

REGIONAL GRADIENT ANALYSIS AND SPATIAL PATTERN OF WOODY PLANT COMMUNITIES OF OREGON FORESTS

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Abstract. Knowledge of regional-scale patterns of ecological community structure, and of factors that control them, is largely conceptual. Regional- and local-scale factors associated with regional variation in community composition have not been quantified. We analyzed data on woody plant species abundance from 2443 field plots across natural and seminatural forests and woodlands of Oregon to identify and quantify environmental, biotic, and disturbance factors associated with regional gradients of woody species composition; to examine how these factors change with scale (geographic extent) and location; and to characterize and map geographic patterns of species and environmental gradients.

Environmental correlates of species gradients, species diversity patterns, and the spatial patterning of woody plant communities varied with geographic extent and location. Total variation explained (TVE) by canonical correspondence analyses (CCAs) was 9-15% at three hierarchical geographic extents: the entire state, two half-states, and five subregions. Our high level of unexplained species variation is typical of vegetation gradient analyses, which has been attributed to landscape effects, stochastic processes, and unpredictable historical events. In addition; we found that TVE in canonical correspondence analysis is confounded by sample size. Large numbers of plots and species, as in our study, are associated with lower TVEs, and we propose a mechanism for this phenomenon.

Climate contributed most to TVE (46-60%) at all locations and extents, followed by geology (11-19%), disturbance (6-12%), and topography (4-8%). Seasonal variability and extremes in climate were more important in explaining species gradients than were mean annual climatic conditions. In addition, species gradients were more strongly associated with climatic conditions during the growing season than in winter. The dominant gradient at the state scale was from the lower elevation, moderate, maritime climate along the coast to the higher elevation, drier, continental climate of eastern Oregon. The second canonical axis followed a gradient from the warm, dry, growing seasons of the western interior valleys and eastern Cascade Range to the cooler, wetter mountainous areas. Geologic variables were most strongly correlated with axis 3, and measures of local site and disturbance with axis 4. For most of the state, our findings on the associations of disturbance factors with species gradients were inconclusive due to confounding of land ownership patterns, disturbance histories, and elevation in our sample. Near the coast, where gradients were not confounded, clear-cutting and stand age accounted for only 2 and 1% of TVE, respectively, in partial CCA. Ordinations of our long, regional gradients were influenced more by species presence than by abundance, and few woody species have been totally eliminated from sites by clear-cutting.

Within Oregon and for the range of geographic extents we examined, variation in the environmental correlates of species gradients was more strongly associated with geographic location than with geographic extent, although topographic factors explained slightly more variation at smaller geographic extents. The greatest subregional contrast in vegetation character was between eastern and northwestern Oregon, and the Klamath subregion was intermediate. In the drier climate of eastern Oregon, community structure varied at a finer spatial scale, and climatic and topographic moisture were more strongly associated with species gradients than in the moister areas of western Oregon. Topographic effects were weakest, and climatic effects strongest near the coast, where climate is moderate. Alpha and gamma diversity were greater in western Oregon, but beta diversity was greater in eastern Oregon and greater for shrubs than for trees.

Our findings supported a conceptual model of multiscaled controls on vegetation distribution, and the related notion that local community structure is the result of both regional- and local-scale processes. Despite strong ecological contrasts within the region, we were able to synthesize species-environment relations at the regional level. This suggests that apparent conflicts among local vegetation studies can be explained by real ecological differences among places

Key words: canonical correspondence analysis; forest ecology; gradient analysis; Oregon; plant communities; regional vegetation analysis; species diversity; variance partitioning; woody plants.

INTRODUCTION

Identifying the factors controlling the distribution, abundance, and diversity of species in ecological communities continues to be a central problem in community ecology. Community structure is now considered a product not only of local physical conditions and interactions among species, but also of regional constraints such as climate, and of historical processes such as dispersal and speciation, migration, and extinction (Neilson and Wullstein 1983, Brown 1984, Ricklefs 1987, Menge and Olson 1990, Ricklefs and Schluter 1993). Ecological research in recent decades has focused on intracommunity patterns, especially on the role of competition and other species interactions in community structure. In addition, plant community ecologists have devoted considerable effort to quantifying local- to landscape-scale variation in vegetation. As a result, factors associated with local patterns of community composition often are well known, but differ among localities. Whereas biogeographers and phytosociologists have long recognized the role of environmental and historical factors in regional- to continental-scale patterns of plant community composition, current knowledge remains general and qualitative. Few systematic, quantitative, regional-scale descriptions provide context for landscape differences (but see Denton and Barnes 1987), and the synthesis and collation of plant-community data in regional analysis has been cited as a major research need (Franklin 1988, Franklin and Blinn 1988).

In the Pacific Northwest, much of the research in plant community ecology has involved classification of potential natural vegetation (Wellner 1989), and placement of associations along environmental gradients has only been inferred (e.g., Topik et al. 1988). Most quantitative studies of forest communities of the western United States have been limited to older, natural forests, to incomplete segments of regional environmental gradients, or to certain forest community types, and most were conducted at the landscape scale (Whittaker 1960, Whittaker and Niering 1965, Daubenmire and Daubenmire 1968, Fonda and Bliss 1969, Minore 1972, Dyrness et al. 1974, Zobel et al. 1976, del Moral and Watson 1978, Peet 1981, del Moral and Fleming 1979, Allen and Peet 1990, Allen et al. 1991, Spies 1991; Spies and Franklin 1991, Riegel et al. 1992, Parker 1994). Other regional- and continental-scale studies quantified patterns of species diversity (Glenn-Lewin 1977, Richerson and Lum 1980, Currie and Paquin 1987), but did not evaluate gradients in community composition. In the only regional-scale account of Oregon vegetation, Franklin and Dyrness (1973) synthesized local studies and related vegetation to environmental factors only qualitatively.

We undertook a quantitative, systematic analysis of plant community data spanning a broad region-forest lands in Oregon—to examine contributions of broad-

and local-scale factors to regional variation in community composition, and to explore the influences of physical environment, biotic factors, and disturbance processes. Our primary study objectives were to identify and quantify environmental factors associated with regional gradients in the composition of woody plant communities of forests and woodlands throughout Oregon and its subregions (Fig. 1); to examine how these factors change with geographic extent and location; and to describe and map geographic patterns of compositional gradients. Our study addresses long-standing questions about factors controlling the distribution, abundance, and diversity of species in ecological communities, but considers a somewhat broader region and a much larger dataset than most previous studies, and uses contemporary multivariate statistical and spatial analytical tools.

*Factors associated with regional variation in
species composition*

We hypothesized that macroclimate, an expression of broad-scale temperature and moisture environment, is the primary associate of regional-scale patterns of community composition, and that substrate (geologic parent material and soils) and local factors (microclimate, topography, and site disturbance) are secondary. It is almost axiomatic that, at a continental scale, patterns of vegetation physiognomy and community composition are associated primarily with large-scale climate (Daubenmire 1978, Woodward 1987). Macroclimate is thought to influence communities directly through physiological effects on organisms and by limiting populations. Macroclimate indirectly influences communities by modifying or regulating the importance of local-scale factors and by favoring certain species and growth forms in interspecific competition. Empirical studies that quantified environmental associations with patterns of forest vegetation in the Pacific Northwest (Whittaker 1960, Whittaker and Niering 1965, Daubenmire and Daubenmire 1968, Fonda and Bliss 1969, Waring 1969, Minore 1972, Dyrness et al. 1974, Zobel et al. 1976, del Moral and Watson 1978, del Moral and Fleming 1979, Spies 1991, Spies and Franklin 1991, Riegel et al. 1992, and others), in other mountainous regions of the western United States (Peet 1978, 1981, Allen and Peet 1990, Allen et al. 1991, Parker 1994), and elsewhere (Denton and Barnes 1987) have consistently demonstrated the primary importance of temperature and moisture. The studies, however, either did not distinguish effects of macroclimate from microclimate and other factors, or considered broadscale climate only indirectly by observing vegetation change along complex gradients of elevation or latitude.

Vegetation patterns have been associated with topography in gradient studies at smaller geographic extents, and in larger areas that were prestratified by el-

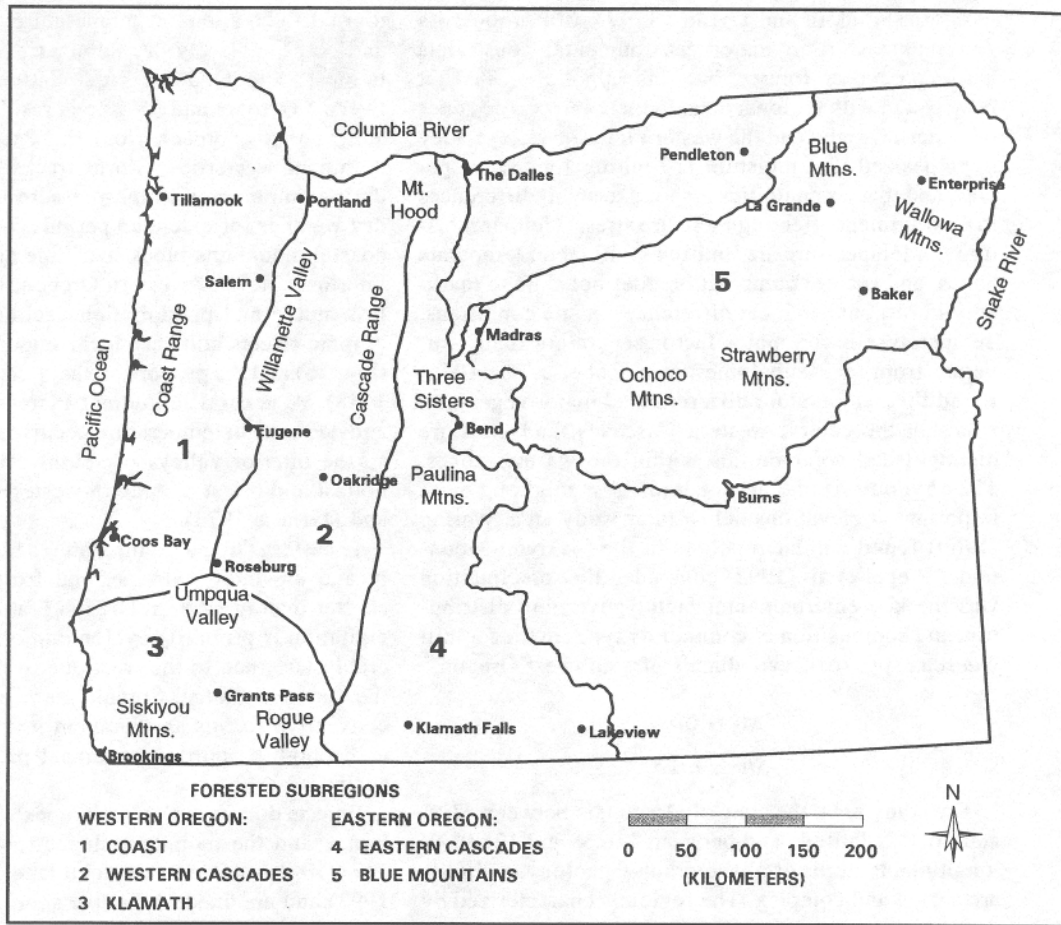


FIG. 1. Oregon study area showing the five forested subregions that are the subject of this study, major cities, and major physiographic features

evation or substrate (e.g., Whittaker 1960, Peet 1978, 1981, Allen and Peet 1990, Allen et al. 1991). However, topographic position did not differentiate vegetation types in the west-central Oregon Cascades (Zobel et al. 1976). Studies in several western mountain systems have shown that soil differences usually are important only secondarily (Whittaker and Niering 1965, Daubenmire and Daubenmire 1968, Fonda and Bliss 1969, Minore 1972, Zobel et al. 1976). Only occasionally is soil chemistry associated with vegetation patterns, such as in the Klamath Mountains and redwood regions (Whittaker 1960, Waring and Major 1964, Waring 1969) and in the pumice region of central Oregon (Volland 1985). Interactions among disturbance and successional processes with other environmental factors in determining regional vegetation patterns are poorly understood, and have been difficult to quantify in regional gradient studies.

The influence of geographic extent and location

Within a local area, the range of climatic conditions is small, and most sites fall within species' physiological tolerances. Thus, shifts in species' relative abun-

dances are thought to be associated with local variations in topography, microclimate, and substrate, and with biotic interactions (Neilson 1987, Neilson et al. 1992), as well as with stochastic disturbances that are highly variable over time and space. We therefore hypothesized that species variation explained by regional climate decreases, and variation explained by local factors increases, with decreasing geographic extent.

Different environmental factors probably assume varying degrees of importance among locales within a region, and limiting factors likely do not vary in parallel from place to place (Neilson et al. 1992). Local shifts in community composition have been proposed to be less pronounced in favorable climates, and more striking where climate is more stressful (Neilson et al. 1992), but rarely has this been demonstrated (but see Neilson and Wullstein 1983). The western United States is climatically diverse, and shifts in controls on community composition among landscapes are poorly understood. Within Oregon, we hypothesized that moisture and topographic factors assume greater importance where climate is drier and more erratic (i.e., in eastern Oregon and the interior valleys of western

Oregon). Franklin and Dyrness (1973: 50) proposed a geographic shift in major environmental constraints across Oregon's forests, but this hypothesis has not been tested with regional data. In their xerophytic zones of eastern Oregon and the western interior valleys, they hypothesized that moisture is limiting for many species, and that communities respond to small differences in environment affecting moisture stress. Neither moisture nor temperature are limiting within their temperate zones, and species composition does not shift so markedly in response to local differences in site conditions. Temperature is the major factor separating their temperate from their subalpine types. Zobel et al. (1976) found that temperature differentiated major vegetation zones in the central western Cascades, and moisture distinguished communities within the warmer zones. They hypothesized that moisture stress might be more important at elevations below their study area. Waring (1969) found similar relations in the Siskiyou Mountains. Riegel et al. (1992) concluded that precipitation was the key environmental factor governing distribution and composition of community types in the foothill *Quercus* spp. (oak) woodlands of southwest Oregon.

