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Understory vegetation in old and young Douglas-fir forests of western Oregon[1]

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Abstract

We studied understory composition in thinned and unthinned Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)/western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stands on 28 sites in western Oregon. These stands had regenerated naturally after timber harvest, 40–70 years before thinning. Commercial thinning had occurred 10–24 years previously, with 8–60% of the volume removed from below with the intent to homogenize spacing among trees. Undisturbed old-growth Douglas-fir stands were present for comparison on 18 of these sites. Total herbaceous cover was greater in thinned (25% cover) stands than in unthinned (13% cover) or old-growth (15% cover) stands. Species richness was also greater in thinned (137) than in unthinned (114) and old-growth (91) stands (P=0.05). Part of the increased richness was caused by the presence of exotic species in thinned stands, but there were also more native grass and nitrogen-fixing species in thinned stands than in unthinned or old-growth stands. Groups of species differed among stand-types. For example, the frequency of tall cordate-leaved species was greater in old-growth stands (P=0.009), but their relative cover was different only between old-growth and unthinned stands (P=0.08). Both the cover and frequency of grasses and sedges in thinned stands were greater than in unthinned or old-growth stands ($P \leq 0.002$). Ordination of shrub cover showed differences among old-growth and unthinned stands compared to thinned stands, mainly because of the amount of *Gaultheria shallon* Pursh and *Polystichum munitum* (Kaulf.) Presl in heavily thinned stands. Ordination of herbaceous community data showed that there were much stronger differences among sites than among stand-types. The lack of difference among stand-types demonstrates the resiliency of herbaceous communities to disturbance associated with past and current forest management. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Thinning; Shrubs; Herbaceous cover; Exotic; Old-growth; Species richness; Ordination

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1. Introduction

Recent concerns over the scarcity of old-growth forests in the Pacific Northwest and mandates to protect associated species are prompting development

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of silvicultural methods that encourage the formation of stand structures that emulate old-growth forests. Desired characteristics include (1) a multistoried canopy consisting of a large range of tree species, ages, and sizes; (2) large-diameter standing snags and fallen trees, and (3) a diverse understory of many species and a variety of available habitats (Franklin and Spies, 1991). While overstory and debris structures are often related to stand age, silvicultural treatments such as thinning (partial removal of the overstory canopy) could be used in young stands to hasten their creation. Understory species development may not be as age (time)-dependent, however, since Spies (1991) found that <20% of understory species were more abundant in older forests than in younger unmanaged forests. The effects of stand management for timber production, including thinning, on understory species composition have been documented on individual sites (e.g. Witler, 1975; Halpern, 1988), but few have analyzed a collection of sites within a broad landscape.

Vascular plant richness in Pacific Northwest forests primarily resides within the shrub and herb layers (Halpern and Spies, 1995). Richness is high in the stage of forest succession prior to canopy closure and stem exclusion due to survival of disturbance-resistant species and addition of early seral species, including exotics, on disturbed sites (Oliver, 1981; Halpern, 1988; Franklin and Spies, 1991). Richness declines as stand density increases, but returns to high levels in mature and old-growth forests as low-intensity disturbances create and maintain openings in the canopy (Long and Turner, 1975; MacLean and Wein, 1977; Alaback and Herman, 1988). This rebound in richness may be explained by the increased number and diversity of microhabitats following such disturbances (Alaback, 1982). Under proper conditions, most thinning operations (particularly those from below) are also low-intensity disturbances, creating germination sites and small openings in dense canopies. Such activity therefore is likely to facilitate survival and establishment of many understory species.

Witler (1975) demonstrated that understory biomass increased immediately after thinning, and the degree of that biomass response increased in proportion to overstory removal. Alaback and Herman (1988) studied the response of two coastal Oregon forest-types to thinning and found no immediate (6 months) difference in understory composition or abundance between thinned and unthinned stands. However, differences in understory species composition and abundance had emerged within 17 years after thinning. Variability in percent cover increased with the amount of volume removed during thinning. Understory species composition was ultimately unaltered by management, but the duration of the shrub stage following cutting was prolonged while the period of relatively low understory cover was shortened (Alaback, 1984).

General increases in understory vegetation richness, frequency, or cover following thinning do not necessarily translate into the development of late-successional understory species composition since changes in species composition can be hidden in richness and diversity indices. Also, competition among and within herb and shrub species can be altered in thinned stands. Expansion of clonal species was encouraged by thinning (Bunnell, 1990; Tappeiner et al., 1991; Huffman et al., 1994). For example, *Gaultheria shallon* Pursh rhizomes expanded by as much as 23% annually following thinning, creating dense patches that could exclude both herbaceous plants and tree seedlings (Huffman et al., 1994). Furthermore, some understory species may be mechanically damaged or eliminated during thinning.

The purpose of this study was to determine if past timber management practices (including both clearcutting >50 years ago and thinning >10 years ago) have had a major effect on understory plant communities. We examined species richness, cover, frequency, and composition in managed and unmanaged Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands of different ages, densities, and stages of succession. We tested the hypothesis that shrub and herb communities are no different among three stand-types: young (50–120 years old) unthinned, young thinned, and old-growth stands. Both types of young stands regenerated naturally following logging.

