

Table 3—Multiple components model representing 5 forest structure components (data are forest age-class means with standard errors in parentheses)

Variable selected	Forest age-class			Structure coefficient		
	Young	Mature	Old growth	CV1	CV2	
Basal area of conifers ≥ 40 m tall	3.2 (1.1)	25.7 (4.0)	40.1 (2.4)	0.93	-0.15	
Basal area of conifers ≥ 90 cm in d.b.h.	1.1 (.6)	12.5 (2.5)	34.8 (2.4)	.88	.20	
Basal area of conifers < 45 cm in d.b.h.	14.4 (2.5)	6.7 (1.5)	2.0 (.4)	-.79	-.03	
Density of hardwood saplings 1-2 m tall	322.3 (53.4)	274.5 (76.3)	633.0 (70.6)	.42	.41	
Percentage cover of hardwoods ≤ 8 m tall	12.5 (2.3)	16.8 (4.3)	25.0 (2.2)	.47	.19	
Density of hardwood snags ≥ 20 cm in d.b.h. and ≥ 2 m tall	6.7 (2.3)	20.0 (5.1)	5.1 (1.2)	-.10	-.56	
Basal area of hardwoods 45-90 cm in d.b.h.	5.3 (1.3)	2.8 (1.0)	5.4 (.7)	.09	.34	
Density of hardwood seedlings 25-50 cm tall	1307.1 (305.0)	1370.4 (314.2)	1496.7 (144.3)	.18	.07	
Wilks' lambda	0.048			Eigenvalue	4.97	2.48
Exact <i>F</i> statistic (df = 16, 92) (significant at $P < 0.001$)	20.45			(%)	67	33
Classification success (%)	100	100	100			

powerful in discriminating among the forest age-classes. The variables selected represented five of the six forest components (table 3). No down-wood (log) variables were retained.

The most important variables discriminating the age-classes were the basal areas of conifers ≥ 40 m tall, ≥ 90 cm in d.b.h., and < 45 cm in d.b.h. The density of hardwood saplings 1 to 2 m tall, the percentage cover of hardwoods ≤ 8 m tall, the basal area of hardwoods 45 to 90 cm in d.b.h., and the density of hardwood snags ≥ 20 cm in d.b.h. and ≥ 2 m tall were of moderate importance. The eighth variable, the density of hardwood seedlings 25 to 50 cm, made a very minor contribution to the model.

Features most distinctive of old growth (fig. 12) were high basal areas of conifers ≥ 40 m tall and conifers ≥ 90 cm in d.b.h., and a low basal area of conifers < 45 cm in d.b.h. A high cover of hardwoods ≤ 8 m tall and a high density of hardwood saplings 1 to 2 m tall also contributed (table 3). Young forests were distinguished by low basal areas of conifers ≥ 40 m tall and conifers ≥ 90 cm in d.b.h., along with a high basal area of conifers < 45 cm in d.b.h. Mature forests were typified by basal area values that were all intermediate to old-growth and young forests. Another feature of the mature age-class was a relatively high density of hardwood snags ≥ 20 cm in d.b.h. and ≥ 2 m tall. Two other features, the density of hardwood saplings 1 to 2 m tall, and the basal area of hardwoods 45 to 90 cm in d.b.h. were both lower in mature stands than in young and old-growth forests.

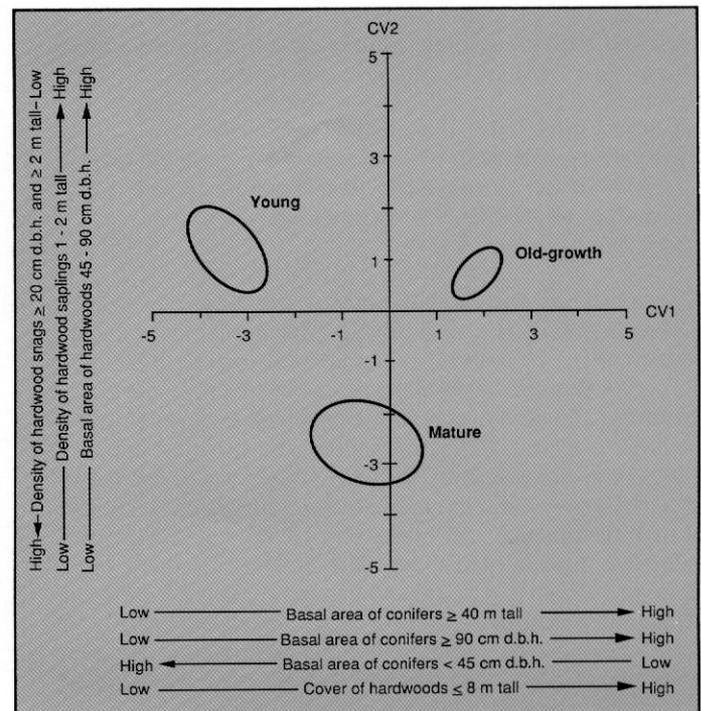


Figure 12—Ordination of forest age-classes according to seven variables. Significant separation of age-class means occurred for both canonical variates (CV1 and CV2). Plotted are the 95 percent confidence ellipses around age-class centroids.

Of the 14 validation stands used to test the model, all 10 old-growth and three of the four mature stands were correctly assigned. One mature stand dominated by trees ≥ 185 years old and on a productive site was incorrectly assigned to old growth.

The jackknife classification of the training set (56 stands) correctly assigned 100 percent of the old-growth stands, 79 percent of the mature stands, and 100 percent of the young stands. One mature stand, about 135 years old, was incorrectly assigned to the young class. It was an unmanaged stand characterized by a considerably higher density of hardwoods, and a lower density of conifers 45 to 90 cm in d.b.h. than was typical of mature stands. Another mature unmanaged stand, 190 years old, was incorrectly assigned to old-growth. It had a moderate density of large conifers ≥ 90 cm in d.b.h. and high densities of hardwoods ranging from seedlings to large trees. The third stand was also incorrectly assigned to the old-growth class. The stand was logged 115 years ago but retained several residual large conifers per hectare and had a high density of hardwoods.

Discussion

As indicated by our multiple components model and by our analyses of individual forest components, features associated with tree size provide the strongest discrimination among different-aged Douglas-fir/hardwood forests. In the multiple components model, the most distinctive features of old-growth forests were a high basal area of very large Douglas-fir trees and a low basal area of small Douglas-fir trees. The reverse was true of young forests and intermediate values were typical of mature forests.

The four discriminant models based on variables representing the tree height and tree diameter components were the most powerful of the 11 individual-components models. The remaining models indicated that features of tree reproduction, understory, and dead-wood components, on their own, provide little-to-moderate discrimination. The variation in such features, between stands as well as within a stand, can be extreme. Changes in microhabitat conditions affect seedling and sapling densities, and understory cover values. Tree reproduction, especially of Douglas-fir, varies from scattered individuals to densely populated patches associated with canopy openings regardless of forest age. The influences of total canopy cover on tree reproduction and understory growth are similar for different-aged forests. Regardless of age-class, hardwood reproduction is mainly from crown sprouts. Reproduction from seed is variable, showing patterns in distribution similar to those of Douglas-fir. As a result, seedling and sapling densities, and understory cover can each include a wide range of stand values that typically overlap among different-aged forests.