METHODS

Study area

The study area, the state of Oregon, is between 41.9° and 46.4° N latitude and between 116.5° and 124.9° W longitude. Patterns of physiography, geology, and soils are varied and complex. The region is characterized by the north-south oriented Cascade and Coast ranges, as well as the Siskiyou Mountains in southwest Oregon and the Blue-Ochoco-Strawberry-Wallowa complex of mountains in the Blue Mountains subregion of eastern Oregon (Fig. 1). The Cascade Range, which is the major topographic and climatic divide in Oregon, is bisected at the northern Oregon boundary by the Columbia River. Elevations range from sea level to >3000 m (Fig. 2a). Geologic formations date from the Paleozoic (over 400 x 10⁶ yr old) to the Holocene (Walker and MacLeod 1991) (Fig. 3). Vulcanism has shaped much of the landscape, but sedimentary and metamorphic rocks are plentiful, and deposition of parent materials by alluvial, colluvial, and eolian processes is common (Walker and MacLeod 1991). Soil types are primarily inceptisols, spodosols, and ultisols (Franklin and Dyrness 1973). Volcanic activity during the Pleistocene and Holocene has mantled large tracts at higher elevations in the Cascade Range and in central Oregon with pumice and ash.

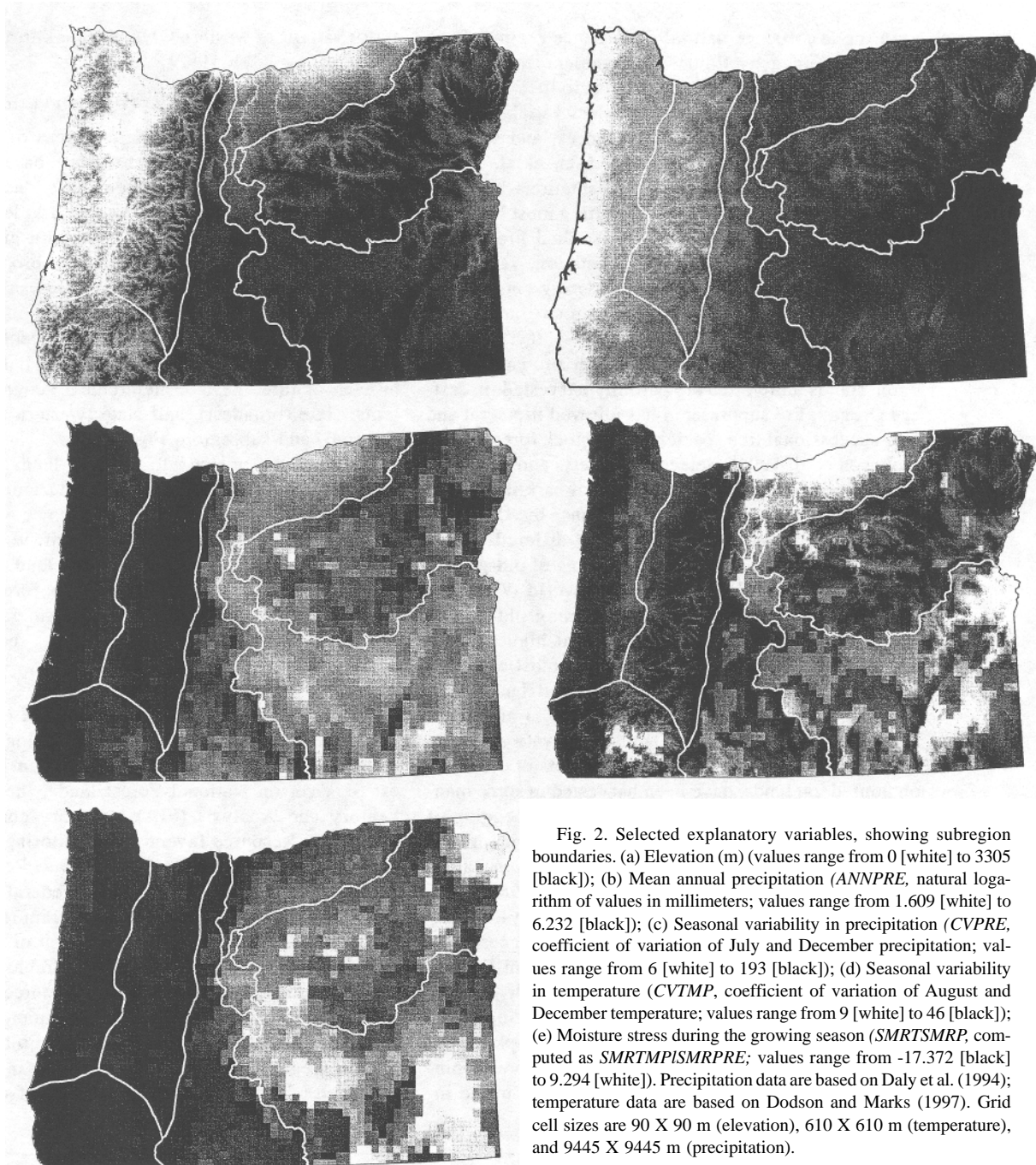
Climatic variation in the region is influenced by the interplay among westerly winds of maritime air masses, northeasterly winds of continental air masses, and the blocking effects of mountain ranges (Franklin and Dyrness 1973). Western Oregon has a maritime climate characterized by mild temperatures; a long frost-free season; prolonged cloudy periods; narrow seasonal and

diurnal fluctuations in temperature; mild, wet winters and cool, relatively dry summers; and heavy precipitation (Table 1). Most precipitation falls as rain between 1 October and 31 March, resulting from cyclonic storms that approach from the Pacific Ocean on the dominant westerlies. Storm tracks shift to the north during summer, and high-pressure systems bring fair, dry weather for extended periods. To varying degrees, coastal mountains block maritime air masses from the interior valleys of western Oregon, where climates are less muted and precipitation declines markedly. Orographic effects influence local amounts of precipitation (Fig. 2b) and the proportion that falls as snow (Franklin 1988). A general latitudinal increase in precipitation and decrease in temperature occurs from south to north, so the interior valleys of southwest Oregon have the hottest and driest climate in western Oregon (Franklin and Dyrness 1973).

In eastern Oregon, temperatures fluctuate more widely and are more extreme, and frost-free seasons are shorter than in western Oregon (Table 1, Fig. 2d). Precipitation is primarily cyclonic in origin but is considerably less than to the west due to the rain shadow of the Cascade Range. Summers are very dry, although convective storms are common in mountainous areas, and a high proportion of annual precipitation falls as snow.

Forests dominate the landscapes west of the Cascade Range and the mountain slopes to the east, covering 11 x 10⁶ ha (46%) of the total land area (Powell et al. 1993) and confined to the five subregions of our study (Fig. 1). About 60% of the forest land is publicly owned, 23% is owned by the timber industry, and 17% belongs to nonindustrial private landowners (Powell et al. 1993) (Figs. 4 and 5).

Coniferous tree species dominate most of Oregon's forest communities (Franklin and Dyrness 1973, blaring and Franklin 1979, Franklin 1988). Outside of the mixed-evergreen zone of southwest Oregon, where several evergreen hardwood trees codominate, hardwoods tend to occupy harsh sites or specialized habitats or serve as pioneers. The present climate of wet, mild winters and relatively dry summers favors evergreen, needle-leaved conifers by permitting extensive photosynthesis outside of the growing season and reducing net photosynthesis during the summer (blaring and Franklin 1979). The mesic temperate coniferous forests of northwestern Oregon contain the greatest biomass accumulation and some of the highest productivity rates of any forests in the world (Franklin 1988). Many of the dominant tree species (e.g., *Tsuga heterophylla* and *Thuja plicata*) are endemic to the Pacific Northwest, and others find their center of distribution and attain maximum development here. Southward, where the climate is warmer and drier, *Pinus lambertiana*, *Calocedrus decurrens*, and *Lithocarpus densiflorus* are added to the flora. The forest zones of interior southwest Oregon represent northern extensions of the



mixed-conifer forest of the Sierra Nevada and the mixed sclerophyll forest of the California Coast Ranges. In eastern Oregon, Pacific coastal elements mix with Rocky Mountain elements. *Pinus ponderosa* characterizes forests at lower elevations, and *Abies lasiocarpa* those at higher elevations. Franklin and Dyrness (1973) provide detailed descriptions of Oregon plant communities.

Disturbance regimes vary tremendously across Oregon. Before European settlement, natural disturbance

regimes were dominated by infrequent, catastrophic fires (Agee 1993). Periodic, low-intensity underburns were common in some places (Teensma 1987, Morrison and Swanson 1990), as were fires set by American Indians (Agee 1993). Natural fire-return intervals ranged from 15 yr in drier eastside pine forests, to 400 yr in moist, coastal forests, to 800 yr in subalpine forests (Agee 1993). Windstorms, pathogens, and other disturbance agents also have influenced forest development.

In the last 100 yr, natural disturbance regimes have been supplanted by timber management and wildfire suppression. Timber management activities generally are more frequent and intense and less variable in size and intensity than natural disturbances, and simplify stand and landscape structure (Hansen et al. 1991). Intensive management of forest plantations in northwestern Oregon consists of clear-cutting most live trees and snags, site preparation by prescribed fire or herbicides to control competing vegetation, replanting with a single species (usually *Pseudotsuga menziesii*), periodic thinning to maintain vigorous and evenly spaced crop trees, and harvesting at 40-100 yr intervals (Hansen et al. 1991). In southwestern and eastern Oregon, stands more often are partially harvested. In eastern Oregon, fire suppression has allowed fire-seral and late-successional tree species to overstock forest stands (Johnson et al. 1994). Selective harvests and overstory removals have converted large areas of parklike forests of *Pinus ponderosa* to greater dominance by *Abies* spp.

Forest management practices have differed among land ownerships and over time. Logging of old-growth forest from federal lands began after World War II and accelerated in the 1970s. Most remaining old growth is concentrated on federal lands and at higher elevations (Bolsinger and Waddell 1993). Almost all of the vegetation plots in our study on federal lands were established in older, natural stands (Figs. 4 and 5). In contrast, virtually all forest lands in private and state ownership, and almost all vegetation plots in our study on nonfederal lands, have been harvested in some manner (Fig. 4) and are < 120 yr old (Fig. 5). Logging of the most accessible and productive lands in private ownership began in the mid-1800s, and some areas have been harvested a second time. By the 1980s, 97% of the nonfederal timberland was in an early- or mid-successional stage, and only 3% was late successional (Pacific Resource Inventory, Monitoring, and Evaluation Program, Pacific Northwest Research Station, Portland, Oregon, unpublished data). Grazing, fuelwood harvesting, introduction of nonnative plant species, and urbanization also have altered forest composition, especially near population centers in the in-

terior valleys of western Oregon (Franklin and Dyrness 1973, Riegel et al. 1992).

Three hierarchical geographic extents

We divided the major forested areas of the state a priori into five geographic subregions, based primarily on physiography (Fig. 1). Boundary placement was somewhat arbitrary but consistent with widely accepted physiographic provinces (e.g., Franklin and Dyrness 1973, Bailey et al. 1994). We aimed to broadly stratify the region into relatively homogenous subregions to examine within-region ecological variation, and to analyze effects of geographic extent on ecological pattern. We conducted most of our analyses independently at each of three nested, hierarchical geographical extents: state (broadest), half-state (western and eastern Oregon), and subregion (Fig. 1).

We limited our study to forested lands because of availability of field plot data. The data sources defined forest as areas with at least 10% canopy cover of trees, including closed forest and open woodland. We did not include small inclusions of nonforest land, usually associated with soil conditions, within forested areas. These natural openings comprise a considerable portion of the landscape in the Blue Mountains subregion.

Vegetation data

We obtained vegetation data collected on ~10000 field plots installed by the Area Ecology Program (Ecology) of the Pacific Northwest Region, USDA Forest Service, on National Forest lands; the Forest Inventory and Analysis (FIA) inventory conducted by the Pacific Resource Inventory, Monitoring, and Evaluation Program of the Pacific Northwest Research Station, USDA Forest Service, on nonfederal lands; and the Forestry Intensive Research Program (FIR) of Oregon State University on USDI Bureau of Land Management lands in southwest Oregon (Table 2). We obtained digital data files from each source, extracted vegetation and site data elements common to all data sets, and compiled the extracted data into a single database. Vegetation measurements used in our study consisted of crown cover for woody plant species. For

FIG. 3. Geologic types of Oregon, generalized from Walker and MacLeod (1991). VOLC = igneous: volcanic and intrusive rocks; SILR = igneous: silicic rocks (granite, diorite, rhyolite, and dacite); MAFO = igneous: mafic rocks (basalt, basaltic andesite, andesite, gabbro), Miocene and older; MAFY = igneous: mafic rocks (basalt, basaltic andesite, andesite, gabbro), Pliocene and younger; UMAF = igneous: ultramafic rocks (serpentine); PYRO = igneous: mafic pyroclastic rock, ash, ejecta, vent deposits, Miocene and older; PYRY = igneous: mafic pyroclastic rock, ash, ejecta, vent deposits, Pliocene and younger; SILV = igneous: silicic vent deposits; META = metamorphic; SEDR = sedimentary: siltstones, sandstones, mudstones, conglomerates; TUF0 = sedimentary: tuffaceous rocks and tuffs, pumicites, silicic flows, Miocene and older; TUFY = sedimentary: tuffaceous rocks and tuffs, pumicites, silicic flows, Pliocene and younger; DEPO = depositional: dune sand, alluvial, glacial, glaciofluvial, loess, landslide and debris flow, playa, lacustrine, fluvial; MIXR = mixed rocks.

FIG. 4. History of clear-cutting (CLEARCUT) on field plots, and major federal land ownerships, in Oregon. FS = Forest Service; BLM = Bureau of Land Management; NPS = National Park Service. Unshaded areas are private and other public ownerships.

FIG. 5. Stand age (AGE) and major federal land ownerships in Oregon. FS = Forest Service; BLM = Bureau of Land Management; NPS = National Park Service. Unshaded areas are private and other public ownerships.