2. Methods

2.1. Site selection

This research compared understory vegetation in 28 ‘pairs’ of thinned and unthinned young Douglas-fir

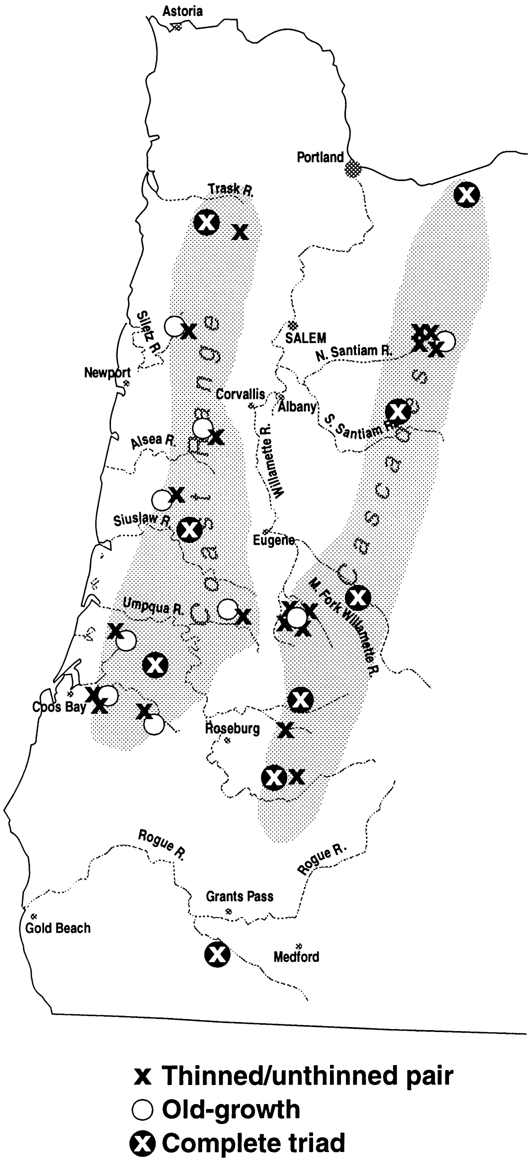

Fig. 1. Location of research sites in western Oregon (map adapted from Franklin and Dyrness, 1988).

stands with vegetation in 18 nearby old-growth stands distributed across western Oregon (Fig. 1). One pair of young stands and the nearest old-growth stand were called a 'triad.' Ten pairs of young stands had no old-growth comparison. In addition to the 28 pairs and 18 old-growth stands, one unthinned stand had a second adjacent thinning (a total of 29 thinned stands). For shrub composition, we had access to data from one additional triad and one additional pair (a total of 80 stands).

We used Bureau of Land Management stand records to locate young stands that met the following criteria: (1) stand age of 50–120 years; (2) a recorded operational thinning or salvage in part of the stand between 1970 and 1985; (3) remainder of the original stand untreated but otherwise similar (e.g. similar elevation, slope, and aspect); (4) no additional stand treatments (e.g. fertilization) in either the thinned or unthinned portion; (5) located near an older ($\geq$200 years) stand exhibiting old-growth structure (18 of 28 pairs); and (6) all three stand-types contained >10 ha of interior environment. Thinnings were from below with the intent to homogenize spacing, and they ranged from light (8% merchantable volume removal) to extremely heavy (60% volume removal); site indices ranged from 24 to 43 (King, 1966) at age 50 with height in meters. Detailed pre-treatment data from thinned and unthinned stands were not available, but the broad classification of habitat-type and the overstory classification based on aerial photos were once identical for every thinned–unthinned pair. Paired stands had to be immediately adjacent without major changes in elevation, slope, aspect, or soils. We also avoided apparent differences in soil depth and type as well as riparian influences.

These young Douglas-fir stands were regenerated naturally between 1880 and 1930, typically following cutting and burning associated with timber harvesting. They were composed primarily of one age cohort with a few large trees or snags remaining from a previous stand (Bailey, 1996). The old-growth stands showed little evidence of recent human disturbance and displayed structures typically associated with late-successional forests as described by Franklin and Spies (1991). The 18 triads and 28 pairs had the following range of physical characteristics: elevation, 250–800 m; slopes, 3–63%; precipitation, 100–300 cm year^{-1}; January low temperatures, -2°C to 0°C (US weather service). Most sites were in the Western Hemlock Zone (Franklin and Dyrness, 1988) where *Tsuga heterophylla* (Raf.) Sarg. is considered the climax species. Douglas-fir may be climax at the southern edge of this zone, and it is the climax species in the Douglas-fir zone. Other stand data are available in Bailey and Tappeiner (1998).

2.2. Data collection

Stands were inventoried from mid-June through mid-September in 1993–1995, 10–24 years after thinning, which allowed sufficient time for changes in the understory community to develop. Paired young stands and nearby old-growth stands were surveyed within days of one another to minimize the likelihood of observing differences in species composition due to time of year. Stand entry location and direction and distance to the first sample point were pre-assigned for each stand using aerial photos and stand maps, which ensured that sampling was not biased. Sample points were located 75 m from any stand edge so that only the interior of each stand was sampled. Six to 12 (typically 10) sample points were established systematically on a grid with 50–75 m intervals between points, depending on the total stand size. At each sample point, five 17.6 m^2 circular plots were established, one at the point center and four that were 15 m from point center in each cardinal direction. Overstory characteristics were collected at the center point and reported in Bailey and Tappeiner (1998).

For sampling purposes, understory plants were divided into three strata (after MacLean and Wein (1977)): 'tall shrubs' ($\geq$150 cm in height), 'low shrubs' (50–150 cm tall), and 'herbs.' We included large ferns in the low shrub stratum because of their size and apparent functional effect. Herbs were defined as being without woody aboveground stems, but some woody plants that were normally <50 cm tall were included in the herb stratum. An individual plant could only occupy one stratum, but several individuals of the same species could occupy different strata if the plant sizes differed. In the rare case that significant portions of one plant appeared in several strata, it was assigned to the strata in which it had the greatest cover. A complete species list is included in Bailey (1996). Taxonomic classifications follow Hitchcock and Cronquist (1973).