The accumulation and distribution of coarse woody debris are affected by environment, disturbance, decay rates, and topography (Harmon and others 1986). Wet sites typically have greater amounts of coarse wood than do dry sites (Spies and others 1988). Recruitment of coarse woody debris as snags and logs often occurs in waves related to some event. Stands with histories of hot or frequent fire can contain small quantities of dead wood. Managed stands can inherit large quantities of wood on the ground as slash. Low numbers of large snags, and higher numbers of stumps are also carried over. Decay progresses at different rates depending on species, size, microclimate, and cause of mortality. Topography affects accumulations and distributions by influencing storm patterns, the direction of tree-fall, and the movement of material by gravity. Such influences are important regardless of stand age, and help explain similarities among different-aged forests in certain features of coarse woody debris.

Our multiple components model provides forest managers with a set of features that, in combination, are distinctive of young, mature, and old-growth Douglas-fir/hardwood forests. Together, these features act as a powerful tool for discriminating among the forest age-classes. The models composed of variables selected by analyses of individual forest components can further assist managers in identifying important features of each forest age-class. For example, the analysis of the snag component showed that managed young forests generally have higher sound-snag and rotten-snag densities than does old growth. Old-growth forests, however, typically have higher densities of large conifer snags > 40 cm in d.b.h. and > 4 m long. As another example, analyses of the features of the log component showed that managed young stands and old growth generally have relatively high densities and biomasses of logs > 44 cm in diameter and ≥ 4 m long, while mature stands typically contain low quantities.

Testing our model with the validation data set and the jackknife classification helps confirm certain ideas about the development of old-growth features. Age alone may be a poor indicator of old-growth structure. Old-growth conditions develop gradually, with the rate related to the environmental conditions and the disturbance history of the stand (Spies and Franklin 1988). Certain features of old growth, such as a high density of very large trees, do appear on productive sites before 200 years. Stands on sites that are poor at producing large conifers may require much longer periods or may never develop certain features commonly associated with old growth. On managed sites, logging practices can retain large conifers and hardwoods at densities more characteristic of old growth than younger stands.

Forest Definitions

We define young, mature, and old-growth Douglas-fir/hardwood forests by using ranges of means observed in the majority of the stands we sampled in each age-class. The ranges, therefore, represent typical stand values and not minimums or maximums. To provide the most thorough descriptions, we included features beyond those selected by our stepwise discriminant analyses. The major features we used to define each forest age-class, such as tree densities for dominant height- and diameter-classes, and total snag and log densities, all exhibited standard errors that were $< \pm 20$ percent of the age-class mean. Other features, such as those of seedling densities and understory cover, are more affected by changes in microhabitat conditions and tend to show greater variation.

Young Douglas-fir/hardwood forests

Canopy <40 m tall, single-tiered, total cover 65 to 80 percent.

Trees 12 to 40 m tall, conifers 105 to 525 per ha and hardwoods 160 to 660 per ha. Dominant stems, conifers <45 cm in d.b.h., 260 to 780 per ha; hardwoods <45 cm in d.b.h., 225 to 1215 per ha. Stand basal area, 30 to 75 percent hardwoods.

Saplings 1 to 8 m tall, conifers 150 to 450 per ha and hardwoods 300 to 1200 per ha.

Seedlings <1 m tall, conifers 100 to 2500 per ha and hardwood seedlings or sprouts 1500 to 7000 per ha.

Understory cover ≥ 8 m tall, conifers 2 to 10 percent and hardwoods 5 to 20 percent.

Ground cover < 2 m tall, 10 to 25 percent. Moss and lichen cover including epiphytes on the ground, 1 to 5 percent.

Snags ≥ 10 cm in d.b.h., 45 to 135 per ha. Hardwood snags 20 to 60 percent of snag density. Large snags >40 cm in d.b.h. and >4 m tall, 0.5 to 5 per ha.

Logs ≥ 10 cm in diameter, 200 to 530 per ha. Hardwood logs 20 to 65 percent of log density. Large logs >44 cm in diameter and ≥ 4 m long, 7 to 48 per ha.

Biomass of snags and logs, 10 to 50 metric tons per ha.

Mature Douglas-fir/hardwood forests

Canopy <55 m tall, two-tiered but indistinct, total cover 65 to 80 percent.

Trees 12 to 40 m tall, conifers 60 to 215 per ha and hardwoods 120 to 330 per ha; ≥ 40 m tall, conifers 30 to 60 per ha. Dominant stems, conifers 45 to 90 cm in d.b.h., 40 to 70 per ha; hardwoods <45 cm in d.b.h. 255 to 760 per ha. Stand basal area, 15 to 45 percent hardwoods.

Saplings 1 to 8 m tall, conifers 50 to 400 per ha, and hardwoods 30 to 1100 per ha.

Seedlings <1 m tall, conifers 250 to 1200 per ha and hardwood seedlings or sprouts 3000 to 9000 per ha.

Understory cover ≤ 8 m tall, conifers 1 to 5 percent and hardwoods 5 to 35 percent.

Ground cover <2 m tall, 5 to 55 percent. Moss and lichen cover including epiphytes on the ground, 1 to 20 percent.

Snags 210 cm in d.b.h., 35 to 125 per ha. Hardwood snags 20 to 90 percent of snag density. Large snags ≥ 40 cm in d.b.h. and ≥ 4 m tall, 0.5 to 4 per ha.

Logs ≥ 10 cm in diameter, 225 to 385 per ha. Hardwood logs 45 to 75 percent of log density. Large logs >44 cm in diameter and ≥ 4 m long, 0.5 to 16 per ha.

Biomass of snags and logs, 5 to 30 metric tons per ha.

Old-growth Douglas-fir/hardwood forests

Canopy >55 m tall, two-tiered and well to defined, total cover 65 to 80 percent.

Trees 12 to 40 m tall, conifers 15 to 55 per ha and hardwoods 105 to 280 per ha; 240 m tall, conifers 35 to 50 per ha. Dominant stems, conifers ≥ 90 cm in d.b.h. 20 to 40 per ha; hardwoods <45 cm in d.b.h. 425 to 690 per ha. Stand basal area, 15 to 40 percent hardwoods.

Saplings 1 to 8 m tall, conifers 30 to 300 per ha and hardwoods 650 to 1500 per ha.

Seedlings <1 m tall, conifers 150 to 1100 per ha and hardwood seedlings or sprouts 3500 to 9900 per ha.

Understory cover ≤ 8 m tall, conifers 1 to 5 percent and hardwoods 15 to 30 percent.

Ground cover <2 m tall, 10 to 65 percent. Moss and lichen cover including epiphytes on the ground, 5 to 25 percent.