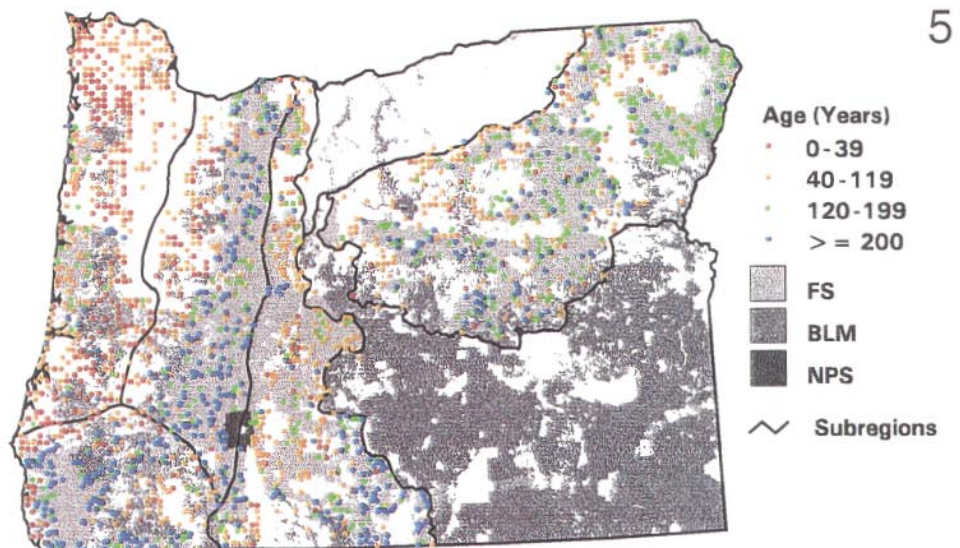
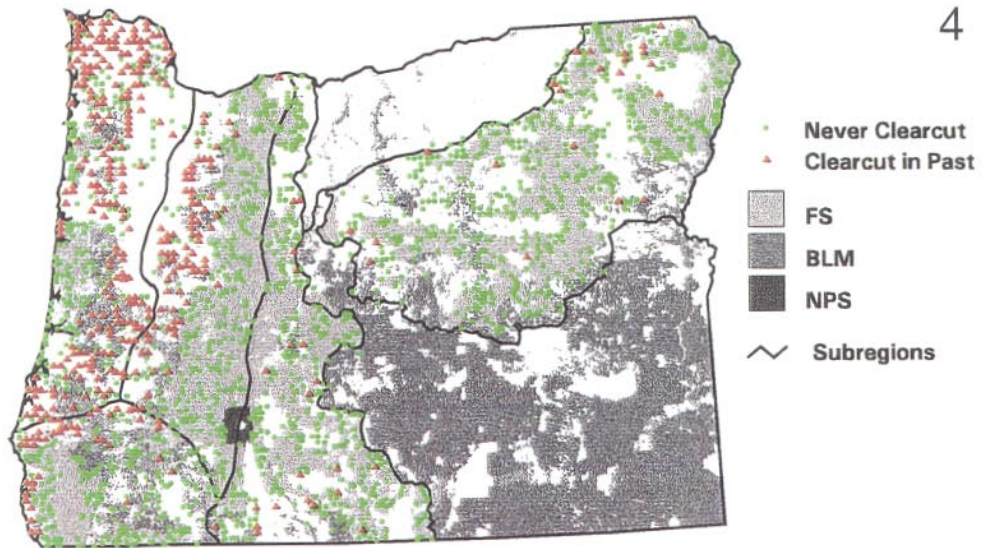
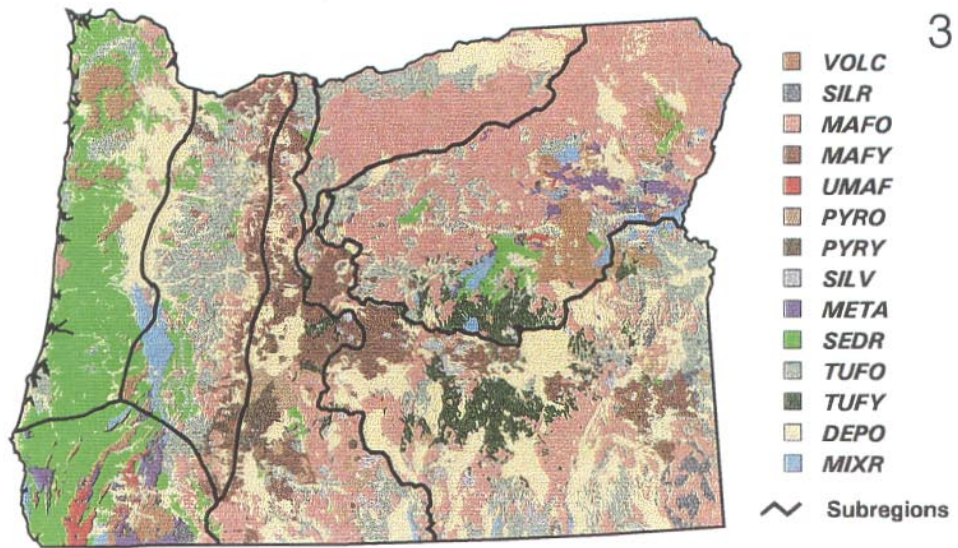


TABLE 1. Mean and coefficient of variation (CV) of continuous explanatory variables by geographic area. See Table 3 for explanation of codes for variables.

Variable	Half-state					
	Oregon		Western Oregon		Eastern Oregon	
	Mean	cv	Mean	cv	Mean	cv
<i>ASPECT</i>	1.03	67	1.10	63	0.96	71
<i>SLOPE</i>	26.16	84	33.34	68	18.85	98
<i>SOLAR</i>	6.84	17	6.60	19	7.09	14
<i>AGE</i>	140.44	79	138.74	97	142.17	56
<i>TREOCOV</i>	54.05	58	69.28	44	38.52	64
<i>ELEV</i>	1048.74	55	627.70	72	1477.78	22
<i>ANNPRES</i>	6.91	10	7.44	5	6.37	6
<i>WTRPRE</i>	6.49	12	7.11	5	5.85	8
<i>SMRPRE</i>	5.24	9	5.48	7	4.98	7
<i>CVPRE</i>	110.83	17	125.30	4	99.09	18
<i>CONTPRE</i>	9.82	51	6.03	24	13.68	32
<i>SMRTSMRP</i>	2.45	22	2.42	22	2.48	22
<i>ANNTMP</i>	6.71	43	8.41	28	4.97	45
<i>MAXTMP</i>	30.10	18	34.08	12	26.04	12
<i>MINTMP</i>	-28.27		-22.31		-34.35	
<i>WTRTMP</i>	0.76		3.41		-1.93	
<i>SMRTMP</i>	12.70	19	13.46	18	11.94	19
<i>CVTMP</i>	26.08	24	20.92	18	31.34	9

Note: CV not shown for variables that can have negative values (*MINTMP* and *WTRTMP*).

all component data sets, crown cover was visually estimated on fixed-radius plots (Table 2).

The component data sets were collected under different objectives and sampling designs (Table 2). The Ecology and FIR plots were selected subjectively without preconceived bias (Mueller-Dombois and Ellenberg 1974), primarily from older, natural stands. The Ecology plots were established across all National Forest lands statewide (Fig. 4), and the FIR plots on Bureau of Land Management lands in southwest Oregon. The FIA plots were established systematically across all nonfederal forest lands statewide (Fig. 4), at intersections of a 5.5 x 5.5 km grid. Plot sizes and configurations varied among the component data sets, and thus also with geographic location, ecological conditions, and ownership (Table 2). We subsampled from the complete vegetation data set, to reduce it to a manageable size, to even-out strong differences in sampling intensity among the component data sets, to introduce an element of randomness, and to reduce the possibility of geographic bias. To obtain an even geographic distribution of the subsample, we randomly selected 10 plots from each 635-km² hexagon in the tessellation developed by White et al. (1992). This yielded 2443 plots for analysis, encompassing 30 families, 71 genera, and 181 species. Nomenclature follows Hitchcock and Cronquist (1973) and Hickman (1993).

Explanatory variables

We compiled data on the physical environment and disturbance history of each plot from field-recorded measures and through overlay of plot locations with mapped features in a geographic information system (GIS) (ARC/INFO software, version 7.0; Environmental Systems Research Institute [ESRI] 1991) (Table 3).

We used field-recorded data for slope, aspect, elevation, overstory crown cover, stand age, and history of clear-cut timber harvesting. We used a cosine transformation of aspect: $ASPECT = \cosine(45 - \text{DEGREES}) + 1$ (Beers et al. 1966). This equation transforms a circular variable, where large values are close to small values, into a measure of aspect that is relevant for vegetation. Values range from 0.0 on the most exposed (southwest) slopes to 2.0 on the least exposed (northeast) slopes. For the Ecology and FIR plots, *AGE* was based on the oldest of several trees on the plot, determined by increment boring. For FIA plots, *AGE* was based on all over- and mid-story trees on each plot, determined by increment boring. Where a history of clear-cutting was recorded on FIA plots, we coded $CLEARCUT = 1$. We assumed all other plots never had been harvested ($CLEARCUT = 0$).

We derived climate data from precipitation map surfaces generated by the Precipitation-elevation Regressions on Independent Slopes Model (PRISM) (Daly et al. 1994) and temperature map surfaces generated by a model developed by Dodson and Marks (1997). Both models use digital elevation models (DEMs) to account for topographic effects in interpolating weather measurements from an irregular network of weather stations to a uniform grid. Thirteen precipitation surfaces (mean annual and 12 mean monthlies) were generated at 10-km resolution from 1961-1990 weather data. We log-transformed all precipitation surfaces, because vegetation does not respond linearly to amount of precipitation. A 1.0-cm difference in precipitation is more important at low than at high levels. We generated 15 temperature surfaces (mean annual, all-time recorded minimum, all-time recorded maximum, and 12 mean monthlies) at 500-m resolution from 1981-1992 weath-

TABLE 1. Extended.

Subregion									
Coast		Western Cascades		Klamath		Eastern Cascades		Blue Mountains	
Mean	cv	Mean	cv	Mean	cv	Mean	cv	Mean	cv
0.95	71	0.88	80	1.08	61	1.14	60	1.08	66
32.78	74	30.81	70	38.00	54	12.03	115	23.31	84
6.37	18	6.82	17	6.63	21	7.35	10	6.92	16
66.57	90	184.72	84	177.45	78	130.67	68	149.70	48
67.55	46	73.44	39	65.59	46	33.43	62	41.85	63
266.16	63	886.97	49	777.89	52	1489.28	22	1470.24	22
7.54	5	7.44	4	7.29	7	6.33	6	6.39	6
7.21	5	7.08	4	7.00	8	5.92	7	5.81	9
5.54	7	5.62	5	5.19	8	4.72	7	5.15	6
124.32	5	123.54	3	129.42	3	108.24	12	88.13	16
5.72	20	7.10	13	4.85	26	10.83	30	15.55	26
2.54	16	2.32	21	2.63	27	2.60	20	2.30	22
9.47	15	7.37	35	8.40	30	5.45	35	4.65	50
37.33	5	31.87	14	32.55	11	25.83	13	26.18	12
-20.62		-24.98		-20.82		-32.70		-35.42	
5.01		1.81		3.44		-1.07		-2.50	
13.94	11	12.99	20	13.45	22	12.16	17	11.79	20
18.58	16	23.48	8	20.55	22	29.06	7	32.84	7

er data. We assigned precipitation and temperature values from each map surface to plot locations, by using bilinear interpolation (LATTICESPOT function, ESRI 1991). From the mean monthly precipitation and temperature values for each plot, we computed indices that approximate conditions during the growing season (*SMRPRE*, *SMRTMP*, *SMRTSMRP*) and the cool season (*WTRPRE*, *WTRTMP*), as well as seasonal variability and continentality (Table 3). Continental climates experience greater diurnal and seasonal variability in temperature (reflected in *CVTMP*), less seasonal variability in precipitation because of increased prevalence of rainfall from summer connective storms (reflected in *CVPRE* and *CONTPRE*), and colder minimum temperatures (reflected in *MINTMP*) than do maritime climates (Table 3).

We estimated each plot's potential solar radiation from latitude, elevation, aspect, and slope using program SOLARPD (Smith 1993). SOLARPD com-

putes total insolation, including direct (direct beam) and indirect (skylight), based on the algorithms of Lowry and Lowry (1989). Calculations assume an average profile for atmospheric transmissivity and absorptivity for humid, temperate climates, and do not adjust for cloud cover.

We obtained data on lithology and geologic age from a geologic map of Oregon (Walker and MacLeod 1991) obtained as a GIS coverage from the Corvallis Forestry Sciences Laboratory, USDA Forest Service, 3200 SW Jefferson Way, Corvallis, Oregon. We assigned a type to each field plot using the INTERSECT command (ESRI 1991). We grouped the types into 14 generalized geologic types, which we converted to dummy variables. Because direct gradient analysis can only accept $K - 1$ dummy variables for a categorical variable with K categories, we dropped the uninformative "mixed rocks" (*MIXR*) category (Table 3, Fig. 3) from our analyses.

TABLE 2. Sources, sample sizes, and sample designs of vegetation data sets. See Figs. 4 and 5 for locations of sampled ownerships.

Data source	Sub-sample		Ownerships sampled	Sample design
	Total N	sample N		
Area Ecology Program	7542	1482	National Forest, statewide	Plots selected subjectively without preconceived bias (Mueller-Dombois and Ellenberg 1974) from mid- to late- successional stands. Fixed-radius plots, 378 1350 m ² .
Forest Inventory and Analysis	1474	849	Private and other public, statewide	Plots established at intersections of 5.5-km systematic grid across stands of all ages. Plots were a cluster of five subplots, each with a series of variable- and fixed-radius plots. Variable-radius plots for trees were 15, 20, 30, or 80 metric basal-area factor to an other limit of 4047-6750 m ² fixed-radius plots; 91-908 m ² fixed-radius plots for shrubs.
Forestry Intensive Research Program	983	112	Bureau of Land Management, southwest Oregon	Plots selected subjectively in mid- to late-successional stands. Plot size 500 m ² .

TABLE 3. Codes and definitions of explanatory variables used in canonical correspondence analysis, by variable subset.