Number, height, and average crown radius of individual stems of all tall shrub species were recorded for all circular plots at all sample points. Percent cover, by species, of low shrubs and large ferns was visually estimated in 10% cover classes on all circular plots. Herb cover was recorded for every species on two–four 1 m^2 subplots clustered at each circular plot (up to 12 subplots per sample point); individual species cover was summed for total cover. Percentage cover was estimated visually and recorded in 10% cover classes. For both the low shrub and herb strata, trace coverage was recorded as 1%. Cover was summed to a maximum of 100%, but it typically included empty space or bare ground. This estimate of relative cover may influence how these data compare with other studies that use absolute cover.

Leaf area index (LAI) was measured with a LAI-2000 canopy meter (LI-COR, Lincoln, NE) standardized to clear sky readings and recorded with 2 h of solar noon. LAI for shrub strata was measured at point center only. Readings were taken above tall shrubs for canopy LAI, above low shrubs (but below tall shrubs) for tall shrub LAI, and above herbaceous vegetation (but below low shrubs) for low shrub LAI. The difference between the readings was the LAI for each strata. The height of all three strata was recorded at each point center.

2.3. Data analysis

Observational studies assume that paired subjects were initially identical and that observed differences are due to treatment effects (Cochran et al., 1983). In an effort to comply with this fundamental assumption, we set several criteria for stands used in this study, as described above. The advantage of retrospective, observational studies lies in their ability to evaluate changes after long time periods (Mueller-Dombois and Ellenberg, 1974). This study furthers that advantage by evaluating operational practices covering large areas. Comparisons of 'triads' (young pairs and old-growth stands) are presented even though they violate the shared-past assumption (Cochran et al., 1983). This violation is considered minor, however, given that the study question shifts away from one of treatment effect to a simple question of how old-growth stands may differ.

We compared mean density (number of stems), cover, and frequency of understory species and species groups among stand-types within and across 28 pairs and 18 triads. For data that met the basic assumptions of parametric statistics (i.e. normally distributed, independent data with equal variances), we used t-tests or ANOVA comparisons, and present means ($\pm$standard deviations) and P-values from the t- or F-statistic. For data that did not meet these basic assumptions, we

Table 1
Tests for significant differences in frequency for 14 species identified by Spies (1991) as more frequent in old-growth Douglas-fir stands than in young stands

Species	*P*-value
Achlys triphylla (Smith) DC.[a]	0.40
Adenocaulon bicolor Hook.[a]	0.45
Anemone deltoidea Hook.[a]	0.33
Blechnum spicant (L.) Roth.[b]	0.86
Coptis laciniata Gray[b]	0.79
Cornus canadensis L.[b]	0.62
Disporum hookeri (Torr.) Nicholson [a,b]	0.28
Goodyera oblongifolia Raf. [a,b]	0.06[c]
Linnaea borealis L. [a,b]	0.87
Monotropa uniflora L.[b]	0.37
Smilacina racemosa (L.) Desf.[a]	0.41
Synthyris reniformis (Dougl.) Benth.[a]	0.09[d]
Tiarella trifoliata var. *unifoliata* (Hook.) Kurtz.[b]	0.07[e]
Vancouveria hexandra (Hook.) Morr. & Dec.[b]	0.61

[a] Coast range.
[b] Cascade range (Oregon).
[c] Unthinned>thinned at $\alpha=0.1$, with old-growth intermediate.
[d] Unthinned>old-growth at $\alpha=0.1$, with thinned intermediate.
[e] Thinned>unthinned at $\alpha=0.1$, with old-growth intermediate.
P-values are from tests of differences across stand types.

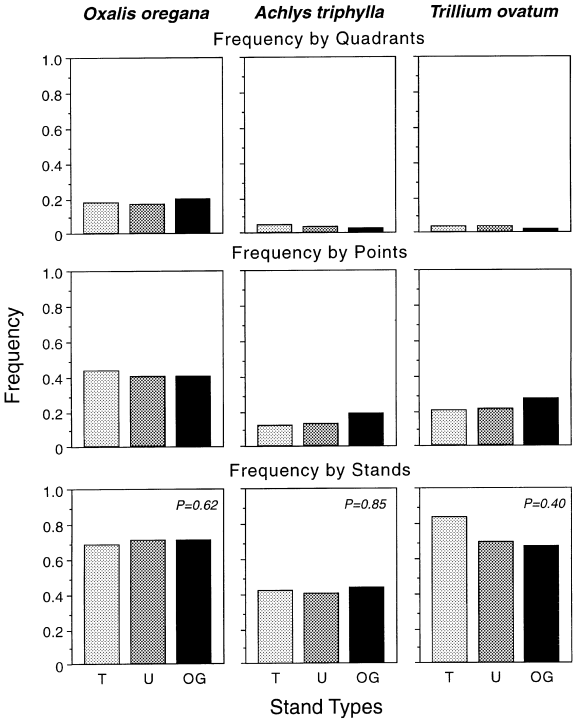

Fig. 2. Frequency of three native herbaceous species by stand-type at three scales: among 1 m^2 quadrats, among points (typically 10–12 quadrats), and among stands (typically 10 points). *Achlys triphylla* (Smith) DC. was more frequent than *Trillium ovatum* Pursh on quadrats, but less frequent among points and stands. *Oxalis oregana* Nutt. was the most common species of all 212 herbaceous species at the quadrat and point scales but not at the stand level. *P*-values reflect tests for statistical differences among stand-types. T, U, and OG refer to young thinned, young unthinned, and old-growth stands, respectively. For *Oxalis oregana*, mean cover was 9% for both thinned and unthinned stands and 6% for old-growth stands. For *Achlys triphylla* and *Trillium ovatum*, mean cover was <1% and <0.1%, respectively, for all three stand-types.

used Wilcoxon rank-sum test comparisons, and present medians with 25th and 75th quartiles and *P*-values from a Kruskal–Wallis χ^2 approximation (SAS Institute Inc., 1989). Pairwise *t*-test comparisons and blocking by triad were both necessary to account for site-to-site differences.