Snags ≥ 10 cm in d.b.h., 20 to 40 per ha. Hardwood snags 15 to 75 percent of snag density. Large snags ≥ 40 cm in d.b.h. and ≥ 4 m tall, 0.5 to 11 per ha.

Logs ≥ 10 cm in diameter, 215 to 385 per ha. Hardwood logs 20 to 55 percent of log density. Large logs >44 cm in diameter and ≥ 4 m long, 14 to 38 per ha.

Biomass of snags and logs, 10 to 110 metric tons per ha.

Old-growth Douglas-fir/hardwood forest overstories are strongly two-tiered. The hardwoods attain maximum heights roughly half the height of Douglas-fir and dominate the lower tier. In the upper tier, Douglas-fir dominates as widely spaced individuals or as groups of trees. Within the forest, the prevalence of either tier shifts from place to place. Forest openings with hardwood and conifer regeneration at various stages add to the high spatial diversity.

In addition to the forest canopy, the hardwood element of Douglas-fir/hardwood forest influences other forest components. Hardwoods contribute importantly to snag and log densities, but because of the smaller dimensions of hardwoods, along with several other factors (such as different climatic and disturbance regimes), snag and log biomasses are low in comparison to Douglas-fir forests farther north where other conifers share dominance. Densities of large snags and large logs are also typically lower.

New Standards for Old-Growth Douglas-Fir/Hardwood Forests

Our research indicates that the minimum standards prepared by the Old-Growth Definition Task Group (1986) for old-growth Douglas-fir/hardwood forests require revision (table 4). We introduce standards for some additional features not included in the interim definition, but identified as key features by our analyses. Along with new minimum standards, we present average values \pm 95-percent confidence limits for each key feature.

The most diagnostic feature of nonmanipulated old-growth Douglas-fir/hardwood forests is the presence of large old trees in densities adequate to form an upper tier that dominates over a hardwood layer. Stands that fail to meet minimum standards for other features, such as those for large snags and large logs can qualify as old growth. For example, wet and mesic sites are more likely to exceed the minimum values, and dry sites are more likely to approach or even drop below the minimum criteria. We believe that the new minimum standards will include the majority of old-growth Douglas-fir/hardwood stands in northwest California and southwest Oregon.

Table 4-Interim and new standards for old-growth Douglas-fir/hardwood forests in northwestern California and southwestern Oregon

Stand characteristic	Interim minimum standards from Old-Growth Definition Task Group 1986 ^a	New minimum standards	New average standards \pm 95% confidence limits
Live trees	Douglas-fir and evergreen hardwood (tanoak, Pacific madrone, and canyon live oak) associates (40 to 60 percent of canopy)	Douglas-fir and evergreen hardwood associates (e.g. tanoak, Pacific madrone, and canyon live oak), hardwoods account for ≥ 10 percent of the total stand basal area	Basal area of hardwoods average 30 ± 5 percent of the total stand basal area
	Douglas-fir or sugar pine ≥ 15 per ha of trees >80 cm in diameter or >200 years old	Douglas-fir or minor conifers (e.g. sugar pine, Port-Orford-cedar, iucense-cedar, or redwood) ≥ 14 per ha of trees ≥ 90 cm diameter or >200 years old	Douglas-fir or minor conifers average 29 ± 3 per ha of trees ≥ 90 cm in diameter or >200 years old
	Intermediate and small size-classes may be evergreen hardwoods or include a component of conifers (e.g., Douglas-fir or white fir)	Intermediate and small size-classes of hardwoods and Douglas-fir, >10 percent total cover of trees ≤ 8 m tall, may include minor conifers	Intermediate and small size-classes with high numbers of hardwoods and moderate numbers of Douglas-fir or minor conifers, small sires ≤ 8 m tall average 25 ± 5 percent cover of hardwoods and 2 ± 1 percent cover of conifers

Table 4—continued

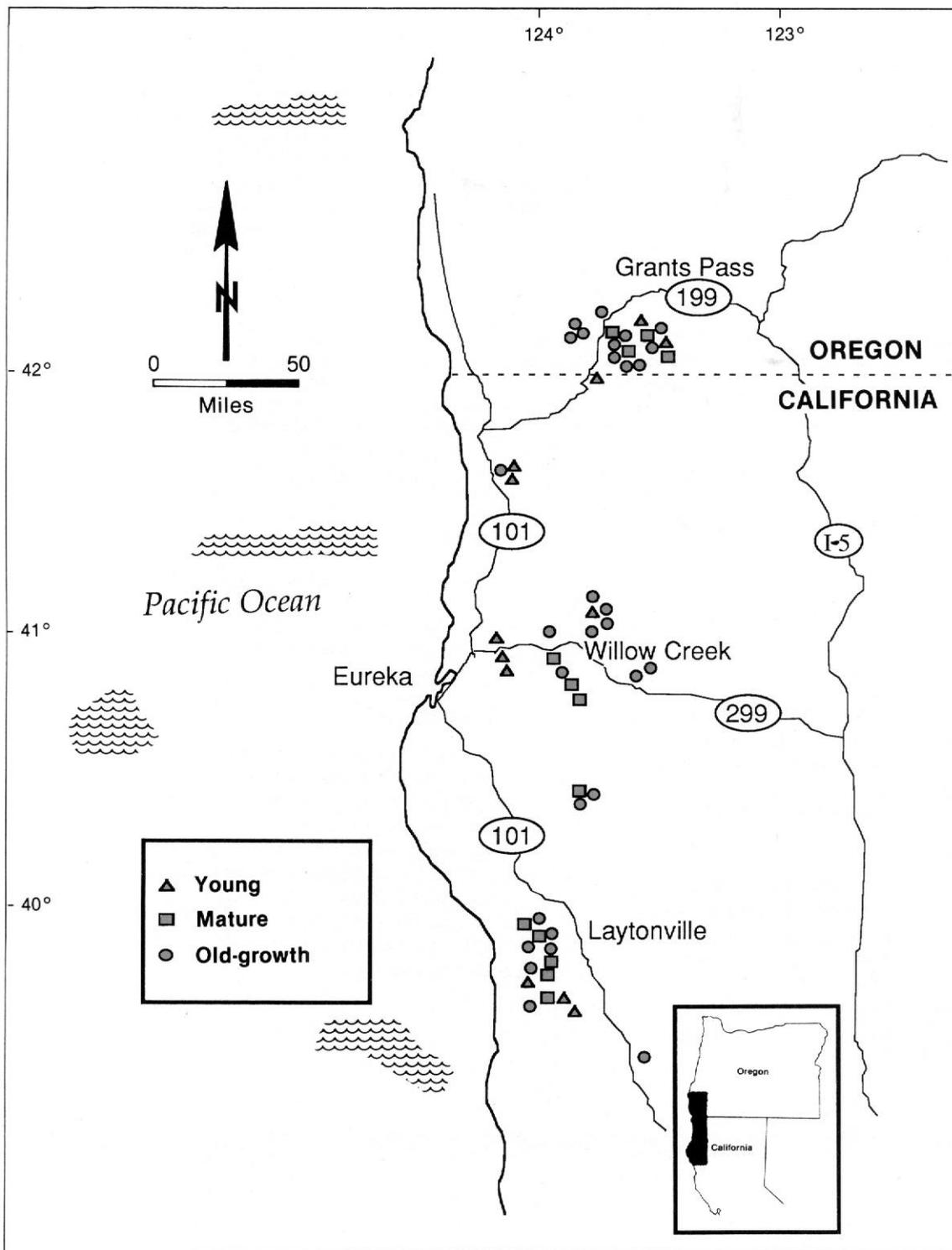
Stand characteristic	Interim minimum standards from Old-Growth Definition Task Group 1986 ^a	New minimum standards	New average standards ± 95% confidence limits
Canopy	Douglas-fir emergent above evergreen hardwood canopy	Distinct two-tiered canopy with an upper tier of Douglas-fir with trees reaching heights >40 m and a lower tier of conifers and hardwoods <40 m tall and a total canopy cover of >60 percent	Conifers ≥ 40 m tall average 44 ± 2 trees per ha, conifers 12 to 40 m tall average 39 ± 15 trees per ha, hardwoods 12 to 40 m tall average 221 ± 43 trees per ha, and an average total canopy cover of 71 ± 3 percent
Snags	Conifer snags >4 per ha that are >50 cm in diameter and >4.5 m tall	Conifer or hardwood snags >13 per ha that are ≥10 cm in diameter including >0.25 per ha of conifer snags that are ≥40 cm in diameter and ≥4 m tall	Conifer or hardwood snags ≥10 cm diameter average 32 ± 6 per ha including 5 ± 2 per ha of conifer snags that are ≥40 cm diameter and ≥4 m tall
Logs	Logs >22 metric tons per ha including 5 pieces per ha >60 cm in diameter and >15 m long	Logs >2.5 metric tons per ha including >1 piece per ha >44 cm in diameter and ≥4 m long, of which >0.25 piece per ha are >15 m long	Logs average 26 ± 8 metric tons per ha including 25 ± 6 pieces per ha that are >44 cm in diameter and ≥4 m long, of which 5 ± 2 pieces per ha are >15 m long