Code	Definition
Topography	
<i>ASPECT</i>	Cosine transformation of aspect (degrees), 0.0 (southwest) to 2.0 (northeast)
<i>SLOPE</i>	Slope (percent)
<i>SOLAR</i>	Total potential solar radiation (joules/m ² x 10 ⁻⁸)
Disturbance	
<i>AGE</i>	Stand age (years)
<i>CLEARCUT</i>	History of clearcut harvest (1 = clearcut, 0 = not clearcut)
<i>TREOCOV</i>	Crown cover of all overstory trees (percent)
Climate	
<i>ELEV</i>	Elevation (m)
<i>ANNPRE</i>	Mean annual precipitation (natural logarithm, mm)
<i>WTRPRE</i>	Mean precipitation in November-March (natural logarithm, mm)
<i>SMRPRE</i>	Mean precipitation in May-September (natural logarithm, mm)
<i>CVPRE</i>	Coefficient of variation of mean monthly precipitation of the wettest and driest months, usually December and July
<i>CONTPRE</i>	Percentage of mean annual precipitation falling in June-August
<i>SMRTSMRP</i>	Moisture stress during the growing season, <i>SMRTMPISMRPRE</i>
<i>ANNTMP</i>	Mean annual temperature (°C)
<i>MAXTMP</i>	All-time maximum recorded temperature (°C)
<i>MINTMP</i>	All-time minimum recorded temperature (°C)
<i>WTRTMP</i>	Mean monthly temperature (°C) from November-March
<i>SMRTMP</i>	Mean monthly temperature (°C) from May-September
<i>CVTMP</i>	Coefficient of variation of mean monthly temperature of the coldest and warmest months, usually January and August, calculated after resealing °C (-40° to 40°) to (0° to 255°)
Geology	
<i>VOLC</i>	Igneous: volcanic and intrusive rocks
<i>SILR</i>	Igneous: silicic rocks (granite, diorite, rhyolite, and dacite)
<i>MAFO</i>	Igneous: mafic rocks (basalt, basaltic andesite, andesite, gabbro), Miocene or older
<i>MAFY</i>	Igneous: mafic rocks (basalt, basaltic andesite, andesite, gabbro, Pliocene and younger)
<i>UMAF</i>	Igneous: ultramafic rocks (serpentine)
<i>PYRO</i>	Igneous: mafic pyroclastic rock, ash, ejecta, vent deposits, Miocene and older
<i>PYRY</i>	Igneous: mafic pyroclastic rock, ash, ejecta, vent deposits, Pliocene and younger
<i>SILV</i>	Igneous: silicic vent deposits
<i>META</i>	Metamorphic
<i>SEDR</i>	Sedimentary: siltstones, sandstones, mudstones, conglomerates
<i>TUFO</i>	Sedimentary: tuffaceous rocks and tuffs, pumicites, silicic flows, Miocene and older
<i>TUFY</i>	Sedimentary: tuffaceous rocks and tuffs, pumicites, silicic flows, Pliocene and younger
<i>DEPO</i>	Depositional: dune sand, alluvial, glacial, glaciofluvial, loess, landslide and debris flow, playa, lacustrine, fluvial
<i>MIXR</i>	Mixed rocks
Spatial	
<i>X</i>	Longitude (decimal degrees)
<i>Y</i>	Latitude (decimal degrees)
<i>Y2</i>	Y ²
<i>X3</i>	X ³
<i>X2Y</i>	X ² Y

We obtained the latitude (Y) and longitude (X) of each plot. The derivation and accuracy of these coordinates varied greatly among the component data sets. To account for complex spatial trends, we developed quadratic and cubic combinations of X and Y (sensu Borcard et al. 1992). We identified the five spatial variables (Table 3) that explained the most species variation in a preliminary gradient analysis for use in subsequent analyses.

Gradient analyses

Direct gradient analyses.—Our primary analytical tool was canonical correspondence analysis (CCA) (ter Braak 1986, 1987a, b, ter Braak and Prentice 1988), a direct gradient analysis method used widely in com-

munity ecology (Palmer 1993). We chose CCA, because our goal was to better understand environmental factors associated with vegetation pattern. In CCA, sites and species are arranged in a multidimensional space, with the restriction that the ordination axes must be linear combinations of the specified environmental variables. We used program CANOCO, version 3.12 (ter Braak 1987a), recompiled with increased array sizes to accommodate our large data set. In all CCAs, we log-transformed species relative abundance values to dampen the influence of dominant species. All other CANOCO defaults were used. All CCA plot scores in this paper are linear combinations. In CCA and in this paper, the fraction of species variation explained by a set of explanatory variables (total variation explained,

TVE) is the sum of all constrained eigenvalues divided by the total variation (TV) in the species data (or "total inertia," sensu ter Braak 1987a), which is the sum of all unconstrained eigenvalues. The TV is the ratio of the dispersion of the species scores to the dispersion of the plot scores (ter Braak 1987a), a property of the species-by-plot data matrix. Data matrices with greater TV contain many species and little overlap of species occurrence among plots.

CCA with variance partitioning.—We performed CCA with variance partitioning (ter Braak 1988, Borcard et al. 1992, Økland and Eilertsen 1994), using partial CCA, to quantify the relative contributions of variable subsets to explained variation. In partial CCA, species variation associated with explanatory variables that are not of direct interest (i.e., covariables) is partialled out, in order to examine a selected set of explanatory variables of interest. The usual explanatory variables are replaced by the residuals obtained by regressing each of the variables of interest on the covariables. We analyzed several combinations of two sets of explanatory variables, denoted $\{A\}$ and $\{B\}$ in the general sense (sensu Økland and Eilertsen 1994). We denoted variation explained by $\{A\}$ as A and by $\{B\}$ as B . We found the fraction of variation explained by $\{A\}$ and not shared with $\{B\}$, denoted $A|B$, by partial CCA (ter Braak 1988), using the variables in $\{B\}$ as covariables and $\{A\}$ as the constraining variables. We found the fraction of variation explained by $\{B\}$ and not shared with $\{A\}$, denoted $A|B$, by partial CCA using the variables in $\{A\}$ as covariables and $\{B\}$ as the constraining variables. We found the fraction of variation explained that is shared by $\{A\}$ and $\{B\}$, denoted $A \cap B$, by $(A - A|B)$.

We grouped factors thought to operate at a local scale into the topography ($\{T\}$) and disturbance ($\{D\}$) subsets, regional-scale factors into the macroclimate ($\{C\}$) and geologic ($\{G\}$) subsets, and measures and transformations of spatial position into the spatial ($\{S\}$) subset (Table 3). We performed CCA with variance partitioning to quantify relative contributions to explained variation of environmental vs. spatial factors ($\{T \cup D \cup C \cup G\}$ vs. $\{S\}$), of local vs. regional factors ($\{T \cup D\}$ vs. $\{C \cup G\}$), and of each variable subset vs. the other three subsets ($\{T\}$ vs. $\{D \cup C \cup G\}$, $\{D\}$ vs. $\{T \cup C \cup G\}$, $\{C\}$ vs. $\{T \cup D \cup G\}$, and $\{G\}$ vs. $\{T \cup D \cup C\}$).

Stepwise CCA.—We performed stepwise CCA on all woody species, tree species only, and shrub species only, for each geographic area. We excluded spatial variables because they explained very little of the species variation in CCA with variance partitioning. We added explanatory variables to the model in the order of greatest additional contribution to TVE, but only if they were significant ($P \leq 0.01$), where significance was determined by a Monte Carlo permutation test using 99 permutations (H_0 : additional influence of variable on vegetation is not significantly different from

random), and if adding the variable did not cause any variance inflation factors to exceed 20. Variables with large inflation factors are strongly multicollinear with other variables and contribute little unique information to the model (ter Braak 1987a). We excluded them to improve model interpretability and parsimony. Although several of the explanatory variables included in the stepwise models still were intercorrelated, CCA is robust to this multicollinearity (Palmer 1993).

We graphed results as biplots (Fig. 6), in which arrow length and position of the arrowhead indicate the correlation between the explanatory variable and the CCA axes, arrow direction indicates how the variable is correlated with the CCA axes, and smaller angles between arrows indicate stronger correlations between variables (ter Braak 1986, 1987a, b). We evaluated CCA model fit for plots using residual distances, an ordination diagnostic provided by CANOCO (ter Braak 1987a). Residuals are the squared chi-square distances between each plot and the centroid of all plots in m -dimensional species space for CCA axes 1-4 (ter Braak 1987a).

Indirect gradient analyses.—In order to more fully explore how successfully the environmental variables used in the constrained ordination explained species variation, we analyzed the vegetation data using detrended correspondence analysis (DCA), an indirect gradient analysis method (Gauch 1982), and with detrended canonical correspondence analysis (DCCA) using the same explanatory variables identified in the stepwise CCAs. Species relative abundance was log-transformed cover; all other defaults were used. We used detrending by segments, with 26 segments for both DCA and DCCA, so we could compare results from the two methods (Palmer 1993). We compared eigenvalues and gradient lengths from the two methods. By rescaling in DCA and DCCA, gradient length is set equal to species turnover (standard deviations, SD) so as to make gradient length interpretable and readily comparable between different datasets (Peet et al. 1988). We also computed Spearman's rank correlations (PROC CORR) (SAS 1990) of plot scores from DCA and DCCA.

Mapping of dominant gradients.—We kriged (Isaacs and Srivastava 1990) the plot scores from stepwise CCA in a GIS (command KRIGING, ESRI 1991) to help visualize the ordination results through interpolation. Kriging is a linear, weighted-average interpolation method that considers spatial autocorrelation in the data and does not require that the data be normally distributed or uncorrelated. We selected the Gaussian model as having the best fit between actual and predicted semivariograms for CCA axes 1-4 at the state scale. We interpolated the plot scores to a lattice with 8000-m spacing, equal to the average distance between adjacent field plots, and then contoured the lattice using command LATTICECONTOUR (ESRI 1991). We kriged the Blue Mountains subregion independently from the other four subregions because it is not geo-

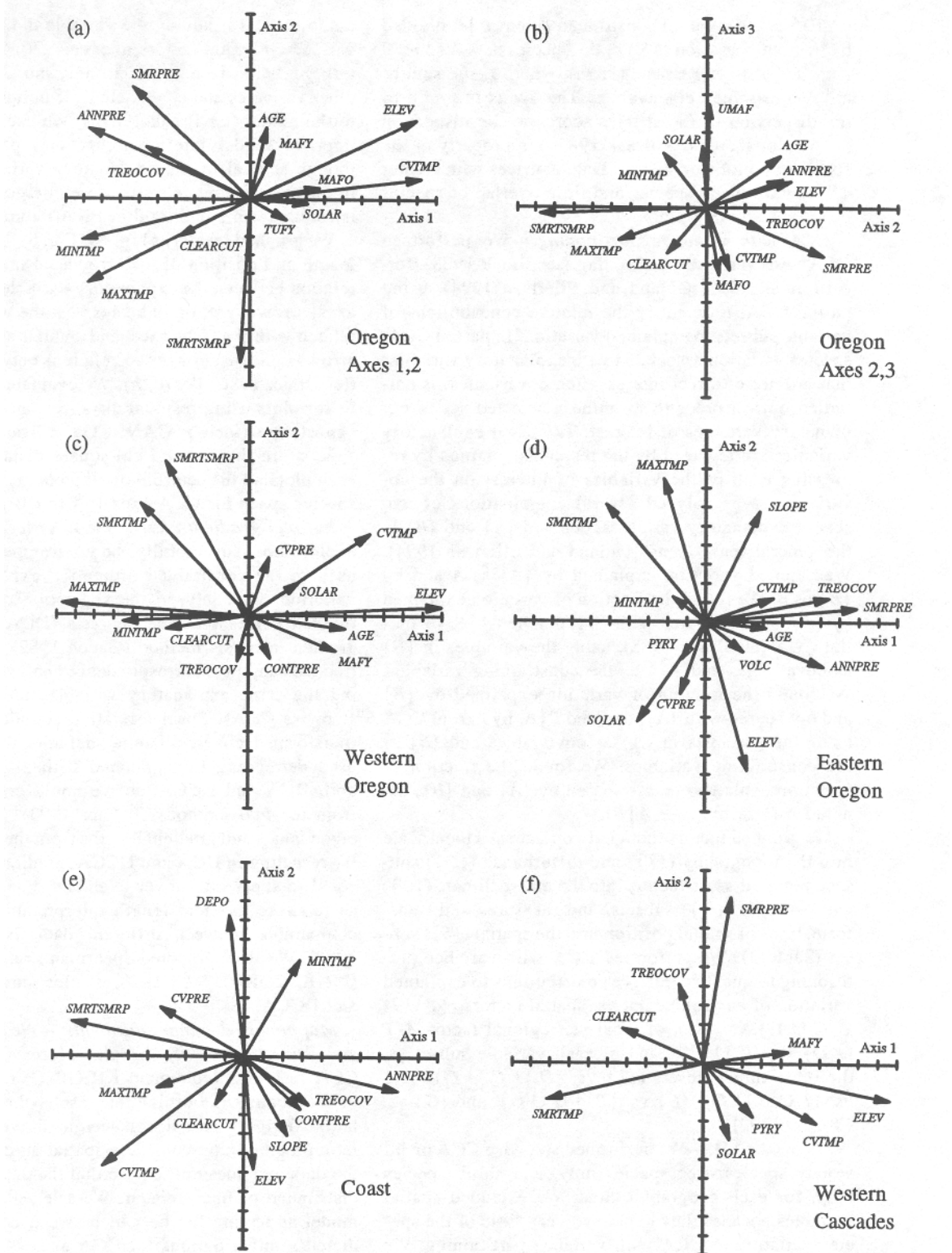


FIG. 6. Biplots from canonical correspondence analysis of all woody species. All axes have been resealed to range from -1.0 to 1.0. Axes for explanatory variables that were not significant or that had very low correlations with the canonical axes are not shown.