We examined total (all species) density and cover, which improved our ability to compare stand-types within and across pairs and triads. We also tallied the total number of species for richness and diversity calculations. We excluded the southernmost triad from richness and diversity, because it had 75 species not present elsewhere, and we did not want our results to be skewed by a single site from a different geographic area.

We also analyzed data for individual species that were common across most sites, 14 species of which Spies (1991) identified as significantly more frequent in old-growth Douglas-fir stands than in young unmanaged stands (Table 1). Most shrub and herb species, however, were rare or occurred sporadically within stands. Comparisons among stand-types were dependent on a species occurring on at least one sample point in each stand-type – atypical except for the most common 20% of our 229 species. Rarity resulted in non-normally distributed cover and frequency data (i.e. skewed by the predominance of zeros for the vast majority of species; see Fig. 2), which weakened statistical comparisons. Our data also showed markedly different variances among stand-types and individual sites (related to this rarity issue).

Given that many species occurred on <1% of the plots and that related species function in similar ecological roles across broad landscapes, we aggregated species into six groups based on field observations of intermixed species, assumed ecological function, and interest in site invasion. This functional grouping concept was adapted from Keddy (1992). The species groups are as follows:

1. Nitrogen-fixing species: Species that can fix nitrogen hold competitive advantages on disturbed sites due to their abilities to established and prosper on N-depleted soils. They require additional mineral and light resources to exploit this ability. Young stands in this study have recent disturbance histories; thinned stands were most recently disturbed and have more light and soil resources available in the understory. Thinned stands should contain the greatest abundance of N-fixing species. Species in this group include *Ceanothus* spp., *Cytisus scoparius* L. Link, *Lathyrus* spp., *Lotus micranthus* Benth., *L. purshiana* (Benth.) Clements & Clements, *Lupinus* spp., *Medicago lupulina* L., *Swainsona salsula* (Pall.) Taub., *Thermopsis montana* Nutt., *Trifolium eriocephalum* Nutt., *Vicia americana* (Muhl.), and *V. cracca* L.
2. Tall, cordate-leaved species: Species that display horizontally oriented, cordate leaves on erect stems are effective light gatherers in heavily shaded environments where the risk of desiccation is low (Givinish, 1987). These species may therefore be unusually susceptible to harvest disturbance and should be most common in old-growth stands, which lack such histories. Species in this group include *Actaea rubra* (Ait.) Willd., *Asarum caudatum* Lindl., *Dicentra formosa* (Andr.) Walp., *Maianthemum dilatatum* (Wood) Nels. & Macbr., *Mitella caulescens* Nutt., *M. ovalis* Greene, *Tellima grandiflora* (Pursh) Dougl., *Tiarella trifoliata* var. *Unifoliata* (Hook.) Kurtz., and *Trillium ovatum* Pursh.
3. Grass and sedge species: The presence of thin-leaved grass and sedge species indicates high light environments where desiccation is common. They can also spread rapidly via seed into disturbed sites. Thinned stands, with the lowest canopy LAIs and most recent soil disturbance, should contain the most grass and sedge species. Species in this group include *Bromus* spp., *Carex* spp., *Cynosurus echinatus* L., *Elymus glaucus* Buckl., *Festuca* spp., *Holcus lanatus* L., *Luzula* spp., *L. campestris* L. DC., *L. parviflora* (Ehrh.) Desv., and *Poa* spp.
4. Achlorophyllous species: Species lacking chlorophyll during some part of their life history include monotropoid, orchidoid, ericoid, and parasitic species. They are unique in how they use shaded, understory environments and are ill-adapted for rapid dispersal, given their host specificity and mycotrophic dependency (Taylor and Bruns, 1997). Species in this group include *Corallorhiza maculata* Raf., *C. mertensiana* Bong., *Goodyera oblongfolia* Raf., *Hemitomes congestum* Gray, *Hypopitys monotropa* Crantz, *Monotropa uniflora* L., *Pleuricospora fimbriolata* Gray, and *Pyrola aphylla* Smith.
5. Matted vines: Species with vine-like growth forms are capable of rapid expansion into disturbed sites to capture new light and soil resources. They often develop thick vegetative mats that may preclude establishment and growth of other species. Thinned stands should have the greatest frequency and cover of these species. Species in this group include *Galium aparine* L., *G. oreganum* Britt., *G. triflorum* Michx., *Nemophila parviflora* Dougl., *Rubus ursinus* Cham. & Schlecht., and *Whipplea modesta* Torr.
6. Exotic species: This group includes species that were established in Oregon after Euro-American settlement (approximately 1900) according to Hitchcock and Cronquist (1973). They possess a combination of regenerative and survival strategies that has enabled their populations to invade and persist with native species. They are potentially assisted by the disturbances associated with young thinned (and potentially unthinned) stands in this study. Species in this group include *Caucalis microcarpa* H. & A., *Cyrsanthemum leucanthemum* L., *Cirsium arvense* (L.) Scop., *C. vulgare* (Savi) Tenore, *Cynosurus echinatus, Cytisus scoparius, Digitalis purpurea* L., *Epilobium angustifolium* L., *Holcus lanatus, Lactuca muralis* (L.) Fresen., *Rubus laciniatus* Willd., *Rumex crispus* L., *Senecio Jacobaea* L., *Swainsona salsula, Urtica dioica* L., and *Vicia cracca.*

Not every species fit into one of these groups, and several species occupy two groups. We analyzed aggregate frequency and cover for each group independently. The statistical tests were more powerful with the data for species groups than for individual species, and grouping species increased our ability to detect cover and frequency differences among stand-types.