^a The Old-Growth Definition Task Group uses the name Douglas-fir on mixed evergreen sites in their interim definition. Values from the interim minimum standards have been converted to metric equivalents.

The new minimum standards are intended to assist managers in identifying nonmanipulated and manipulated stands that contain key old-growth features. Additionally, the minimum standards can be used as guidelines for retaining features associated with old growth when manipulating stands. We view the mean values and 95 percent confidence limits as being more appropriate for identifying optimal old-growth conditions. We also suggest that the new old-growth definition be used to supplement the minimum and average standards. The old-growth definition goes beyond the standards for large trees, snags, and logs in providing criteria for additional understory features. The definitions for young and mature stands will also assist managers when making age-class comparisons over a wide range of structural features.

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Location of study sites.

Habitat Association Patterns of Breeding Birds and Small Mammals in Douglas-Fir/Hardwood Stands in Northwestern California and Southwestern Oregon

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Abstract

We surveyed birds and small mammals in 45 forest stands from southern Oregon, near Cave Junction, south into northern California, near Branscomb. Over this 350-km distance, we found 71 species of birds and 7 species of mammals that were common enough for detailed analysis. Fourteen species of birds and two mammals reached peak abundances in older (mature and old-growth) forests; however, none appeared limited to these forests. The species were: Allen's hummingbird, hairy woodpecker, pileated woodpecker, Hammond's flycatcher, western flycatcher, gray jay, chestnut-backed chickadee, red-breasted nuthatch, brown creeper, winter wren, golden-crowned kinglet, wrentit, hermit warbler, black-headed grosbeak, Douglas' squirrel, and the California

red-backed vole. In addition, about half of the species were correlated with total conifer or hardwood stems. The abundance of many species also differed among the three geographic regions we sampled. These differences could also be associated with elevation because our northern stands tended to be at higher elevations than were the southern stands. Our community analysis of the birds showed separations between different regions, and between the avian communities of young forests and those of older (mature and old-growth) forests. The mature and old-growth bird communities were not readily separable from each other.

Introduction

The Douglas-fir forests of northwestern California are a major source of timber products in the United States, with almost half of the Nation's timber supply contained in the old-growth forests of the West (Society of American Foresters Task Force 1983: 1). Clearcutting has been the primary method of harvesting timber in the region for the past 30 years. Morrison (1988) has documented the great reduction of old-growth timber in many forests of the Pacific Northwest, which includes Washington, Oregon, and northern California.

Present management guidelines state that the USDA Forest Service shall "maintain viable populations" of all vertebrates found on each National Forest (National Forest Management Act 1976, 16 U.S.C. 1600-1614), yet the impacts of the decline of old-growth forests on vertebrate populations in northwestern California are uncertain, with only a few studies on the subject (Hagar 1960, Raphael 1984, Raphael and others 1988). Our study's goal is better understanding of the association patterns of flora and fauna across a chronosequence of forests in the Northwest; it was conducted as a part of research that extends north into Washington (Carey and Spies, this volume; Ruggiero and Carey 1984).

We studied the relative abundance of small mammals and diurnal birds along an age gradient of selected forest stands in northwestern California and southwestern Oregon during the summers of 1984 and 1985. We surveyed the entire diurnal avian community and trapped small mammals to determine if the relative abundance of each species differed between the stands, and to determine which habitat variables correlated with the abundances of each species. We detected 23 small mammal species and 102 bird species over 2 years of field work; in this paper, we concentrate on the more common species.

Methods

Study Areas

We selected 45 principal study stands (table 1) in three regions of northwestern California and southwestern Oregon to represent a successional gradient typical of the Douglas-fir communities (see frontispiece). We selected stands nonrandomly based on accessibility by road, presence of a representative age-class of trees, and moderate topography. The stands were conveniently divided into three geographical regions of 15 stands each (table 1): Cave Junction in the north, Willow Creek in the central area, and Branscomb in the south. Stands ranged in elevation from about 400 m to 1550 m, and most were dominated by Douglas-fir in association with tanoak and madrone. Six low-elevation plots had some redwood, and four high-elevation stands in the Cave Junction region were dominated by white fir.

Bird Counting Techniques

Diurnal birds were counted in 1984 and 1985 during the breeding seasons from May to June. Each stand was visited 5 to 7 times each field season, with counts conducted over the entire breeding season at the rate of about once per week for each stand. We minimized observer bias by rotating observers at each stand. In 1984, we had 5 to 6 observers per region, so each stand was usually counted once per observer. During the 1985 field season, we had only 3 to 4 observers

in each region, so stands were usually visited on the average of twice per observer. Counts were conducted on 12 fixed stations placed 150 m apart at least 100 m from adjoining habitat types. Observers counted at each station for 8 minutes, recording horizontal distance to each bird seen or heard. All counts were initiated within 15 minutes of official sunrise and took approximately 3.5 hours to complete, to minimize time-of-day bias.