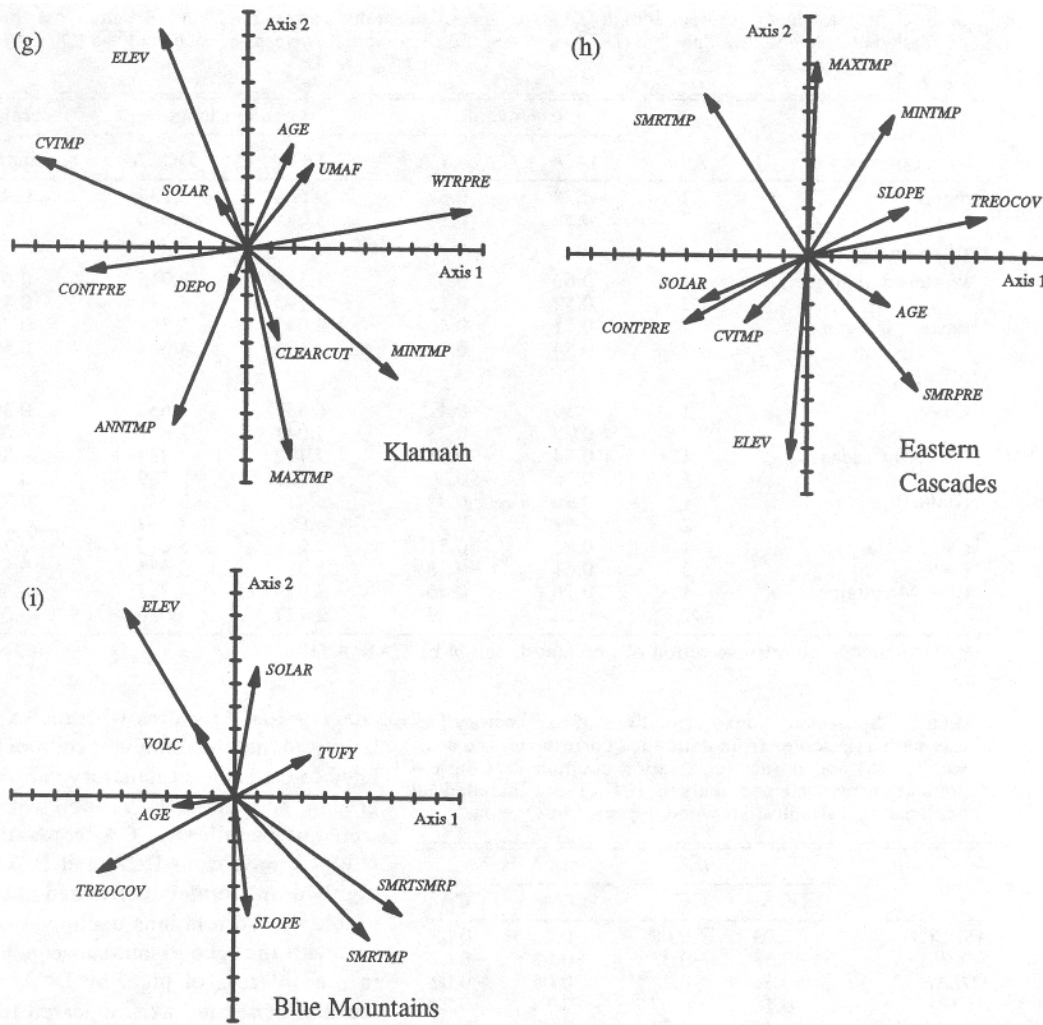


FIG. 6. Continued.

graphically contiguous. We selected sizes of the sampling windows and contour intervals subjectively to achieve comparable appearance among contour maps.

Species diversity measures

We computed measures of the three levels of species diversity defined by Whittaker (1960) for each geographic area and vegetation layer. We estimated alpha diversity ($\bar{\alpha}$), or intracommunity diversity, as the mean number of species sampled (species richness) on a field plot. We estimated gamma diversity (S), the diversity of an entire landscape or region, from the total number of species sampled on all plots within each geographic area. We computed two measures of beta diversity, which is defined as the change in species composition along environmental gradients and often is measured as the degree to which the species compositions of samples differ. We used Whittaker's (1960) measure of beta diversity, $\beta_w = (S/\bar{\alpha}) - 1$, and total variation (TV) from stepwise CCA. The TV is the ratio of the dis-

persion of the species scores to the dispersion of the plot scores (ter Braak 1987a). Data matrices with greater TV contain many species with little overlap of species occurrence among plots, and thus higher beta diversities.

RESULTS

Comparison of direct and indirect gradients

Eigenvalues and gradient lengths were moderately higher for detrended correspondence analysis (DCA) than for detrended canonical correspondence analysis (DCCA) for the first two axes in most of the geographic areas (Table 4), indicating that a portion of the species variation was not accounted for by the explanatory variables in DCCA. However, the strong correlations between the DCA axis 1 and the explanatory variables (Table 5) suggested that much of the variation in vegetation is related to the measured explanatory variables. Furthermore, the striking similarity between correlations of DCA scores and canonical correspondence

TABLE 4. Eigenvalues, gradient lengths (1 SD), Spearman's rank correlations, and *P* values for the first two axes from detrended correspondence analysis (DCA) and detrended canonical correspondence analysis (DCCA) of all woody species, by geographic area.

Geographic area	Axis	Eigenvalue		Gradient length		Spearman's rank correlation [†]	<i>P</i>
		DCA	DCCA	DCA	DCCA		
Oregon	1	0.78	0.67	9.664	5.237	0.93	<0.01
	2	0.59	0.36	8.045	4.940	0.63	<0.01
Half-state							
Western Oregon	1	0.62	0.42	7.557	3.715	0.67	<0.01
	2	0.52	0.35	7.795	4.071	-0.45	<0.01
Eastern Oregon	1	0.71	0.46	9.043	5.397	0.73	<0.01
	2	0.54	0.32	4.693	4.569	0.59	<0.01
Subregion							
Coast	1	0.59	0.41	6.537	3.653	0.80	<0.01
	2	0.29	0.23	4.041	2.372	0.03	0.46
Western Cascades	1	0.64	0.45	7.192	4.233	0.89	<0.01
	2	0.36	0.20	4.136	2.789	0.71	<0.01
Klamath	1	0.56	0.42	6.419	3.079	0.83	<0.01
	2	0.51	0.23	4.988	2.697	0.23	<0.01
Eastern Cascades	1	0.81	0.51	8.917	5.675	0.70	<0.01
	2	0.61	0.28	5.317	3.375	0.50	<0.01
Blue Mountains	1	0.76	0.46	8.949	4.867	0.80	<0.01
	2	0.54	0.30	2.127	4.086	-0.08	0.71

[†] Sign reflects arbitrary selection of gradient direction by CANOCO.

TABLE 5. Spearman's rank correlations of explanatory factors with axis scores from detrended correspondence analysis (DCA) and intraset correlation coefficients from canonical correspondence analysis (CCA) that included all explanatory variables, all woody species in Oregon.

	Axis 1		Axis 2	
	DCA	CCA	DCA	CCA
ASPECT	0.03	0.08	0.00	0.03
SLOPE	-0.38	-0.35	-0.03	-0.01
SOLAR	0.36	0.27	0.06	-0.02
AGE	0.16	0.07	-0.14	0.27
CLEARCUT	-0.36	-0.33	0.00	-0.14
TREOCOV	-0.58	-0.51	-0.33	0.21
ELEV	0.77	0.82	-0.01	0.32
ANNPRE	-0.82	-0.85	-0.49	0.30
WTRPRE	-0.82	-0.80	-0.47	0.25
SMRPRE	-0.67	-0.58	-0.52	0.48
CVPRE	-0.68	-0.67	-0.22	-0.03
CONTPRE	0.72	0.68	0.22	0.04
SMRTSMRP	0.06	-0.06	0.49	-0.68
ANNTMP	-0.59	-0.63	0.13	-0.48
MAXTMP	-0.75	-0.80	0.03	-0.34
MINTMP	-0.79	-0.83	-0.15	-0.16
WTRTMP	-0.72	-0.76	0.02	0.02
SMRTMP	-0.29	-0.33	0.31	-0.58
CVTMP	0.81	-0.84	0.21	-0.19
VOLC	-0.05	-0.05	-0.05	-0.01
SILR	0.04	-0.03	0.01	-0.04
MAFO	0.27	0.33	0.14	0.05
MAFY	0.10	0.11	-0.11	0.18
UMAF	-0.02	-0.05	0.01	<0.01
PYRO	0.12	0.13	0.03	-0.01
PYRY	0.14	0.14	-0.05	0.02
SILV	0.08	0.08	0.03	-0.02
METH	0.00	0.01	0.01	-0.01
SEDR	-0.43	-0.42	-0.07	-0.10
TUFO	-0.14	-0.14	-0.02	-0.01
TUFY	0.16	0.17	0.11	-0.08
DEPO	0.00	0.01	-0.07	<0.01

Note: Sign reflects arbitrary selection of gradient direction by CANOCO.

analysis (CCA) scores with the explanatory variables indicated that the dominant compositional gradients related to the same explanatory variables (Table 5). Geographic patterns of DCA scores at the state level also were quite similar to CCA scores for the first two axes. Plot scores from DCA and DCCA for axis 1 were highly or moderately correlated in all geographic areas (Table 4). Correlations declined—sometimes markedly—with the second and subsequent axes. Differences in the ordering of plots by DCA and DCCA beyond the first or second axis appeared to have been caused by poor performance of DCA on our very long gradients. We therefore present DCA results for axis 1 and 2 only. Because of similar geographic patterns and ordering of plots between DCA and DCCA, the similar correlations of DCA and CCA axes with explanatory variables, and the questionable performance of DCA beyond axis 1, we emphasize results from direct gradient analysis in this paper.

Dominant gradients at state, half-state, and subregion scales

Results from stepwise CCAs varied with geographic extent, geographic location, and sample size (numbers of plots and species) (Table 6). Total variation (TV) and sample size increased, and total variation explained (TVE) decreased, with increasing geographic extent (Table 6). In all geographic areas, TV was higher for shrub species than for tree species (Table 6). TVE was highest for all woody species (15%) and for shrubs (12%) in the Klamath subregion, and for trees in the eastern Cascades (19%). Since TVE decreased with increasing sample size, we could not discern whether the explanatory power of the models changed with geo-

TABLE 6. Summary of results from stepwise canonical correspondence analyses by vegetation layer and geographic area. TV = total variation; TVE = total variation explained.

Geographic area	Plots (no.)	Species (no.)	TV	TVE (decimal fraction of TV)	Eigenvalue			
					Axis 1	Axis 2	Axis 3	Axis 4
Oregon								
Woody	2443	192	24.324	0.09	0.67	0.37	0.26	0.21
Trees	2443	51	14.084	0.13	0.64	0.39	0.23	0.18
Shrubs	2331	141	32.707	0.07	0.71	0.36	0.29	0.23
Half-state								
Western Oregon								
Woody	1233	158	15.468	0.11	0.42	0.37	0.26	0.17
Trees	1233	46	10.066	0.16	0.44	0.36	0.25	0.16
Shrubs	1208	112	19.076	0.09	0.40	0.37	0.29	0.17
Eastern Oregon								
Woody	1210	130	18.499	0.09	0.46	0.35	0.22	0.11
Trees	1210	37	10.301	0.13	0.44	0.26	0.17	0.12
Shrubs	1123	93	25.674	0.07	0.57	0.35	0.25	0.14
Subregion								
Coast								
Woody	461	97	9.705	0.12	0.41	0.27	0.15	0.09
Trees	461	28	6.549	0.16	0.40	0.26	0.12	0.07
Shrubs	459	69	11.064	0.10	0.41	0.28	0.17	0.08
Western Cascades								
Woody	465	119	9.309	0.12	0.45	0.21	0.16	0.09
Trees	465	34	5.953	0.16	0.47	0.22	0.11	0.05
Shrubs	445	85	12.161	0.08	0.41	0.20	0.15	0.10
Klamath								
Woody	307	124	10.565	0.15	0.42	0.31	0.22	0.15
Trees	307	37	7.357	0.13	0.36	0.26	0.11	0.11
Shrubs	304	87	13.209	0.12	0.45	0.35	0.25	0.15
Eastern Cascades								
Woody	479	99	12.556	0.13	0.51	0.32	0.22	0.16
Trees	479	30	7.127	0.19	0.49	0.35	0.19	0.13
Shrubs	453	69	18.713	0.07	0.48	0.26	0.24	0.16
Blue Mountains								
Woody	731	94	15.582	0.09	0.46	0.34	0.13	0.09
Trees	731	24	7.746	0.14	0.47	0.29	0.12	0.09
Shrubs	670	70	20.180	0.06	0.44	0.40	0.11	0.09

graphic extent or location. Because sample size did not appear to affect the proportions of TVE attributable to different subsets of explanatory variables, we present our findings as proportions.

We present results of stepwise CCAs at state, half-state, and subregion scales below. The half-state and subregion analyses revealed much variation in associations between environmental and compositional gradients. The within-region differences underscored the importance of ecological modeling approaches that consider a location's particular biota, physical environment, and history. For each geographic area, species with highest and lowest scores on stepwise CCA axes are shown in Table 7.

Oregon.—At the state scale, the dominant compositional gradient (CCA axis 1) reflected a gradient from the maritime climate of the Coast to the more continental climate of eastern Oregon (Figs. 6a and 7a). Plots with the lowest scores on axis 1 were at lower

elevations and experienced lower seasonal variability in temperature, warmer maximum and minimum temperatures, higher rainfall, and a higher incidence of clear-cutting (Fig. 6a). These plots were concentrated along the length of the coast (Fig. 7a) within the *Picea sitchensis* zone of Franklin and Dyrness (1973). Plots with high scores on axis 1 were at higher elevations and were characterized by greater seasonal variability in temperature, cooler maximum and minimum temperatures, lower precipitation, and less clear-cutting (Fig. 6a). The highest plot scores were concentrated along the eastern boundary of the eastern Cascades subregion south of Bend and the southern boundary of the Blue Mountains subregion, at the transition to the shrubsteppe (Fig. 7a). High-scoring plots fell largely within the *Pinus ponderosa* and *Juniperus occidentalis* zones of Franklin and Dyrness (1973).

With minor exceptions, the axis 1 gradient was longitudinal from the Coast to the foothills of the eastern

TABLE 7. Species with $\geq 1\%$ constancy that scored highest and lowest in stepwise canonical correspondence analyses of all woody species, by geographic area and axis.