Two multivariate ordination methods, detrended correspondence analysis (DCA) and non-metric multidimensional scaling (NMS) procedures in PC-ORD (McCune and Mefford, 1995), were used to analyze patterns in cover and frequency data. Both methods are used to indicate consistent shifts in species composition across samples. DCA is a standard procedure for viewing ecological data, and it adequately recovers information along the first axis if additional axes are of minor importance (van Groenewoud, 1992). We relativized cover data, such that values for all species ranged from 0 to 1, to equate the respective influence of various species (McCune and Mefford, 1995); frequency data are inherently relativized. We used a 'global' NMS ordination (McCune and Mefford, 1995) for herbaceous data since DCA axis 1 only captured 42% of the variability in the original full species-by-stand matrix. Furthermore, DCA is most powerful with a more vertical matrix (herbaceous data was dominantly horizontal), and the original data matrix was replete with outliers, which distort ordination space. NMS ordination is not sensitive to outliers, non-normal data, or matrix dimensions, and it has a more meaningful second axis relative to DCA.

Both ordination techniques were applied to the full stand-by-species matrix for herbs: 75 stands and 59 species that were found on at least 5% of the sites (i.e., >2 sites). Those analyses indicated a strong regional signal in the data, which prompted analysis of a reduced matrix comprised of 18 northern Coast Range stands and their 42 non-rare species. Only DCA was used to analyze the stand-by-species matrix for low shrubs (80 stands and four common species) since these data better met the assumptions of DCA. We correlated axes with individual species to determine which species might be driving the ordination of sites and stand-types. We also correlated axes with a secondary matrix containing physical data: mean annual precipitation, temperature, stand elevation, and aspect (sine-transformed).

3. Results

3.1. Richness

We recorded 212 herb species for the entire study; 75 of these species were unique to one triad in southwest Oregon (Fig. 1), and none were legally protected as 'threatened' or 'endangered.' Total species richness was higher in thinned stands than in unthinned stands or old-growth forests (Table 2), presumably based on the increased α-diversity (within-stand diversity) in the understory environment of thinned stands. Ten of the triads in this study analyzed by Mayrsohn (1995) had greatest richness in thinned stands (38 species) whereas corresponding unthinned and old-growth stands averaged 31 species each, significantly less than thinned stands ($P<0.05$). Richness of exotic species was greatest in thinned stands. However, exotics did not solely account for the higher total richness; nitrogen fixers, grasses, and vines were also richer in thinned stands (Fig. 3). Only two species unique to thinned stands were exotic (Table 3). Richness did not convey all the information in this data set. For example, old-growth and thinned stands were identical in terms of tall cordate-leaved species richness even though their frequencies were significantly different (Table 4).

3.2. Species frequency

Four low shrub species and three tall shrub species were sufficiently frequent (occurred at many sample points) to use parametric statistics and better detect stand-type differences. All sample points on all sites had some low shrub species present and typically contained multiple species. *Gaultheria shallon and Polystichum munitum* (Kaulf.) Presl were the most common shrubs, with median frequencies >0.8 across

Table 2
Herbaceous species richness by stand type

Species richness	Thinned stands	Unthinned stands	Old-growth stands
Total number of species	211	199	198
Average richness/site			
All species[a]	38	31	31
Of 59 common species	21	18	16

[a] Source: Mayrsohn (1995).

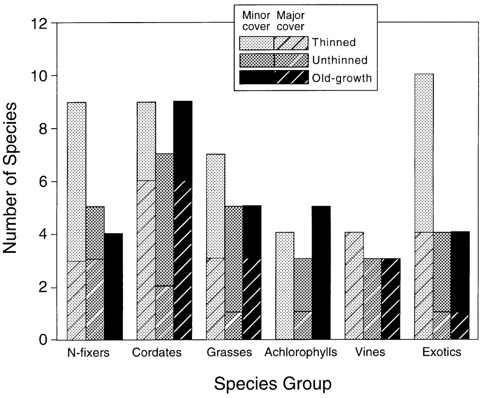

Fig. 3. Species richness (number of species) by stand-type for the six species groups. Major cover corresponds to individual species cover that averaged $\geq$1% across 10 1 m^2 subsamples at any point in any stand; minor cover was <1%.

all stand-types (P=0.21 and 0.95, respectively, for stand-type comparison). *Pteridum aquilinum* (L.) Kuhn. was more frequent in thinned and unthinned stands than in old-growth forests ($P\leq0.0001$), with median frequencies of 0.9, 0.7, and 0.2, respectively. *Acer circinatum* Pursh was more common in old-growth stands than in either thinned or unthinned stands (P=0.08), with median frequencies of 0.15, 0.05, and 0.04, respectively.

Every sample point on every site had some herbs; therefore, tests of frequency based on all 212 species were meaningless. At the opposite extreme, tests of individual species' frequencies detected few differences, given their respective sporadic occurrence in stands. For example, of 14 species associated with old-growth according to Spies (1991), only three species in our study showed significantly different frequencies (P<0.15) among stand-types: *Tiarella trifoliata* var. *unifoliata*, *Synthyris reniformis* (Dougl.) Benth., and *Goodyera oblongifolia*. (Table 1). *Rubus ursinus* was the only other individual herbaceous species that consistently increased in frequency across stand-types ($P\leq0.0001$), and it was most frequent in thinned stands.