We used the number of individuals detected per station as a relative index of population abundance, which corrects for differences in effort. We did not establish an arbitrary distance from the observer beyond which detection would be excluded because the unit of analysis was the stand as a whole, not individual stations within the stand. Double registrations of an individual consequently would not affect the conclusions. We include in this report only those species that we recorded more than about 10 times during the survey in abundances greater than or equal to a total of 0.001 birds per station, which included all but the rarest species.

Mammal Trapping

For the mammal studies, we included an additional two stands at Butte Creek, near Dinsmore, California. A single trapping-grid for snap and livetrapping was laid out in each stand in a pattern of 12 rows with 12 trap stations per row. Trap stations were placed at 15-m intervals in a 165-m x 165-m grid.

In 1984, two Museum Special snaptraps were placed at each trap station within 1.5 m of the grid coordinate in all 47 stands. We trapped in six stands simultaneously (two in each region) for 5 days (4 nights) until all stands were sampled (July 3 to August 31). In 1985, a single Sherman livetrapp (7.6 cm x 8.9 cm x 22.0 cm) was used at the same stations in 43 of the stands, and we trapped again in six stands during each 5-day session from July 9 to August 30. We did not livetrapp in four stands (two in Branscomb area and two in Cave Junction area). We also used pitfall traps to sample small mammal populations in all 47 stands during both 1984 and 1985. A pitfall grid consisted of six rows of six pitfall traps per row spaced at 15-m intervals in each stand. Snap and pitfall grids were usually separated by more than 100 m. Traps were constructed from two No. 10 cans taped together and sunk until the top was flush with the ground. A funnel collar prevented animals from escaping. We propped a cedar shake 3 to 4 cm above the opening of each pitfall trap to act as a cover, and examined the traps at 5-day intervals for 50 days in October and November 1984, and for 30 days in October 1985. In the analyses below, we used the number of mammals captured, without standardizing the data for effort (table 4). Total trap nights were adjusted for inoperative traps.

Table 1-List of study stands by region, with stand abbreviation, elevation, mean age, age-class, and mean density in stems per 1000 m² of hardwood and conifer trees

Region	Stand	Elevation	Canopy trees		Mean density of trees	
			Age	Age-class	Hardwoods	Conifers
Cave Junction						
(AC)	Althouse Flat	427	107	Mature	0.531	1.890
(BP)	Buck Peak	1366	60	Young	.034	.919
(CG)	California Gray Back	1556	265	Old	.000	1.352
(FR)	Frog Pond	1439	196	Mature	.000	3.141
(GG)	Galaxy Grove	1334	259	Old	.000	2.639
(HC)	Happy Camp Road	1053	179	Mature	.179	1.879
(HO)	Holcomb Peak	1411	235	Old	.042	3.235
(LG)	Little Grayback	1205	72	Young	.016	1.359
(LH)	Left Hand	1362	96	Young	.044	2.997
(OC)	Oregon Caves Road	872	192	Mature	.316	1.157
(PM)	Page Mountain	1519	204	Old	.007	3.450
(SK)	Skag Hope	1305	267	Old	.011	3.890
(TU)	Tunnel Site	624	65	Young	.368	1.679
(UH)	Upper Horse	1502	91	Young	.013	1.581
(WC)	Waters Creek	614	240	Old	.246	1.338
Willow Creek						
(BA)	Bald Mountain East	846	43	Young	.862	0.701
(BE)	Brannon Mountain	750	236	Old	.597	1.379
(BM)	Beartooth Mountain	1144	327	Old	.383	2.176
(BR)	Brush Mountain	1050	116	Mature	.420	1.773
(CC)	Cedar Creek	665	347	Old	.396	1.728
(EB)	East Fork Big Creek	1134	246	Old	.589	1.383
(FN)	Fawn Prairie	750	44	Young	.983	.945
(GR)	Gray II	972	101	Mature	.292	1.481
(HP)	Hennessy Peak	949	100	Mature	.172	1.700
(LE)	Lord Ellis	778	48	Young	1.366	1.024
(LR)	Ladder Rock	805	319	Old	.828	2.072
(SF)	South Fork	659	289	Old	.470	1.291
(SH)	Sharber	747	283	Old	.673	.932
	Tish Tang	680	204	Old	.888	1.484
(WR)	Waterman Ridge West	633	85	Mature	1.091	1.140
Branscomb						
(AP)	Alpine	444	210	Old	.730	1.899
(BT)	Barnes	467	53	Young	.357	.329
(DP)	Darby	587	240	Old	.317	1.021
(EC)	Elder Creek	555	155	Mature	.402	2.361
(EH)	Elkhorn Ridge Hydric	518	137	Old	.230	.603
(EX)	Elkhorn Ridge Xeric	518	140	Mature	.487	.291
(FC)	Fox Creek	543	187	Old	.576	1.757
(FP)	Fanny's Place	445	122	Mature	.375	1.372
(HN)	Harwood's Ninty	695	118	Mature	1.010	.424
(HT)	Homestead	726	40	Young	1.071	1.300
(MS)	Mud Springs	689	70	Young	.691	.678
(SC)	Skunk Creek	529	291	Old	.278	1.223
(SG)	Standley Grove	481	450	Old	.082	3.555
(TM)	Ten Mile	445	241	Old	.317	1.718
(WH)	White House	427	136	Mature	.655	1.451

Vegetation Sampling

Vegetation was quantified on each of the 12 bird-count stations in each stand. On the snap-livetrapping grid we measured 16 plots overlaying the 144 trap stations. Nine vegetation plots were also uniformly distributed among the 36 pitfall stations. For this analysis, we used the mean number of all hardwood and conifer stems greater than 50 cm in d.b.h. within 15 m of each mammal-trapping station and 25 m for bird observations. We reasoned that, for this study, individual plant species would be too detailed for our analysis.

Stand ages were based on data supplied by B. Bingham (pers. comm.) from core samples of three to five dominant Douglas-firs on each of three plots in each young and mature stand (up to about 180 years). In old-growth stands, tree cores could not always be taken because trees were so large and had rotten cores; thus, some stand ages were estimated from rings counted on stumps in adjacent clearcuts or beside nearby roads, or they were based on ages provided by local Forest Service offices.

We minimized the number of variables for the small mammal community by comparing the capture rates associated with logs that have fallen relatively recently, hard logs of decay-classes 1 and 2 of Thomas (1979: 80), and soft logs of decay classes 3 to 5.

Data Analysis

The objective of this analysis was to estimate how much variation in bird abundance among stands could be explained by stand age or geographical region, and whether abundance was affected by interaction between stand age and region. For most analyses, stand age was considered as a continuous variable, and entered into calculations as a square-root transformation. Region was considered a categorical variable. A probability level of $P < 0.05$ was used to signify statistical significance.