Axis 1	Axis 2
Oregon	
Low	
<i>Picea sitchensis</i>	<i>Quercus garryana</i>
<i>Umbellularia californica</i>	<i>Quercus kelloggii</i>
<i>Alnus rubra</i>	<i>Fraxinus latifolia</i>
<i>Rhamnus purshiana</i>	<i>Juniperus occidentalis</i>
<i>Menziesia ferruginea</i>	<i>Arctostaphylos viscida</i>
<i>Vaccinium ovatum</i>	<i>Rhus diversiloba</i>
<i>Vaccinium parviflorum</i>	<i>Lonicera hispidula</i>
<i>Rubus spectabilis</i>	<i>Ceanothus integerrimus</i>
<i>Oplopanax horridum</i>	<i>Rubus discolor</i>
<i>Sambucus racemosa</i>	<i>Symphoricarpos</i> spp.
High	
<i>Juniperus occidentalis</i>	<i>Tsuga mertensiana</i>
<i>Cercocarpus ledifolius</i>	<i>Abies amabilis</i>
<i>Pinus contorta</i>	<i>Abies lasiocarpa</i>
<i>Artemisia tridentata</i>	<i>Abies procera</i>
<i>Chrysothamnus viscidiflorus</i>	<i>Abies magnifica</i> var. <i>shastensis</i>
<i>Chrysothamnus nauseosus</i>	<i>Pinus monticola</i>
<i>Haplopappus bloomeri</i>	<i>Gaultheria ovatifolia</i>
<i>Purshia tridentata</i>	<i>Vaccinium scoparium</i>
<i>Symphoricarpos oreophilus</i>	<i>Vaccinium alaskaense</i>
<i>Ribes cereum</i>	<i>Rubus lasiococcus</i>
Axis 3	Axis 4
Oregon (continued)	
Low	
<i>Larix occidentalis</i>	<i>Quercus chrysolepis</i>
<i>Salix scouleriana</i>	<i>Quercus kelloggii</i>
<i>Physocarpus malvaceus</i>	<i>Pinus lambertiana</i>
<i>Lonicera utahensis</i>	<i>Cornus nuttallii</i>
<i>Spiraea betulifolia</i>	<i>Arbutus menziesii</i>
<i>Philadelphus lewisii</i>	<i>Lonicera ciliosa</i>
<i>Acer glabrum</i>	<i>Lonicera hispidula</i>
<i>Ribes lacustre</i>	<i>Arctostaphylos viscida</i>
<i>Oplopanax horridum</i>	<i>Berberis piperiana</i>
<i>Symphoricarpos albus</i>	<i>Whipplea modesta</i>
High	
<i>Chamaecyparis lawsoniana</i>	<i>Picea sitchensis</i>
<i>Abies magnifica</i> var. <i>shastensis</i>	<i>Alnus rubra</i>
<i>Lithocarpus densiflorus</i>	<i>Umbellularia californica</i>
<i>Umbellularia californica</i>	<i>Vaccinium ovatum</i>
<i>Quercus chrysolepis</i>	<i>Rubus spectabilis</i>
<i>Pinus monticola</i>	<i>Sambucus racemosa</i>
<i>Arctostaphylos viscida</i>	<i>Menziesia ferruginea</i>
<i>Berberis piperiana</i>	<i>Arctostaphylos uva-ursi</i>
<i>Arctostaphylos patula</i>	<i>Chrysothamnus viscidiflorus</i>
<i>Ceanothus prostratus</i>	<i>Purshia tridentata</i>
Axis 1	Axis 2
Western Oregon	
Low	
<i>Picea sitchensis</i>	<i>Picea sitchensis</i>
<i>Fraxinus latifolia</i>	<i>Tsuga mertensiana</i>
<i>Rhamnus purshiana</i>	<i>Abies amabilis</i>
<i>Rubus discolor</i>	<i>Abies procera</i>
<i>Rubus spectabilis</i>	<i>Pinus contorta</i>
<i>Menziesia ferruginea</i>	<i>Menziesia ferruginea</i>
<i>Sambucus racemosa</i>	<i>Oplopanax horridum</i>
<i>Myrica californica</i>	<i>Vaccinium scoparium</i>
<i>Rosa</i> spp.	<i>Vaccinium alaskaense</i>
<i>Symphoricarpos</i> spp.	<i>Rubus spectabilis</i>
High	
<i>Pinus contorta</i>	<i>Quercus kelloggii</i>
<i>Pinus monticola</i>	<i>Quercus garryana</i>
<i>Tsuga mertensiana</i>	<i>Pinus ponderosa</i>
<i>Abies magnifica</i> var. <i>shastensis</i>	<i>Ceanothus cuneatus</i>

TABLE 7. Continued.

Axis 1.	Axis 2
<i>Picea engelmannii</i>	<i>Ceanothus integerrimus</i>
<i>Abies amabilis</i>	<i>Arctostaphylos viscida</i>
<i>Vaccinium scoparium</i>	<i>Lonicera hispidula</i>
<i>Ribes viscosissimum</i>	<i>Rhus diversiloba</i>
<i>Arctostaphylos nevadensis</i>	<i>Amelanchier pallida</i>
<i>Gaultheria ovatifolia</i>	<i>Berberis piperiana</i>
Eastern Oregon	
Low	
<i>Juniperus occidentalis</i>	<i>Pinus albicaulis</i>
<i>Quercus garryana</i>	<i>Pinus contorta</i>
<i>Artemisia arbuscula</i>	<i>Pinus monticola</i>
<i>Artemisia tridentata</i>	<i>Tsuga mertensiana</i>
<i>Chrysothamnus nauseosus</i>	<i>Abies lasiocarpa</i>
<i>Chrysothamnus viscidiflorus</i>	<i>Abies magnifica</i> var. <i>shastensis</i>
<i>Haplopappus bloomeri</i>	<i>Vaccinium scoparium</i>
<i>Purshia tridentata</i>	<i>Arctostaphylos patula</i>
<i>Arctostaphylos patula</i>	<i>Haplopappus bloomeri</i>
<i>Ceanothus prastratus</i>	<i>Ceanothus velutinus</i>
High	
<i>Tsuga mertensiana</i>	<i>Quercus garryana</i>
<i>Abies lasiocarpa</i>	<i>Philadelphus lewisii</i>
<i>Pinus albicaulis</i>	<i>Physocarpus malvaceus</i>
<i>Taxus brevifolia</i>	<i>Holodiscus discolor</i>
<i>Picea engelmannii</i>	<i>Acer glabrum</i>
<i>Vaccinium scoparium</i>	<i>Prunus virginiana</i>
<i>Vaccinium membranaceum</i>	<i>Ribes</i> spp.
<i>Ribes lacustre</i>	<i>Symphoricarpos albus</i>
<i>Sorbus scopulina</i>	<i>Spiraea betulifolia</i>
<i>Berberis nervosa</i>	<i>Rubus parviflorus</i>
Coast	
Low	
<i>Quercus kelloggii</i>	<i>Abies procera</i>
<i>Quercus garryana</i>	<i>Cornus nuttallii</i>
<i>Fraxinus latifolia</i>	<i>Castanopsis chrysophylla</i>
<i>Arbutus menziesii</i>	<i>Prunus emarginata</i>
<i>Calocedrus decurrens</i>	<i>Vaccinium membranaceum</i>
<i>Rosa eglanteria</i>	<i>Oplopanax horridum</i>
<i>Rosa</i> spp.	<i>Berberis aquifolium</i>
<i>Amelanchier alnifolia</i>	<i>Berberis nervosa</i>
<i>Symphoricarpos</i> spp.	<i>Ribes</i> spp.
<i>Rhus diversiloba</i>	<i>Acer circinatum</i>
High	
<i>Picea sitchensis</i>	<i>Pinus contorta</i> var. <i>contorta</i>
<i>Chamaecyparis lawsoniana</i>	<i>Chamaecyparis lawsoniana</i>
<i>Tsuga heterophylla</i>	<i>Fraxinus latifolia</i>
<i>Abies procera</i>	<i>Salix hookeriana</i>
<i>Menziesia ferruginea</i>	<i>Arctostaphylos columbiana</i>
<i>Vaccinium alaskaense</i>	<i>Myrica californica</i>
<i>Vaccinium membranaceum</i>	<i>Baccharis pilularis</i>
<i>Oplopanax horridum</i>	<i>Cytisus scoparius</i>
<i>Myrica californica</i>	<i>Amelanchier alnifolia</i>
<i>Rubus spectabilis</i>	<i>Ceanothus velutinus</i>
Western Cascades	
Low	
<i>Fraxinus latifolia</i>	<i>Quercus kelloggii</i>
<i>Quercus garryana</i>	<i>Quercus garryana</i>
<i>Quercus kelloggii</i>	<i>Pinus ponderosa</i>
<i>Rhamnus purshiana</i>	<i>Abies magnifica</i> var. <i>shastensis</i>
<i>Acer macrophyllum</i>	<i>Arctostaphylos nevadensis</i>
<i>Prunus emarginata</i>	<i>Arctostaphylos patula</i>
<i>Rubus discolor</i>	<i>Berberis piperiana</i>
<i>Rubus laciniatus</i>	<i>Ribes binominatum</i>
<i>Symphoricarpos</i> spp.	<i>Ribes viscosissimum</i>
<i>Rhus diversiloba</i>	<i>Lonicera hispidula</i>

TABLE 7. Continued.

Axis 1	Axis 2
High	
<i>Abies lasiocarpa</i>	<i>Thuja plicata</i>
<i>Abies magnifica</i> var. <i>shastensis</i>	<i>Tsuga heterophylla</i>
<i>Pinus contorta</i>	<i>Oplopanax horridum</i>
<i>Tsuga mertensiana</i>	<i>Rubus pedatus</i>
<i>Picea engelmannii</i>	<i>Rubus spectabilis</i>
<i>Vaccinium scoparium</i>	<i>Vaccinium ovalifolium</i>
<i>Arctostaphylos nevadensis</i>	<i>Vaccinium alaskaense</i>
<i>Ribes viscosissimum</i>	<i>Vaccinium parvifolium</i>
<i>Ribes binominatum</i>	<i>Sambucus racemosa</i>
<i>Sorbus sitchensis</i>	<i>Oemleria cerasiformis</i>
Klamath	
Low	
<i>Cercocarpus montanus</i>	<i>Fraxinus latifolia</i>
<i>Cercocarpus ledifolius</i>	<i>Cercocarpus montanus</i>
<i>Quercus garryana</i>	<i>Cercocarpus ledifolius</i>
<i>Quercus kelloggii</i>	<i>Quercus garryana</i>
<i>Fraxinus latifolia</i>	<i>Alnus rubra</i>
<i>Ceanothus cuneatus</i>	<i>Rubus discolor</i>
<i>Ceanothus sanguineus</i>	<i>Rubus spectabilis</i>
<i>Symphoricarpos albus</i>	<i>Baccharis pilularis</i>
<i>Ceanothus integerrimus</i>	<i>Ceanothus thyrsiflorus</i>
High	
<i>Sequoia sempervirens</i>	<i>Abies magnifica</i> var. <i>shastensis</i>
<i>Pinus contorta</i> var. <i>contorta</i>	<i>Pinus monticola</i>
<i>Alnus rubra</i>	<i>Ribes binominatum</i>
<i>Berberis pumila</i>	<i>Acer glabrum</i>
<i>Juniperus communis</i>	<i>Vaccinium membranaceum</i>
<i>Rhododendron occidentale</i>	<i>Quercus sadleriana</i>
<i>Baccharis pilularis</i>	<i>Arctostaphylos nevadensis</i>
<i>Rhamnus californica</i>	<i>Arctostaphylos patula</i>
<i>Rubus spectabilis</i>	<i>Ceanothus pumilus</i>
Eastern Cascades	
Low	
<i>Juniperus occidentalis</i>	<i>Abies lasiocarpa</i>
<i>Cercocarpus ledifolius</i>	<i>Abies procera</i>
<i>Artemisia arbuscula</i>	<i>Tsuga mertensiana</i>
<i>Artemisia tridentata</i>	<i>Pinus albicaulis</i>
<i>Chrysothamnus viscidiflorus</i>	<i>Pinus monticola</i>
<i>Chrysothamnus nauseosus</i>	<i>Pinus contorta</i>
<i>Salix geyeriana</i>	<i>Vaccinium scoparium</i>
<i>Purshia tridentata</i>	<i>Arctostaphylos nevadensis</i>
<i>Haplopappus bloomeri</i>	<i>Ribes viscosissimum</i>
<i>Spiraea douglasii</i>	<i>Spiraea douglasii</i>
High	
<i>Abies lasiocarpa</i>	<i>Quercus garryana</i>
<i>Abies procera</i>	<i>Pseudotsuga menziesii</i>
<i>Tsuga mertensiana</i>	<i>Larix occidentalis</i>
<i>Vaccinium scoparium</i>	<i>Lonicera ciliosa</i>
<i>Vaccinium membranaceum</i>	<i>Corylus cornuta</i> var. <i>californica</i>
<i>Berberis nervosa</i>	<i>Ceanothus integerrimus</i>
<i>Acer circinatum</i>	<i>Spiraea betulifolia</i>
<i>Spiraea betulifolia</i>	<i>Holodiscus discolor</i>
<i>Rubus ursinus</i>	<i>Symphoricarpos</i> spp.
<i>Corylus cornuta</i> var. <i>californica</i>	<i>Berberis nervosa</i>
Blue Mountains	
Low	
<i>Abies lasiocarpa</i>	<i>Betula occidentalis</i>
<i>Pinus albicaulis</i>	<i>Taxus brevifolia</i>
<i>Pinus contorta</i>	<i>Philadelphus lewisii</i>
<i>Taxus brevifolia</i>	<i>Berberis nervosa</i>
<i>Picea engelmannii</i>	<i>Holodiscus discolor</i>
<i>Chimaphila menziesii</i>	<i>Acer glabrum</i>
<i>Chimaphila umbellata</i>	<i>Physocarpus malvaceus</i>
<i>Vaccinium scoparium</i>	<i>Rubus parviflorus</i>
<i>Sorbus scopulina</i>	<i>Amelanchier alnifolia</i>
<i>Lonicera involucrata</i>	<i>Rosa</i> spp.

TABLE 7. Continued.

Axis 1	Axis 2
High	
<i>Juniperus occidentalis</i>	<i>Pinus albicaulis</i>
<i>Cercocarpus ledifolius</i>	<i>Abies lasiocarpa</i>
<i>Haplopappus bloomeri</i>	<i>Juniperus occidentalis</i>
<i>Artemisia arbuscula</i>	<i>Artemisia tridentata</i>
<i>Artemisia tridentata</i>	<i>Artemisia arbuscula</i>
<i>Artemisia rigida</i>	<i>Artemisia rigida</i>
<i>Chrysothamnus nauseosus</i>	<i>Chrysothamnus viscidiflorus</i>
<i>Chrysothamnus viscidiflorus</i>	<i>Vaccinium scoparium</i>
<i>Purshia tridentata</i>	<i>Haplopappus bloomeri</i>
<i>Prunus</i> spp.	<i>Purshia tridentata</i>

Cascades, reflecting the strong climatic influence of the Pacific Ocean and the north-south orientation of the Coast and Cascade ranges. The dominant gradient in the Blue Mountain subregion was more latitudinal. Forests in the northern part of the Blue Mountain subregion receive a stronger maritime influence, and were most similar in composition to forests of the Cascades (Fig. 7a). Positions of selected species in ordination space are shown in Fig. 8. Species with highest and lowest scores on the CCA axes are shown in Table 7.