3.3. Density and cover

Density or cover of vegetation in each stratum was greatest in thinned stands. Total tall shrub density (all species) was greater in old-growth and thinned stands than in unthinned stands (P=0.03). Thinned stands had greatest tall shrub density in 14 of 28 pairs,

Table 3
Species richness (number of species) by stand-type across 17-old-growth stands and 27 thinned–unthinned paired young stands, and a list of species unique to a given stand-type

Stand-type	Total number of herbaceous species	Species unique to stand-type
Old-growth forest	91	(none)
Young unthinned	114	*Erechtites minima* (Poir.) DC.
Young thinned	133	*Anaphalis margaritacea* (L.) B. & H. *Aralia californica* S. Wats. *Chrysanthemum leucanthemum* L.[a] *Elymus glaucus* Buckl.[b] *Epilobium minutum* Lindl. *Hydrophyllum occidentale* Wats. Gray *Hypopitys monotropa* Crantz.[c] *Lupinus* spp.[d] *Mimulus dentatus* Nutt. *Oenanthe sarmentosa* Presl. *Rubus laciniatus* Willd.[a] *R. Leucodermis* Dougl. *Senecio triangularis* Hook. *Varetrum californicum* Durand

[a] Exotic species.
[b] Grass species.
[c] Monotropoid.
[d] Nitrogen-fixing species.

Table 4
Frequency and percent cover for each species group across 18 stands of each type

Species group	Stand-type	Frequency	Total cover (%)
Nitrogen-fixing species	Thinned	0.25 (0–0.67) a	0.20 (0–1.50) a
	Unthinned	0 (0–0.20) b	0 (0–0.05) b
	Old-growth	0 (0–0.00) b	0 (0–0.00) b
		($P=0.0002$)	($P=0.006$)
Tall, cordate-leaved species[a]	Old-growth	0.42 (0.35–0.49) a	0.25 (0.07–0.74) a
	Thinned	0.28 (0.21–0.35) b	0.16 (0.03–0.46) a,b
	Unthinned	0.22 (0.16–0.28) b	0.09 (0.03–0.21) b
		($P=0.009$)	($P=0.08$)
Grasses and sedges[a]	Thinned	0.66 (0.39–0.95) a	0.57 (0.32–2.5) a
	Unthinned	0.49 (0.17–0.81) b	0.32 (0.02–0.79) b
	Old-growth	0.34 (0.09–0.59) b	0.12 (0.05–0.38) b
		($P=0.002$)	($P=0.0003$)
Achlorophyllous species	Unthinned	0.16 (0–0.3) a	0.03 (0–0.04) a
	Old-growth	0.10 (0–0.2) a	0.01 (0–0.05) a
	Thinned	0.09 (0–0.1) a	0.01 (0–0.02) a
		($P=0.21$)	($P=0.57$)
Matted vine species	Thinned	1.0 (0.9–1.0) a	8.3 (1.5–10.4) a
	Unthinned	1.0 (0.9–1.0) a	1.6 (1.4–3.30) b
	Old-growth	0.6 (0.4–0.9) b	0.9 (0.3–2.64) b
		($P=0.0001$)	($P=0.0001$)
Exotic species	Thinned	0.1 (0.1–0.3) a	0.08 (0.01–0.30) a
	Old-growth	0 (0–0.1) b	0 (0–0.11) b
	Unthinned	0 (0–0.0) c	0 (0–0.00) c
		($P=0.0001$)	($P=0.0001$)

[a] Data were normally distributed. Values represent means±one standard deviation.

P-values represent comparisons among stand-types. Within a species group, different letters designate statistically significant differences at $\alpha=0.05$.

significant across all pairs at $P=0.002$. Tall shrub density for individual species was not consistently different across stand-types except for *Rosa gymnocarpa* Nutt., which was greater in thinned stands across 28 pairs ($P=0.05$). Potential relationships between tall and low shrub cover and overstory characteristics are presented in Bailey and Tappeiner (1998).

Total low shrub cover was, on average, 13% greater in thinned stands than in either unthinned or old-growth stands ($P=0.005$). This difference can be attributed to two species: *Pteridium aquilinum* and *Gaultheria shallon*. *P. aquilinum* cover was 0% and 1% in unthinned and old-growth stands, respectively, and 5% in thinned stands (median values, rank test $P<0.0001$). *G. shallon* cover was 5% and 8% in unthinned and old-growth stands, respectively, but 23% in thinned stands (median values, rank test $P=0.02$). *Polystichum munitum* cover was not consistently different across triads ($P=0.80$), but among pairs it was marginally greater in unthinned stands ($P=0.15$). *Berberis nervosa* Pursh cover was not consistently different across pairs or triads.

Total herbaceous cover was also consistently greater in thinned stands across 18 triads ($P=0.03$) relative to both unthinned and old-growth stands, and across 28 pairs ($P=0.005$) relative to unthinned stands. Thinned stands averaged 25% total herbaceous cover (±6%), approximately 10–12% greater than either unthinned or old-growth stands. Total herbaceous cover was not different between unthinned and old-growth stands, which averaged 13% and 15% total cover, respectively. Cover was not different among stand-types for most of the individual 212 herbaceous species or even for the 59 most common species, given their respective sporadic occurrence within stands.

None of the 14 species associated with old-growth (Table 1) according to Spies (1991), which were all included in the 59 most common species in this study, had significantly greater cover in old-growth stands than in either young stand on these sites. However, Spies (1991) summarized data from a larger number of sites and used absolute rather than relative cover.

3.4. Leaf area index

Tall shrub LAI was not different between thinned and old-growth stands, as with density, though unthinned stands had lower LAI (P=0.001). Low shrub LAI was consistently greater in thinned stands (1.4 $m^2\,m^{-2}$) than in old-growth and unthinned stands, both 0.8 $m^2\,m^{-2}$ ($P\leq0.0001$). Combining LAI for the two shrub strata and comparing across stand-types yielded differences among all three stand-types (P=0.0005), with thinned stands averaging 1.7, old-growth stands averaging 1.2, and unthinned stands averaging 0.9. This suggested some compensatory interaction between tall and low shrubs, at least in old-growth stands.