We considered that the bird counts, as discrete variables, approximated normal distributions with means linear on the independent variables and with equal variances.

A general linear model (GLM) in SAS (Freund and others 1986: 145) was used to compare relations between the abundance of each bird species with stand age and region. This comparison was treated as an analysis of covariance with

interaction between age and region, with region as the covariate. The interaction term determines if the relation (the slope of the line describing the relation between age and abundance) was statistically different among regions.

The SAS procedure "GLM," produces two sets of statistics, Type I and III Sums of Squares, which we used in constructing table 2. If the interaction between age and region was not significant, then we used the statistics from Type I (the unadjusted treatment sums of squares), where age was entered into the model after region. If the interaction term was significant, then we used Type III (adjusted treatment sum of squares), which takes into account the other variables before calculating the effect of the variable under consideration. For example, if an age and region interaction was significant, then the statistic appearing in table 2 was the effect of age **after** accounting for the effects of both region and the interaction of age and region.

We also treated stand age as a classification variable when separating the sites into young, mature, or old-growth, based on a discriminant function analysis of vegetation data sampled from the entire stand (Bingham and Sawyer, this volume). These classifications, based on vegetative structure and composition, sometimes differed from stand age as determined by counting tree rings. Bird abundances are presented in table 2 according to the stand-age classifications of Bingham and Sawyer. A least-squares test (Freund and others 1986) determined significant differences in bird abundances between age-classes and regions.

We compared numbers of species and individuals detected between years and habitat types by using Pearson product-moment correlation coefficients.

Our analysis of the data aggregated the various stands according to similarities in the abundance of bird species found in each stand. For this, we used Ward's method of cluster analysis (SAS 1982: 423), but only for the commoner species, which we defined as the 29 species with average abundances greater than 0.1 birds per station in either 1984 or 1985 (table 3). We acknowledge that this analysis is only an approximation because it is not based on actual densities, but we believe that the figures were indicative of the relative abundance of most species.

Table 2—Comparison of the number of individuals of each bird or mammal species detected or captured per station in the three regions; the significance ($P <$) of region alone as a contribution to a model; the number of individuals per station in young, mature, and old-growth stands; the significance of age alone as a contribution to a model; the significance of the interaction of age and region; and the amount of variance explained by the model (R^2)

Species	Region			Region significance	Age of stands			Age significance	Age*Region significance	R^2
	Branscomb	Willow Creek	Cave Junction		Young	Mature	Old-growth			
Turkey vulture	0.008	0.001	0.000	0.0369	0.000	0.003	0.005	0.3124	0.5512	0.1951
Northern goshawk	.001	.003	.001	.4094	.000	.001	.003	.1561	.7576	.1030
Red-shouldered hawk	.006	.000	.000	.3800	.000	.000	.005	.4709	.5607	.0864
Red-tailed hawk	.004	.006	.008	.7967	.001	.009	.006	.2979	.9966	.0389
Blue grouse	.000	.000	.051	.0001	.033	.002	.021	.9224	.9369	.3848
California quail	.014	.001	.009	.3832	.027	.004	.001	.0128	.4107	.2137
Mountain quail	.325	.075	.071	.0001	.116	.169	.169	.9229	.9037	.3844
Band-tailed pigeon	.002	.013	.003	.0606	.015	.001	.005	.2360	.9301	.1635
Mourning dove	.019	.001	.025	.4213	.013	.024	.008	.4902	.6863	.0717
Flammulated owl	.000	.001	.003	.0932	.000	.002	.002	.1831	.3008	.1936
Northern pygmy-owl	.030	.256	.005	.0828	.005	.025	.024	.2228	.3939	.1834
Anna's hummingbird	.011	.003	.003	.0262	.004	.005	.007	.1425	.0036	.3402
Allen's hummingbird	.046	.002	.006	.0013	.003	.007	.036	.0008	.0001	.5540
Acorn woodpecker	.075	.066	.066	.9853	.030	.093	.069	.9610	.4755	.0381
Red-breasted sapsucker	.025	.031	.030	.9042	.020	.031	.032	.6857	.1850	.0908
Downy woodpecker	.003	.001	.002	.1922	.001	.002	.002	.8319	.8798	.0876
Hairy woodpecker	.055	.048	.054	.8133	.034	.036	.076	.0133	.2767	.2007
White-headed woodpecker	.000	.001	.003	.2019	.000	.000	.003	.0562	.0900	.2403
Northern flicker	.426	.193	.159	.0001	.230	.253	.280	.2669	.3135	.5251
Pileated woodpecker	.152	.110	.089	.0880	.051	.127	.144	.0285	.9227	.2124
Olive-sided flycatcher	.016	.038	.119	.0003	.063	.025	.082	.0890	.5924	.3788
Western wood-pewee	.078	.009	.082	.0259	.044	.064	.056	.2404	.4916	.2185
Hammond's flycatcher	.000	.104	.374	.0001	.091	.157	.198	.0377	.2185	.4611
Dusky flycatcher	.000	.005	.053	.0001	.042	.008	.016	.2122	.2818	.4594
Western flycatcher	1.780	1.175	.520	.4531	.543	1.230	1.420	.0001	.0480	.8194
Ash-throated flycatcher	.015	.000	.000	.2297	.019	.002	.000	.1010	.0752	.2264
Gray jay	.000	.000	.011	.2236	.003	.000	.007	.0360	.0257	.3881
Steller's jay	.978	.748	.555	.0007	.651	.850	.743	.8193	.8286	.3187
Scrub jay	.011	.004	.000	.0116	.010	.005	.002	.0772	.5351	.2720
American crow	.000	.001	.006	.1604	.001	.005	.000	.3631	.3815	.1459
Common raven	.373	.086	.083	.0001	.075	.213	.209	.3174	.4458	.5036
Mountain chickadee	.000	.000	.041	.0031	.016	.002	.022	.3456	.1819	.3149
Chestnut-backed chickadee	.609	.548	.317	.0001	.339	.533	.535	.0113	.9390	.5574
Bushtit	.013	.008	.001	.1262	.005	.010	.006	.7712	.0667	.2083
Red-breasted nuthatch	.264	.544	.830	.0001	.335	.514	.684	.0047	.1853	.5344
White-breasted nuthatch	.000	.014	.002	.1906	.001	.010	.004	.7786	.9520	.0854
Brown creeper	.528	.218	.222	.0001	.118	.313	.438	.0001	.0001	.8521
Bewick's wren	.001	.000	.004	.0783	.004	.001	.001	.1569	.2103	.2164
House wren	.000	.005	.005	.4594	.005	.005	.002	.3365	.7833	.0720
Winter wren	.084	.160	.235	.0452	.173	.068	.229	.0134	.0319	.3381
Golden-crowned kinglet	.013	.270	.774	.2346	.417	.242	.411	.1560	.0301	.6618
Townsend's solitaire	.003	.050	.149	.0018	.139	.034	.057	.0710	.0291	.4630
Hermit thrush	.382	.671	.453	.0413	.551	.422	.543	.9865	.9476	.1528
Swainson's thrush	.000	.023	.008	.1541	.016	.001	.016	.8395	.7464	.1046
American robin	.251	.086	.124	.0024	.053	.195	.173	.1515	.2447	.3293

