrari, C., and R. Naiman. 1994. A multiscale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. *Journal of Vegetation Science* 5:247-258.
- FEMAT (Forest Ecosystem Management and Assessment Team) 1993. Forest ecosystem management: An ecological, economic, and social assessment. USDA Forest Service; USDI Fish and Wildlife Service; U.S. Department of Commerce National Oceanic and Atmospheric Administration National Marine Fisheries Service; USDI National Park Service; USDI Bureau of Land Management; and U.S. EPA.
- Fonda, R. W. 1974. Forest succession in relation to river terrace development in Olympic National Park, Washington. *Ecology* 55:927-942.
- Fonda, R. W., and L. C. Bliss. 1969. Forest vegetation of the montane and subalpine zones, Olympic Mountains, Washington. *Ecological Monographs* 39:271-301.
- Franklin, J. F., and T. A. Spies. 1983. Characteristics of old-growth Douglas-fir forests. In *Proceedings of New Forests for a Changing World, Proceedings of the 1983 Society of American Foresters National Convention*. pp. 10-16.
- Franklin, J. F., and C. T. Dyrness. 1988. *Natural Vegetation of Oregon and Washington*. USDA Forest Service. PNW-8:1-417.
- Fredericksen, T. S., B. D. Ross, W. Hoffman, M. L. Morrison, J. Beyea, B. N. Johnson, M. B. Lester, and E. Ross. 1999. Short-term understory plant community responses to timber-harvesting intensity on non-industrial private forestlands in Pennsylvania. *Forest Ecology and Management* 116:129-139.
- Griffis, K. L., J. A. Crawford, M. R. Wagner, and W. H. Moir. 2001. Understory response to management treatments in northern Arizona ponderosa pine forests. *Forest Ecology and Management* 146:239-245.
- Habeck, J. R. 1968. Forest succession in the glacier peak cedar-hemlock forests. *Ecology* 49:872 - 880.
- Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. *Ecology* 69:1703-1715.
- Halpern, C. B. 1989. Early successional patterns of forest species: Interactions of life history disturbance. *Ecology* 70:704-720.
- Halpern, C. B., and T. A. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecological Applications* 5:913-934.
- Halpern, C. B., S. A. Evans, and S. Nielson. 1999. Soil seed banks in young, closed-canopy forests of the Olympic Peninsula, Washington: Potential contributions to understory reinitiation. *Canadian Journal of Botany* 77:922-935.
- Henderson, J. A., D. H. Peter, R. D. Leshner, and D. C. Shaw. 1989. Forested plant associations of the Olympic National Forest. USDA Forest Service, Pacific Northwest Region. R6 ECOL 001-88.
- Hill, M. O. 1973. Diversity and evenness: A unifying notation and its consequences. *Ecology* 54:428-432.
- Holthausen, R. S., M. G. Raphael, K. S. McKelvey, E. D. Forsman, E. E. Starkey, and D. E. Seaman. 1995. The contribution of federal and non-federal habitat to persistence of the Northern Spotted Owl on the Olympic Peninsula, Washington: Report of the reanalysis team. USDA Forest Service, Pacific Northwest Research Station. PNW-GTR-352.
- Huff, M. H. 1995. Forest age structure and development following wildfires in the western Olympic Mountains, Washington. *Ecological Applications* 5:471-483.
- Jones, G. N. 1936. A botanical survey of the Olympic Peninsula, Washington. University of Washington Press, Seattle.
- Jules, E. S. 1998. Habitat fragmentation and demographic change for a common plant: Trillium in old-growth forest. *Ecology* 79:1645-1656.
- Larsen, D., and Q. Nguyen. 2001. Washington timber harvest—1999. Washington Department of Natural Resources, Office of Budget and Economics.

- Lezberg, A. 1998. Survival of herbaceous species after canopy closure: Role of below-ground traits. M.S. Thesis. University of Washington, Seattle.
- Lezberg, A. L., J. A. Antos, and C. B. Halpern. 1999. Below-ground traits of herbaceous species in young coniferous forests of the Olympic Peninsula, Washington. *Canadian Journal of Botany* 77:936-943.
- 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.
- Lunetta, R. S., and C. D. Elvidge. 1998. Remote sensing change detection: Environmental monitoring methods and applications. Ann Arbor Press, Chelsea, Michigan.
- Manly, B. F. J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, London.