3.5. Species groupings

We detected differences among stand-types in five of six species groupings (Table 4). Aggregate cover of some species group was still quite low (e.g. maximum cover of nitrogen-fixing species was only 1.5%), making comparisons weak. Comparisons based on frequency, however, were often more significant statistically. Species frequency also has ecological relevance both as an indicator of stand history and as a potential source of propagules for future stand development. Though not statistically significant across 18 triads, achlorophyllous species frequency was greater in unthinned than in thinned stands across all 28 pairs (P=0.03) with median frequencies of 0.11 and 0.08, respectively.

3.6. Community composition

DCA ordinations (80 stands×4 species) using low shrub cover were remarkably similar to those using shrub frequency and showed differences among sites and among stand-types (Fig. 4). Thinned stands were most distinct from old-growth and unthinned stands, particularly along axis 1 (Fig. 4). Axis 1 correlated positively with *Gaultheria shallon* cover (r=0.61) and negatively with *Polystichum munitum* cover (r=−0.62), the dominant shrub and fern species. The stands outside of the polygon defined by old-growth and unthinned stands along axis 1 (Fig. 4) were all heavily thinned stands ≤80 years old with dense shrub cover. No other factors (e.g. latitude or climate) were strongly correlated with axis 1. Similarity in ordinations of frequency and cover data suggests that the ordination of stands was controlled by species frequency within and among stands, which was only slightly modified by differences in percent cover.

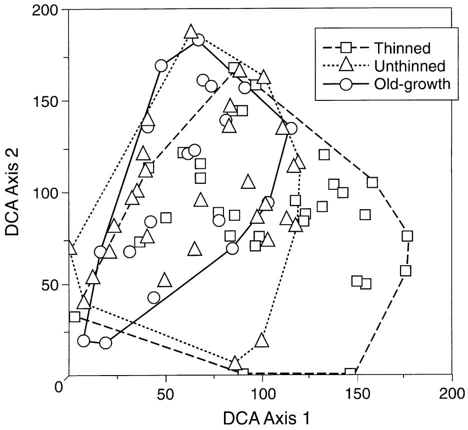

Fig. 4. DCA ordination of small shrub cover data over the entire range of sites (four species and 80 stands). Polygons delineate the range of data in two dimensions by stand-type.

NMS ordinations of herbaceous community data (75 stands×59 species) showed much stronger differences among sites than among stand-types (Fig. 5). Pairs and triads ordinated closely in two dimensions assigned by axes 1 and 2, which captured 78% of the variability in the original data matrix. Southern Oregon pairs and triads tended to occupy the lower range of both axes. These pairs and triads had a high frequency of dry-site species such as *Whipplea modesta* (r=−0.54 and r=−0.49 for axes 1 and 2, respectively) and a low frequency of moist-site species such as *Oxalis oregana* Nutt. (r=0.49 and r=0.37 for axes 1 and 2, respectively). Correlation with a secondary matrix containing mean annual rainfall produced

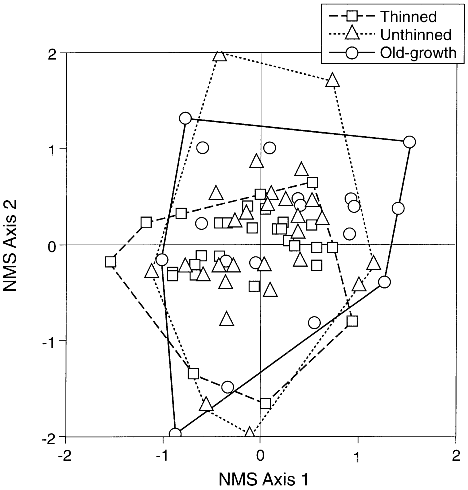

Fig. 5. NMS ordination of herbaceous species frequency data for 75 stands and 59 species. Polygons delineate the range of data in two dimensions by stand-type.

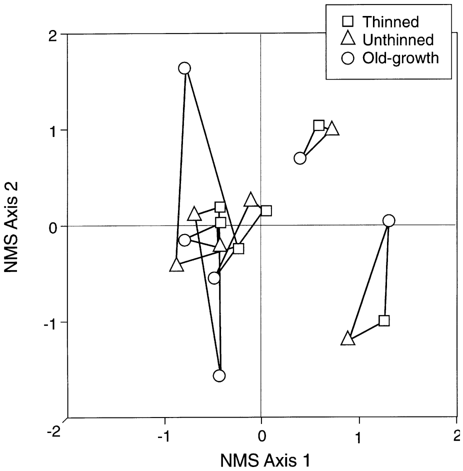

Fig. 6. NMS ordination of herbaceous species frequency data over six triads (42 species and 18 stands). Polygons delineate triads.

r-values of 0.67 and 0.47 for axes 1 and 2, respectively. Pairs of young stands typically ordinated in closer proximity to one another than with their corresponding old-growth stands. When all stand-types were physically adjacent (complete triad), their ordinations were typically most proximate to one another as well. The area of two-dimensional space occupied by each stand-type appears greater for old-growth and unthinned stands than thinned stands (Fig. 5). This suggests that herbaceous communities were more variable in old-growth and unthinned stands than in thinned stands.

Six northern Coast Range triads were subsampled to minimize the tendency for ordinations to distinguish only among sites across different regions or vegetation-types. The results still showed strong differences among sites (Fig. 6). Site-to-site difference was the strongest signal in every herbaceous data submatrix analyzed (e.g. north Cascades, south Cascades). The two primary axes again captured 78% of the variability in the original data matrix. As with the full data set, thinned and unthinned stands were consistently more proximate to each other than to their corresponding old-growth stands, and old-growth and unthinned herbaceous communities were more variable than were unthinned stands (Fig. 6). Within this smaller geographic area, the correlation of axis 1 with rainfall decreased to $r=-0.32$.