The second CCA axis was a gradient in growing season moisture stress, from areas of warm, dry growing seasons at lower elevations to areas of cool, wet growing seasons at higher elevations (Figs. 6a and 7b). Areas of low summer precipitation and high summer temperature included the interior valleys of western Oregon, especially the Rogue and Umpqua Valleys, the foothills of the eastern Cascades from Bend northward to the Columbia River Gorge, and lower elevation areas of the Blue Mountains subregion. Lowest plot scores were concentrated in these areas as well as in the foothills of the Coast Range bordering the Willamette Valley and in scattered locations throughout the Ochoco Mountains (Fig. 7b), and tended to be in younger stands. In addition to *Rubus discolor* (Table 7), several introduced species found primarily in the interior valleys of western Oregon and along the coast were among the lowest scoring species on axis 2, but had low constancy: *Crataegus monogyna*, *Rosa eglantheria*, and *Cytisus scoparius*. Highest plot scores on axis 2 were in older, subalpine forests of the Cascade Range and in high-elevation areas of the northern Coast Range and the Siskiyou, Blue, and Wallowa mountains (Fig. 7b).

Axis 3 was most strongly correlated with geologic variables. Low-scoring plots were on mafic rocks dating to the Miocene and older. High-scoring plots were on ultramafic parent materials, primarily in the Klamath subregion (Figs. 6b and 7c). Axis 3 also reflected a climatic gradient from low to high potential solar radiation, from high to low seasonal variability in temperature, from high to low summer precipitation, and from low to high minimum temperatures (Fig. 6b). The gradient was latitudinal, with low scores in the north and high scores in the south (Fig. 7c). Low-scoring

species on axis 3 were those with affinities for moist or disturbed sites at forest edges or openings, and were predominantly species distributed east of the Cascade crest (Table 7). Highest scoring species included several serpentine associates: *Chamaecyparis lawsoniana* (Zobel 1990) and *Arctostaphylos viscida* with > 1 % constancy (Table 7) and others with < 1 % constancy (*Pinus attenuata*, *P. jeffreyi*, *Ceanothus pumilus*, *C. cuneatus*, *Garrya buxifolia*, *Berberis pumila*, *Rhamnus californica*, *Quercus vaccinifolia*, and *Juniperus communis*).

Axis 4 was less interpretable than the first three axes. Local site and disturbance factors were the strongest environmental correlates. Low-scoring plots were on steep slopes and in older stands with dense canopies, and concentrated in the Klamath Mountains (Fig. 7d). High-scoring plots were on gentle terrain and in younger stands with sparse canopies, primarily along the southern coast and in the Paulina Mountains of central Oregon (Fig. 7d).

Western Oregon.—In western Oregon, the first axis was strongly correlated with elevation and temperature and moderately correlated with stand age and clearcutting (Fig. 6c). Low plot scores were on warm, low elevation sites along the coast and in the interior valleys in stands previously clear-cut, and high scores were on colder, high-elevation sites in older, uncut stands. The second axis was correlated with growing season precipitation and temperature (Fig. 6c). Low scores were in areas with cool, wet summers along the coast and on Mount Hood, and high scores were in areas with hot, dry summers in the Rogue and Umpqua Valleys and in the eastern portion of the Columbia River Gorge.

Eastern Oregon.—In eastern Oregon, axis 1 followed a gradient from younger stands in areas with warm, dry

summers, sparse canopies, and high moisture stress to older stands in areas with cool, wet summers, dense canopies, and low moisture stress (Fig. 6d). Axis 2 followed a gradient from areas of cool temperatures at higher elevations to warmer temperatures at lower elevations. Low-scoring plots also tended to be on flat sites with high solar radiation, and high-scoring plots on steep slopes with low solar radiation. The axis 2 gradient was latitudinal, with low plot scores on

mountain peaks and in the southern portion of the eastern Cascades and high scores in the northern portion of the eastern Cascades and Blue Mountains subregions.

Coast subregion.—In the Coast subregion, axis 1 reflected a gradient in summer moisture stress, annual precipitation, and seasonal temperature variability (Fig. 6e). Lowest plot scores were concentrated in the Umpqua and Willamette valleys, and highest scores were along the northwestern coast. Axis 2 was strongly associated with geology, with high-scoring plots in the coastal dunes, the Willamette Valley floor, coastal forests south of Coos Bay, and wet hardwood sites in the extreme northwest corner of the state. Remaining plots were largely undifferentiated along axis 2. The strongest environmental correlates were depositional soils, elevation, and seasonal temperature variability (Fig. 6e).

Western Cascades subregion.—The dominant compositional gradient in the western Cascades was most strongly associated with temperature (Fig. 6f): elevation, summer temperature, and seasonal temperature variability contributed 45% of TVE (Table 8). Lowest plot scores were in the foothills of the Willamette and Umpqua valleys and on previously clear-cut sites. The lowest scoring tree species on axis 1 were hardwoods (Table 7). Highest plot scores were on the peaks of the Cascade Range in stands without cutting. The second axis was strongly correlated with summer precipitation and less so with overstory cover, solar radiation, and seasonal temperature variability (Fig. 6f). Axis 2 was latitudinal, from low plot scores in the south to high scores in the north.

Klamath subregion.—In the Klamath subregion, axis 1 followed a gradient from a continental climate in the eastern portion of the subregion to a maritime climate with low seasonal temperature variability, high winter precipitation, and high seasonal variability in precipitation along the coast (Fig. 6g). Lowest plot scores on axis 1 were in the Rogue Valley and eastward toward the Cascade crest, and highest scores were along the coast. Axis 2 followed a gradient from low elevations and warm temperatures to high elevations and cool temperatures (Fig. 6g). Plots with low scores also tended to be in younger stands with a history of clearcutting. Low scores were clustered in the Rogue Valley, the southern end of the Umpqua Valley, and along the coast. High plot scores were in the mountainous areas of southwest and southern Oregon. Despite contributing 10% of TVE (Table 8) in the Klamath subregion, ultramafic parent materials were not important until the third CCA axis.

Eastern Cascades subregion.—In the eastern Cascades, axis 1 was most strongly correlated with overstory tree cover and precipitation (Fig. 6h). The axis was strongly dominated by high-scoring plots along the crest of the Cascade Range, especially near the Three Sisters and Mount Hood, which had dense canopies and high summer rainfall. Remaining, lower scoring plots were not well differentiated, but had sparser canopies, warmer and drier summers, and a higher proportion of total precipitation falling in summer (Fig. 6h), and were located throughout the mid- to low elevations of the subregion. Axis 2 correlated most strongly with elevation, high and low temperature extremes, and summer temperature. Lowest scores were in the Three Sisters and Paulina mountains, and the highest scores were in the extreme northern and southern portions of the subregion.

Blue Mountains subregion.—The dominant gradient in the Blue Mountains subregion reflected growing season conditions and overstory canopy cover (Fig. 6i). Plots with low scores on axis 1 had low summer moisture stress and dense canopies, primarily found at high elevations in the Wallowa and Blue Mountains. High plot scores were in low-elevation areas with low summer precipitation, high summer temperatures, and sparse canopies. Axis 2 was associated with elevation, summer climate, and topography. Low plot scores were in areas of low elevation, hot and dry summers, steep slopes, and low solar radiation, and were concentrated in canyons along the Snake River and in the Blue Mountains along the northern Oregon boundary. High scores were concentrated near the peaks of the Wallowa and Strawberry mountains, and in the southern portions of the Ochoco Mountains.

Associations of local and regional factors with species gradients

The relative contributions of explanatory variables to TVE in stepwise and partial CCA were influenced by geographic extent and location, and varied with the scale of the explanatory factor (Tables 8 and 9). Unfortunately, the statistical significance of TVE differences among CCA models cannot be tested, and thus interpretations of differences are somewhat subjective. In partial CCA, regional factors (climate and geology) accounted for more of the TVE (70-79%) than local factors (topography and disturbance) (10-20%) at all geographic locations and extents (Table 9). Local factors contributed less to TVE at the state (10%) than at the subregional scale (14-20%), whereas contributions of regional measures were comparatively strong at all geographic extents (Table 9). Contributions of local

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FIG. 7. Plot scores (linear combinations) from canonical correspondence analysis of all woody species, Oregon: (a) axis 1 (contour interval 0.07); (b) axis 2 (contour interval 0.3); (c) axis 3 (contour interval 0.15); (d) axis 4 (contour interval 0.2).

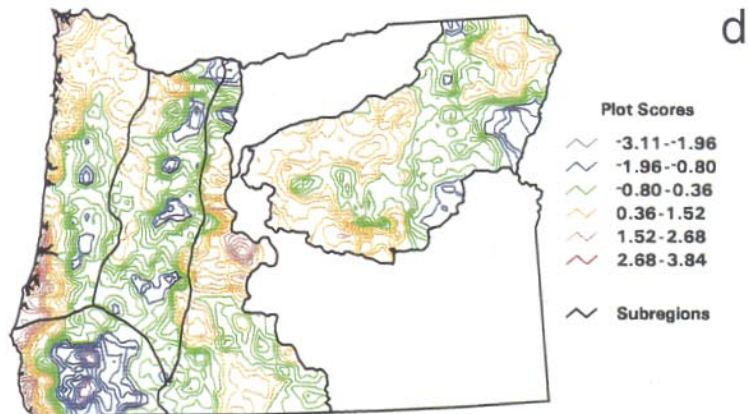
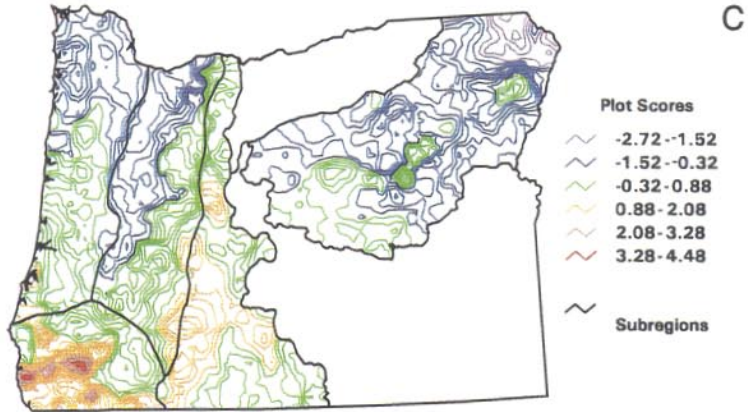
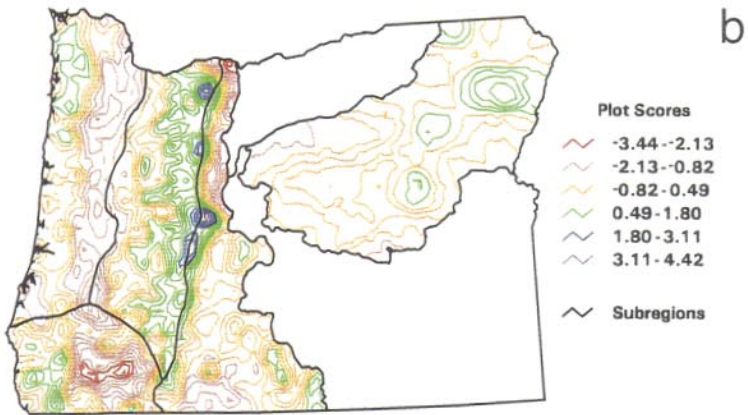
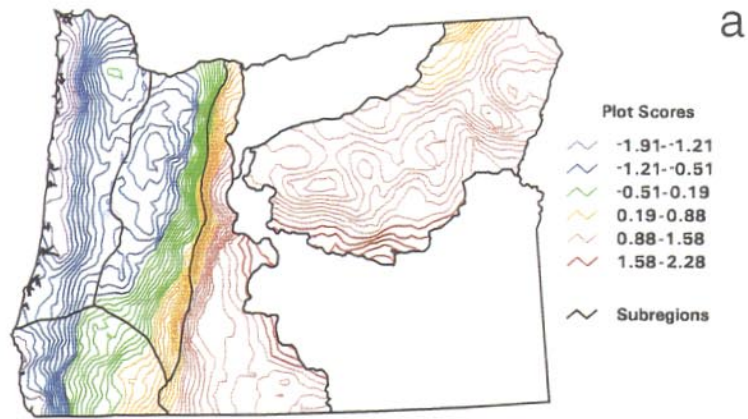


TABLE 8. Increases in total variation explained (TVE) by explanatory variables in stepwise canonical correspondence analysis of all woody species, by geographic area; the three greatest contributors to TVE in each geographic area are shown in boldface.†

Variable	Additional variation explained (proportion of TVE)							
	Half-state			Subregion				
	Oregon	Western Oregon	Eastern Oregon	Coast	Western Cascades	Klamath	Eastern Cascades	Blue Mountains
Topography								
<i>ASPECT</i>	‡	‡	‡	‡	‡	‡	‡	‡
<i>SLOPE</i>	0.05	0.05	0.06	0.03	0.08	0.03	0.09	0.12
<i>SOLAR</i>	0.01	0.02	0.02	‡	0.05	0.03	0.04	0.05
Disturbance								
<i>AGE</i>	0.02	0.02	0.03	‡	‡	0.04	0.07	0.04
<i>CLEARCUT</i>	0.02	0.02	‡	0.04	0.06	0.06	‡	‡
<i>TREOCOV</i>	0.04	0.03	0.11	0.06	0.05	0.05	0.20	0.16
Climate								
<i>ELEV</i>	0.28	0.23	0.15	0.04	0.37	0.19	0.17	0.07
<i>ANNPRE</i>	0.17	§	0.08	0.03	§	§	§	§
<i>WTRPRE</i>	§	§	§	§	§	0.23	§	§
<i>SMRPRE</i>	0.10	§	0.19	§	0.15	§	0.04	§
<i>CVPRE</i>	§	0.08	0.02	0.06	0.04	§	§	§
<i>CONTPRE</i>	§	0.02	§	0.03	‡	0.04	0.05	§
<i>SMRTSMRP</i>	0.03	0.17	§	0.28	§	§	§	0.27
<i>ANNTMP</i>	§	§	§	§	§	0.04	§	§
<i>MAXTMP</i>	0.03	0.03	0.03	0.13	§	0.03	0.04	‡
<i>MINTMP</i>	0.02	0.02	0.03	0.03	‡	0.04	0.06	‡
<i>WRTMP</i>	§	§	§	§	§	§	§	§
<i>SMRTMP</i>	§	0.05	0.06	§	0.04	§	0.11	0.15
<i>CVTMP</i>	0.06	0.06	0.05	0.18	0.04	0.05	0.08	‡
Geology								
<i>VOLC</i>	‡	‡	0.02	‡	‡	‡	‡	0.03
<i>SILR</i>	‡	‡	‡	‡	‡	‡	‡	‡
<i>MAFO</i>	0.01	‡	‡	‡	‡	‡	0.04	‡
<i>MAFY</i>	0.02	0.03	0.02	‡	0.04	‡	§	‡
<i>UMAF</i>	0.07	0.10	0.05	‡	‡	0.10	‡	0.06
<i>PYRO</i>	‡	‡	‡	‡	‡	‡	‡	‡
<i>PYRY</i>	0.01	0.03	‡	‡	0.09	‡	‡	‡
<i>SILV</i>	‡	‡	‡	‡	‡	‡	‡	‡
<i>METH</i>	‡	‡	‡	‡	‡	‡	‡	‡
<i>SEDR</i>	‡	‡	0.02	‡	‡	‡	‡	‡
<i>TUFO</i>	0.01	‡	‡	‡	‡	‡	§	‡
<i>TUFY</i>	0.02	‡	‡	‡	‡	‡	‡	0.05
<i>DEPO</i>	0.01	0.02	‡	0.08	‡	0.06	§	‡

† Increase in TVE is additional species variation explained by adding the variable after previously selected variables already are included, expressed as a proportion of TVE, and thus reflects selection order. Values are for variables included by forward selection ($P < 0.01$, where significance was determined by a Monte Carlo permutation test, H_0 : additional influence of variable on vegetation is not significantly different from random), and where adding the variable did not result in inflation factors > 20 .