- Moir, W. H., F. D. Hobson, M. Hemstrom, and J. F. Franklin. 1979. Forest ecosystems of Mount Rainier National Park. In R.M. Linn (editor), Proceedings of the First Conference on Scientific Research in the National Parks. Volume 1. USDI National Park Service, pp. 201-208.
- Morrison, P. H. 1990. Ancient forests on the Olympic National Forest: Analysis from a historical landscape perspective. The Wilderness Society, Washington, D.C.
- NCDC (National Climatic Data Center), National Oceanic and Atmospheric Administration. 1931-1999. Monthly precipitation and monthly average temperature. Available online at <http://lwf.ncdc.noaa.gov/oa/ncdc.html>
- Oliver, C. D. 1981. Forest development in North America following major disturbances. *Forest Ecology and Management* 3:153-168.
- Rice, P. M. 1998. Invaders database [online]. The University of Montana, Missoula.
- Ryan, M. W., D. F. Fraser, V. G. Marshall, and D. W. F. Pollard. 1998. Differences in the composition of vascular plants, bryophytes, and lichens among four successional stages on southern Vancouver Island. *Landscape Ecology* 72:86-88.
- Schoonmaker, P., and A. McKee. 1988. Species composition and diversity during secondary succession of coniferous forests and the western Cascade Mountains of Oregon. *Forest Science* 34:960-979.
- Simberloff, D. 2001. Introduced species, effects and distribution. In S.A. Levin (editor), *Encyclopedia of biodiversity*. Academic Press, San Diego. pp. 517-529.
- Spies, T. A. 1991. Plant species diversity and occurrence in young, mature, and old-growth Douglas-fir stands in western Oregon and Washington. In L. F. Ruggiero, K. B. Aubry, A. B. Carey and M. H. Huff (editors), *Wildlife and Vegetation of Unmanaged Douglas-fir Forests*. USDA Forest Service General Technical Report PNW-GTR-285, Portland, Oregon. pp. 111-122.
- 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.
- Thomas, J. W., E. D. Forsman, and J. B. Lint. 1990. A conservation strategy for the Northern Spotted Owl: A report of the Interagency Scientific Committee to address the conservation of the Northern Spotted Owl. USDA Forest Service; USDI Bureau of Land Management, Fish and Wildlife Service and National Park Service.
- Thomas, S. C., C. B. Halpern, D. A. Falk, D. A. Liguori, and K. A. Austin. 1999. Plant diversity in managed forests: Understory responses to thinning and fertilization. *Ecological Applications* 9:864-879.
- Thysell, D. R., and A. B. Carey. 2000. Effects of forest management on understory and overstory vegetation: A retrospective study. USDA Forest Service, Pacific Northwest Research Station. General Technical Report PNW-GTR-444.
- Turner, M. G., D. N. Wear, and R. O. Flamm. 1996. Land ownership and land-cover change in the southern Appalachian Highlands and the Olympic Peninsula. *Ecological Applications* 6:1150-1172.
- Tyler, M. W. 2002. Forests of the western Olympia Peninsula: Understory plant species diversity, forest policy, and landscape pattern. Ph.D. Dissertation. University of Washington, Seattle.
- Tyler, M. W., and D. L. Peterson. 2004. Effects of forest policy on landscape pattern of late-seral forest of the western Olympic Peninsula, Washington. *Agriculture, Ecosystems and Environment* 101:289-306.
- USDA (USDA Forest Service) and USDI (USDI Bureau of Land Management). 1994. Record of Decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the Northern Spotted Owl. USDA Forest Service; USDI Bureau of Land Management.
- USDI (USDI Bureau of Land Management) and USDA (USDA Forest Service). 2001a. Interagency vegetation mapping project: Olympic province review release, version 1.0. USDI Bureau of Land Management; USDA Forest Service, Corvallis, Oregon.
- USDI (USDI Bureau of Land Management) and USDA (USDA Forest Service). 2001b. Interagency vegetation mapping project: Olympic province review release, version 1.0, release documentation. Bureau of Land Management; Forest Service, Corvallis, Oregon.
- Whittaker, R. H. 1975. *Communities and ecosystems*. 2nd ed. Macmillan Publishing Co., Inc, New York.
- Zar, J. H. 1996. *Biostatistical analysis*. 3rd ed. Prentice Hall, Upper Saddle River, NJ.

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