Table 2—continued

Species		Region			Region significance	Age of stands			Age significance	Age*Region significance	R ²
		Branscomb	Willow Creek	Cave Junction		Young	Mature	Old-growth			
Varied thrush		0.000	0.057	0.008	0.0132	0.081	0.001	0.008	0.1871	0.0413	0.2756
Wrentit	+	.222	.085	.009	.0118	.054	.079	.155	.0063	.1002	.3728
Solitary vireo	-	.462	.306	.148	.0078	.110	.453	.284	.9630	.6651	.2331
Hutton's vireo	-	.186	.126	.045	.0005	.123	.137	.102	.0931	.3535	.3776
Warbling vireo	+	.781	.291	.147	.0001	.359	.582	.283	.0090	.0001	.6070
Orange-crowned warbler		.109	.011	.000	.0010	.073	.029	.032	.2956	.6806	.3204
Nashville warbler	-	.144	.143	.495	.0021	.306	.280	.224	.3731	.3871	.3060
Yellow-rumped warbler		.001	.037	.321	.0001	.155	.062	.150	.5975	.3089	.4645
Black-th. gray warbler	-	.772	.220	.357	.0030	.484	.632	.279	.0200	.0036	.4468
Townsend's warbler	-	.000	.003	.021	.0001	.011	.008	.006	.5187	.6717	.4841
Hermit warbler	+	1.306	2.279	1.695	.0032	1.155	1.761	2.078	.0040	.0247	.4630
MacGillivray's warbler	+	.000	.009	.033	.0001	.027	.010	.011	.0880	.0964	.5076
Wilson's warbler	+	.550	.205	.022	.0001	.165	.259	.309	.0466	.1203	.5021
Western tanager	-	1.089	.677	.367	.0002	.319	.933	.730	.4929	.2290	.3833
Black-headed grosbeak	-	.537	.583	.242	.0414	.204	.552	.503	.8691	.0235	.3260
Lazuli bunting		.000	.005	.000	.0095	.001	.002	.003	.3790	.8622	.2295
Rufous-sided towhee	-	.350	.007	.009	.0001	.097	.156	.106	.5147	.3277	.6540
Fox sparrow		.000	.000	.013	.0119	.005	.001	.008	.4914	.3890	.2407
Song sparrow		.000	.016	.001	.1153	.017	.002	.003	.1152	.1683	.1998
Dark-eyed junco	-	.490	.374	.600	.1137	.401	.554	.478	.9428	.0791	.2045
Brown-headed cowbird		.001	.006	.040	.0473	.010	.034	.004	.4290	.5470	.1784
Purple finch		.043	.097	.099	.0966	.052	.084	.091	.2313	.2122	.1987
Red crossbill		.011	.015	.031	.0728	.026	.013	.021	.5273	.0249	.2474
Pine siskin		.004	.075	.395	.0001	.164	.127	.182	.0802	.1588	.7240
Lesser goldfinch		.004	.001	.006	.2265	.004	.004	.003	.9962	.8748	.0792
Evening grosbeak		.000	.002	.053	.0001	.031	.012	.017	.4127	.8730	.6541
Chipmunks		.007	.007	.035	.0003	.020	.016	.014	.9837	.9731	.3408
Douglas' squirrel		.072	.315	.443	.0001	.180	.235	.362	.0363	.0755	.4589
Western gray squirrel		.050	.007	.030	.0004	.017	.037	.028	.9808	.8263	.3340

Note: When a significant difference was found between the abundance of a species by age-classes or regions, those that were statistically indistinguishable by a least-squares test are joined by an underline. For nonadjacent, indistinguishable column values (for example, young and old-growth) the underline is disjunct. If all three differ significantly from each other, each is underlined. A plus (+) or minus (-) after the species' name indicates a significantly positive or negative relation to stand age according to the analysis of Raphael (1984).

Results

Bird Abundances

Overall abundance patterns—Seventy-one bird species (table 3) were found in the study plots in both years in numbers greater than 0.001 birds per station. The most abundant species was the hermit warbler, with over 1.7 birds per station in both years. The western flycatcher was next in abundance with more than 1.1 birds per station.

Some birds began to reach the limit of their distributions within the geographic range of this study. For instance, blue grouse and gray jay were only found at Cave Junction in the north, and Hammond's flycatcher was not found at Branscomb in the south. These species could be found in areas we did not count to the north or south, but in limited numbers. They also probably were largely limited by the altitudinal gradient between study stands. The Cave Junction stands were generally at higher elevations and Branscomb tended to be lower.

We divided the species into three groups: year-round residents, short-distance migrants (birds wintering in the United States), and long-distance migrants. More than half (59 percent) of the species were residents, 11 percent were short-, and 30 percent long-distance migrants. By contrast, only 42 percent of individuals (birds per station) were residents, 6 percent short, and the majority (52 percent) long-distance migrants.

Comparison between years—We compared, by correlation, the abundance of each species between years in each stand to determine the concordance of the 2 years' data. The closer the agreement between the 2 years, the greater the likelihood (but, by no means, certainty) that some aspect of the habitat was important in determining the abundance of that species at any sampling point. The less the agreement, the greater the likelihood that stochastic events in the population could be responsible for the abundance of the species.

Table 2—continued

Species		Region			Region significance	Age of stands			Age significance	Age*Region significance	R ²
		Branscomb	Willow Creek	Cave Junction		Young	Mature	Old-growth			
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Wrentit	+	.222	.085	.009	.0118	.054	.079	.155	.0063	.1002	.3728
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Table 3—Mean number of detections of each bird and mammal species per station in 1984 and 1985, the linear correlation (R^2) between years and its sign, and the linear correlation (R^2) between the number of detections and the abundance of hardwood and conifer trees and its sign (significant correlations are indicated as: * = $P \leq .05$, ** = $P \leq .01$, and *** = $P \leq .001$)