4. Discussion

4.1. Comparisons among stand-types

Thinning the overstory canopy of young Douglas-fir stands in western Oregon resulted in consistently higher shrub density, cover, and frequency relative to their unthinned pairs. Richness, frequency, and cover of some herbaceous species and most species groups, including exotics, were also greater in thinned stands than unthinned stands. These differences probably reflect an increase in resource availability (e.g. light), as established by Klinka et al. (1996), and small-scale habitat diversity created by a broad disturbance across a large area. These newly disturbed microhabitats with increased light and other resources were rather uniformly scattered throughout each thinned stand, given the intent of the thinning. Heavier thinnings that remove larger trees and/or groups of trees (or patches) are likely to create more resources for the understory. In comparison to data on vegetation response in clearcuts (Halpern, 1988), shrub and herb responses to thinning from below appear somewhat less in magnitude.

There was little evidence for competitive interaction between strata, as defined by mutual presence and amount of cover by each stratum, given that thinned stands consistently had greater tall shrub density and

LAI, low shrub cover and LAI, and herbaceous cover and frequency than did unthinned stands. Analyses also showed multiple strata responses to thinning at individual points within stands. Apparently, most thinned stands provide sufficient resources for multiple strata to develop simultaneously, at least in the near term.

Thinned stands also consistently showed equal or greater richness, frequency, and cover of herbs and shrubs relative to nearby old-growth forests. The exceptions to this were the leaf area and total density of tall shrubs, density of several tall shrub species, and frequency of tall cordate-leaved herb species; these were greatest in old-growth stands. The cover of tall cordates, however, was apparently enhanced by thinning such that thinned and old-growth stands were not different. Changes in richness, frequency, and cover do not automatically result in changes to species composition. We found little evidence of consistent compositional shifts among any of the stand-types, particularly for herbaceous species, based on ordination.

Similarities in understory vegetation between young (particularly unthinned) stands and old-growth stands suggest that native vascular plants in the Coast and Cascade Ranges are quite resilient to environmental change. The logging and burning when young stands were harvested near the turn of the century were severe disturbances, and early successional species likely dominated these stands for two or more decades. Then during the dense stem exclusion stage of stand development (Oliver, 1981), the flush of early seral growth was suppressed. Despite these extreme environmental fluctuations (total sun to total shade), species richness, composition, total cover, and individual species frequency and cover are indistinguishable $\geq$50 years later. This is consistent with work by Dyrness (1973) and Halpern (1988), who documented that native understory species in the Northwest can survive major environmental change created by clearcutting, and by Graae and Heskjaer (1997) for deciduous forests in Denmark. In young, unthinned stands, this similarity in understories is promoted by natural self-thinning and stem re-initiation, as well as by small-scale disturbances. Such processes are mimicked by thinning, as shown by the response of density, cover, frequency, and richness of understory species in this study.

4.2. *Site-to-site differences*

Site-to-site differences in understory communities dominated any treatment or stand age effect, as demonstrated by ordination analyses that placed pairs and triads in close proximity to one another, and subregions (e.g. northern Coast Range) together. Furthermore, species groups, which lumped species with similar ecological 'roles', were highly effective in distinguishing stand-types. Finally, blocking by triad was significant in all but a few of the hundreds of comparisons made in this analysis, and pairwise *t*-tests were necessary to detect stand-type differences.

For old-growth and unthinned stands, regional differences among triads (e.g. north and south) reflect changes in climate, soils, and landscape history. Differences across thinned stands further include differences in the intensity of and time since thinning disturbance. Low correlations between cover and disturbance measures were due to variations in site history and productivity, stand age, and time since thinning, as well as our limited selection of sites. The size and design of this study preclude using multiple regressions with all influential factors to predict species cover and frequency. This site-to-site variability has major implications on how we monitor rare species within broad landscapes and how we look for potential effects of silvicultural treatments. Sampling with sufficient intensity to construct estimates of cover and frequency that would show differences among stands may become prohibitively expensive when applied broadly.

4.3. *Management implications*

Does thinning in young, dense Douglas-fir stands accelerate the formation of old-growth-type understory communities? The answer is 'yes' given that this and other studies show that thinning increased the density, cover, and frequency of many species that were suppressed under the light-limiting canopy of unthinned stands to higher levels as found in old-growth stands. For example, tall shrub density and tall cordate-leaved herbaceous cover (not frequency) apparently responded strongly to thinning and reached levels comparable to old-growth stands. Also, thinning increased total richness (α-diversity) in the understory community, which may have implications for species composition as the stand ages.

However, as with Schoonmaker and McKee (1988) and Graae and Heskjaer (1997), we found that old-growth forests did not consistently show maximum richness or highest density, frequency, and cover of all herb and shrub species. Increasing frequency and cover of invasive species (e.g. matted vines) in thinned stands may ultimately be counterproductive to the formation of old-growth forest communities, making the answer 'no.' However, the maximum cover observed for such invasive species was only 10%, and managers can monitor invasive species cover, and treat it if necessary, to ensure that it remains low over time. As the overstory canopy regrows and conifer and hardwood structure in the intermediate canopy develops in thinned stands (Bailey and Tappeiner, 1998), herb and shrub cover, with time, are likely to return to lower levels that are more consistent with old-growth stands.

Managers could also compensate for the strong response of understory vegetation to thinning by varying the intensity of thinning within and among stands, leaving a mixture of open (low LAI) and dense (high LAI) canopies to more closely simulate natural stem re-initiation. Such variable-intensity thinning, which creates within-stand heterogeneity, would enhance both α- and β-diversity (in the broader landscape) and represents an alternative to developing a matrix of evenly thinned young stands interspersed with other stand-types. However, continuous cover of any stand-type (particularly young plantations and unthinned mature stands) reduces β-diversity and should be avoided.

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