Species	Year				Tree type	
	1984	1985	R^2	P	Hardwood (R^2)	Conifer (R^2)
Turkey vulture	0.003	0.003	0.47	0.0011	0.01	-0.16
Northern goshawk	.001	.002	-.06	.7017	.03	.11
Red-shouldered hawk	.000	.004	.00	1.0000	-.05	-.11
Red-tailed hawk	.007	.006	-.06	.6836	-.17	-.23
Blue grouse	.020	.014	.37	.0122	-.52***	.27
California quail	.011	.006	.90	.0001	.24	-.24
Mountain quail	.160	.154	.68	.0001	.05	-.12
Band-tailed pigeon	.007	.005	.37	.0115	.29*	-.23
Mourning dove	.012	.018	.88	.0001	.03	-.03
Flammulated owl	.001	.001	-.06	.7208	-.24	.40**
Northern pygmy-owl	.019	.022	.26	.0796	.04	-.29
Anna's hummingbird	.009	.003	-.10	.4978	.00	.19
Allen's hummingbird	.027	.009	.09	.0001	-.17	.32*
Acorn woodpecker	.055	.082	.88	.0001	.15	-.10
Red-breasted sapsucker	.023	.346	.65	.0001	-.31*	.10
Downy woodpecker	.001	.003	-.08	.5931	.07	.00
Hairy woodpecker	.061	.044	.24	.1112	-.29	.27
White-headed woodpecker	.001	.002	-.04	.8022	-.18	.26
Northern flicker	.269	.250	.63	.0001	.08	-.26
Pileated woodpecker	.136	.098	.71	.0001	-.03	-.10
Olive-sided flycatcher	.041	.074	.62	.0001	-.58***	.53***
Western wood-pewee	.045	.068	.63	.0001	-.29	.42**
Hammond's flycatcher	.154	.165	.92	.0001	-.44**	.46**
Dusky flycatcher	.015	.023	.55	.0001	-.48***	.20
Western flycatcher	1.138	1.177	.91	.0001	.17	-.12
Ash-throated flycatcher	.005	.005	.98	.0001	.00	-.26
Gray jay	.005	.003	.21	.1611	-.41**	.33*
Steller's jay	.791	.730	.61	.0001	.12	-.37*
Scrub jay	.005	.005	.21	.1639	.25	-.34*
American crow	.002	.002	.54	.0001	.01	.03
Common raven	.152	.209	.88	.0001	.08	-.21
Mountain chickadee	.014	.013	.76	.0001	-.41**	.13
Chestnut-backed chickadee	.501	.482	.52	.0003	.36*	-.20
Common bushtit	.011	.004	.05	.7498	.21	-.15
Red-breasted nuthatch	.492	.600	.89	.0001	-.51***	.53***
White-breasted nuthatch	.010	.001	.86	.0001	-.10	.00
Brown creeper	.337	.308	.93	.0001	-.19	.28
Bewick's wren	.001	.002	.36	.0144	-.21	.00
House wren	.001	.006	.13	.4139	-.25	.09
Winter wren	.194	.125	.74	.0001	-.33*	.54***
Golden-crowned kinglet	.374	.331	.91	.0001	-.56***	.60***
Townsend's solitaire	.057	.077	.70	.0001	-.52***	.22
Hermit thrush	.447	.557	.71	.0001	.40**	-.31*
Swainson's thrush	.013	.007	.15	.3250	.19	.11
American robin	.165	.143	.69	.0001	-.15	.06
Varied thrush	.020	.024	.67	.0001	.43**	-.12
Wrentit	.090	.121	.96	.0001	-.09	.06
Solitary vireo	.279	.331	.78	.0001	.23	-.19
Hutton's vireo	.109	.129	.65	.0001	.66***	-.50***
Warbling vireo	.447	.366	.91	.0001	.43**	-.28
Orange-crowned warbler	.040	.040	.88	.0001	.09	-.23

Table 3—continued

Species	Year				Tree type	
	1984	1985	R ²	P	Hardwood (R ²)	Conifer (R ²)
Nashville warbler	0.236	0.288	0.85	0.0001	-0.27	-.09
Yellow-rumped warbler	.090	.149	.86	.0001	-.59***	.37*
Black-th. gray warbler	.354	.545	.84	.0001	.29	-.40**
Townsend's warbler	.003	.013	.20	.1873	-.36*	.31*
Hermit warbler	1.729	1.791	.86	.0001	-.22	.43**
MacGillivray's warbler	.011	.017	.37	.0199	-.40**	.15
Wilson's warbler	.206	.312	.94	.0001	.00	-.14
Western tanager	.702	.720	.84	.0001	.28	-.27
Black-headed grosbeak	.407	.501	.81	.0001	.40**	-.32*
Lazuli bunting	.003	.001	-.07	.6561	.18	-.07
Rufous-sided towhee	.081	.163	.94	.0001	.01	-.11
Fox sparrow	.001	.007	.50	.0005	-.37*	.17
Song sparrow	.008	.003	.95	.0001	.23	-.09
Dark-eyed junco	.509	.466	.88	.0001	-.44**	.22
Brown-headed cowbird	.021	.011	.80	.0001	-.10	.04
Purple finch	.068	.091	.31	.0359	-.11	.14
Red crossbill	.007	.031	.56	.0001	-.16	.09
Pine siskin	.162	.154	.83	.0001	-.63***	.42**
Lesser goldfinch	.003	.003	.55	.0001	-.09	-.05
Evening grosbeak	.018	.019	.81	.0001	-.48**	.39**
Chipmunks	.014	.019	.57	.0001	-.49***	.32***
Douglas' squirrel	.228	.325	.84	.0001	-.42***	.44***
Western gray squirrel	.031	.027	.60	.0001	-.02	.18

Although the majority of species had similar detection rates between years, 15 (21 percent) species showed significant differences (table 3). Most of these were rare species that undoubtedly varied because of the low numbers that were detected; only five were fairly abundant, having detection rates in either year in excess of 0.01 birds per station. Common species with abundances that changed significantly between years were the northern pygmy-owl, common bushtit, hairy woodpecker, Swainson's thrush, and Townsend's warbler. No common thread (such as food habits or foraging methods) unites these species; changes such as these are to be expected in a study of several species.

Geographic differences—Geographical variation in abundance is a pattern that overlies the species' response to changes in the amount and suitability of its habitat. Even though the habitat may be suitable, factors that are related to geography (such as climate or competition with existing species) may preclude or severely limit the species' presence, and mute its response to habitat.

By comparing the average number of species recorded on the 15 stands making up each region (fig. 1), we found that the northern Cave Junction stands averaged 37.3 species per stand, the Willow Creek stands averaged 32.4, and the

Branscomb stands 32.6. The Cave Junction stands had significantly greater species richness than the southern stands (Duncan's Multiple Range Test).

We also found distinct patterns in the abundances of individual species in the northern and southern study sites. The majority of the species that showed differences between geographic regions were on a north-south cline (table 2). This cline was also of higher elevation with more true fir in the north, and more hardwoods in the south (table 1). When region was the only significant variable selected in a GLM model, 12 species were more abundant in northern stands, and 14 were more abundant in southern stands. Among the species more abundant in either the north or the south were species with geographic affinities in either direction. Significantly more common to the north were the more montane species, such as blue grouse, olive-sided flycatcher, dusky flycatcher, mountain chickadee, MacGillivray's warbler, Nashville warbler, yellow-rumped warbler, fox sparrow, pine siskin, and evening grosbeak. The brown-headed cowbird and Townsend's warbler were also more abundant in the northern regions. More abundant southern species included turkey vulture, mountain quail, Anna's hummingbird, northern flicker, Steller's jay, scrub jay, common raven, American robin, Hutton's vireo, solitary vireo, orange-crowned warbler, Wilson's warbler, western tanager, and rufous-sided towhee.