‡ Variable was not significant in the stepwise procedure.

§ Variable was significant in the stepwise procedure but excluded because of multicollinearity.

factors to TVE were slightly greater (17%) in eastern Oregon, where climate is more stressful, than in western Oregon (10%). Although subregional differences were slight, local factors were least important in the Coast (14% of TVE) where climate is most maritime and benign, and most important in the Blue Mountains (20% of TVE) where climate is most continental and variable.

At all extents and locations, climate contributed far more to TVE (46-60%) in partial CCA than any other variable subset (Table 9). Climate was particularly important (60% of TVE) in the Coast subregion. Geologic variables were second to climate in total contributions

to TVE (11-19%) in all geographic areas. Disturbance (6-12%) and topography (4-8%) contributed least to TVE in our sample. The contributions of climate, geology, and disturbance variables were unrelated to geographic extent. Contributions of topographic variables to TVE increased very slightly with decreasing geographic extent, from 4% at the state scale to 5-8% at the subregion scale.

Geographic patterns of CCA model fit

Plot-score residuals from stepwise CCA illustrate geographic patterns of model fit (Fig. 9). High residuals were concentrated in locations that represented ends of

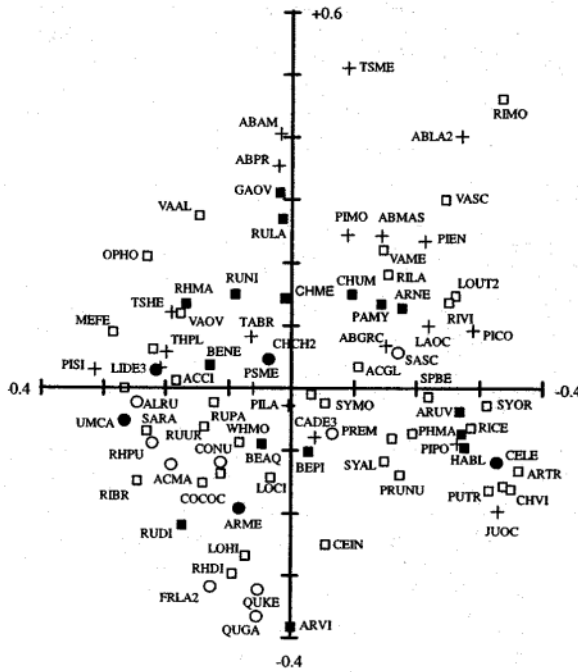


FIG. 8. Scatterplot of species scores on the first two axes from canonical correspondence analysis of all woody species, Oregon, showing species with =1% mass. Symbols indicate membership to growth forms: cross = coniferous tree; solid circle = evergreen broad-leaved tree; open circle = deciduous broad-leaved tree; solid square = evergreen broad-leaved shrub; open square = deciduous broad-leaved shrub. (One needle-leaved shrub, *Juniperus communis*, not shown.) Species codes are as follows: ABAM = *Abies amabilis*, ABGRC = *Abies grandis* or *Abies concolor*, ABLA2 = *Abies lasiocarpa*, ABMAS = *Abies magnifica* var *shastensis*, ABPR = *Abies procera*, ACCI = *Acer circinatum*, ACGL = *Acer glabrum*, ALMA = *Acer macrophyllum*, ALRU = *Alnus rubra*, ARME = *Arbutus menziesii*, ARNE = *Arctostaphylos nevadensis*, ARTR = *Artemisia tridentata*, ARUV = *Arctostaphylos uva-ursi*, ARVI = *Arctostaphylos viscida*, BEPI = *Berberis piperiana*, CADE3 = *Calocedrus decurrens*, CEIN = *Ceanothus integerrimus*, CELE = *Cercocarpus ledifolius*, CHME = *Chimaphila menziesii*, CHUM = *Chimaphila umbellata*, CHVI = *Chrysothamnus viscidiflorus*, COCOC = *Corylus cornuta* var. *cornuta*, FRLA2 = *Fraxinus latifolia*, GAOV = *Gaultheria ovatifolia*, HABL = *Haplopappus bloomeri*, JUOC = *Juniperus occidentalis*, LAOC = *Larix occidentalis*, LIDE3 = *Lithocarpus densiflorus*, LOCI = *Lonicera ciliosa*, LORI = *Lonicera hispidula*, MEFE = *Menziesia ferruginea*, OPHO = *Oplopanax horridum*, PAMY = *Paxistima myrsinites*, PHMA = *Physocarpus malvaceus*, PICO = *Pinus contorta*, PIEN = *Picea engelmannii*, PILA = *Pinus lambertiana*, PIMO = *Pinus monticola*, PIPO = *Pinus ponderosa*, PISI = *Picea sitchensis*, PREM = *Prunus emarginata*, PRUNU = *Prunus* spp., PSME = *Pseudotsuga menziesii*, PUTR = *Purshia tridentata*, QUGA = *Quercus garryana*, QUKE = *Quercus kelloggii*, RHDI = *Rhus diversiloba*, RHMA = *Rhododendron macrophyllum*, RHPU = *Rhamnus purshiana*, RIBR = *Ribes bracteosum*, RICE = *Ribes cereum*, RILA = *Ribes lacustre*, RIMO = *Ribes montigenum*, RIVI = *Ribes viscosissimum*, RUDI = *Rubus discolor*, RULA = *Rubus lasiococcus*, RUNI = *Rubus nivalis*, RUPA = *Rubus parviflorus*, RUUR = *Rubus ursinus*, SARA = *Sambucus racemosa*, SASC = *Salix scouleriana*, SPBE = *Spiraea betulifolia*, SYAL = *Symphoricarpos albus*, SYMO = *Symphoricarpos mollis*, SYOR = *Symphoricarpos oreophilus*, TSHE = *Tsuga heterophylla*, TSME = *Tsuga mertensiana*, UMCA = *Umbellularia californica*, VAAL = *Vaccinium alaskaense*, VAME = *Vaccinium membranaceum*, WHMO = *Whipplea modesta*.

the gradients of the first two CCA axes, where environmental features and community composition diverged most from regional norms. These areas included the foothills of the Willamette Valley west of Salem, the interior valleys of southwest Oregon, the coastal dunes north of Coos Bay, and subalpine areas of the Three Sisters and Wallowa mountains. Extensive areas of the state had large residual scores, as well as high among-plot variability in residual scores. The southern half of the Klamath subregion and most of eastern Oregon exhibited this “salt-and-pepper” pattern of residuals.

Spatial structure in regional gradients

Spatial position alone accounted for 7-15% of TVE (Table 10). Patterns in the relative contributions of spatial position and environment to TVE were more strongly associated with geographic location than with geographic extent. At broader geographic extents, spatial position explained only slightly more species variation, and environmental measures uncorrelated with spatial position explained slightly less, than at smaller extents (Table 10). Spatial position explained slightly more of the TVE in eastern Oregon (14%) and its subregions (11-14%) than in western Oregon (9%) and its subregions (7-9%) (Table 10). Environmental factors in the Coast and western Cascades subregions were more spatially structured (30-34% of TVE) than in the Klamath, eastern Cascades, and Blue Mountains subregions (17-24% of TVE). The subregions also differed somewhat in terms of proportions of TVE attributed to environmental measures uncorrelated with spatial position (E IS), with the Coast having the least and the Klamath the most.

Species diversity patterns

Alpha and gamma diversity were greater in western than in eastern Oregon (Table 11). Alpha diversity was greatest in the Klamath and western Cascades, lowest in the eastern Cascades and Blue Mountains, and intermediate in the Coast for both trees and shrubs. Gamma diversity was greatest in the Klamath subregion for both vegetation layers. Alpha, gamma, and beta diversity of the shrub layer were greater than for trees in all geographic areas. Beta diversity was greater in eastern than in western Oregon for both tree and shrub layers.

DISCUSSION

Environmental correlates of regional species gradients

Elevation.—Elevation contributed more to total variation explained (TVE) than any other variable (Table

←
 TSHE = *Tsuga heterophylla*, TSME = *Tsuga mertensiana*, UMCA = *Umbellularia californica*, VAAL = *Vaccinium alaskaense*, VAME = *Vaccinium membranaceum*, WHMO = *Whipplea modesta*.

TABLE 9. Proportion of total variation explained (TVE) by subsets of constraining variables in six partial canonical correspondence analyses (CCAs) of all woody species, by geographic area. Local variables include topography and disturbance variables, and regional variables include climate and geology variables (see Table 3 for subset affiliations of individual variables).

Constraining variables in partial CCA	Proportion of TVE not shared with covariables							
	Half-state			Subregion				
	Oregon	Western Oregon	Eastern Oregon	Coast	Western Cascades	Klamath	Eastern Cascades	Blue Mountains
Local	0.10	0.10	0.17	0.14	0.16	0.16	0.15	0.20
Regional	0.72	0.79	0.72	0.78	0.72	0.76	0.70	0.70
Topography	0.04	0.04	0.07	0.05	0.08	0.06	0.07	0.08
Disturbance	0.06	0.06	0.10	0.09	0.08	0.09	0.08	0.12
Climate	0.49	0.50	0.49	0.60	0.48	0.46	0.54	0.48
Geology	0.15	0.19	0.16	0.11	0.18	0.19	0.13	0.18

8). However, elevation is a complex-gradient (sensu Whittaker 1960, 1965) that covaries with a host of historical and environmental factors such as soil chemistry, amount and persistence of winter snowpack, and climate. In addition, in much of our dataset the elevation gradient was confounded with land ownership patterns and thus disturbance gradients. *ELEV* and *AGE* were moderately correlated in all geographic areas except for the Coast subregion (Table 12), but only in the western Oregon canonical correspondence analysis (CCA) model were these gradients collinear (Fig. 6). Elevation and clear-cutting were confounded in parts of the western half of the state, where even-aged forest management predominates. *ELEV* and *CLEARCUT* were moderately correlated (Table 12) and CCA gradients were collinear (Fig. 6) at the state scale, in western Oregon, and in the western Cascades and Klamath subregions. Our sample thus did not allow us to distinguish the effects of elevation from stand age in western Oregon, nor elevation from clear-cutting in Oregon, western Oregon, and in the western Cascades and Klamath subregions. *ELEV* contributed most to TVE in these geographic areas (Table 8), and some of this

explained variation could have been associated with the confounded disturbance variables. Nevertheless, the strong association between elevation and species composition we observed in our sample is consistent with other vegetation studies.

We debated excluding elevation from our analysis because it measures spatial position and only indirectly reflects physical environment. Excluding *ELEV* from stepwise CCAs, however, did not appreciably affect TVE, probably because of multicollinearity with other climate measures, nor the relations among species, plots, and explanatory variables. This robustness to multicollinearity among explanatory variables, as well as to omission of important explanatory variables, is a strength of CCA (Palmer 1993). We retained *ELEV* in our analyses because of its value in interpreting results.

Macroclimate.—Results supported our hypothesis of the primary importance of macroclimate and the secondary role of substrate (geology), topography, and disturbance in controlling regional compositional gradients in the predominantly mid- to late- successional forest communities we sampled (Tables 8 and 9). The minor degree of confounding of disturbance measures

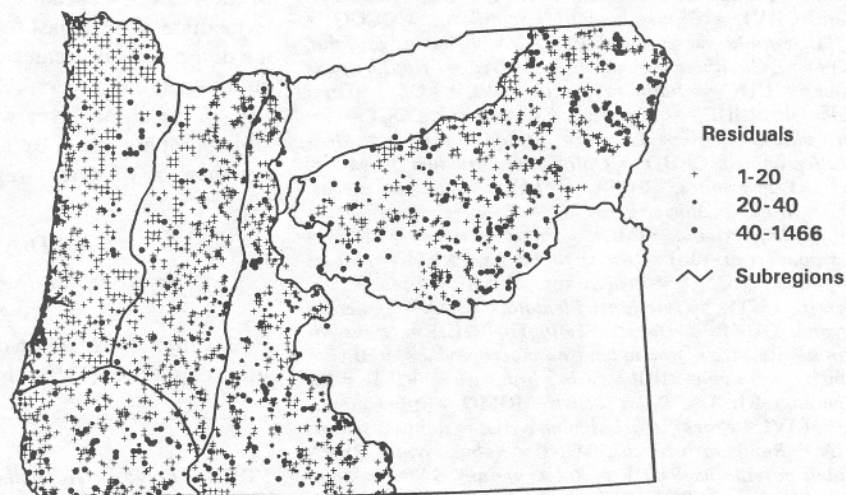


Fig. 9. Residual distances (squared chi-square distance between each plot and the centroid of all plots in m-dimensional species space [ter Braak 1987a]) from first four axes from canonical correspondence analysis of all woody species, Oregon.

TABLE 10. Proportion of total variation explained (TVE) by subsets of explanatory variables in canonical correspondence analyses with variance partitioning, all woody species, by geographic area. S = spatial variables; E = topography, disturbance, climate, and geology variables (see Table 3).

Geographic area	Proportion of TVE†		
	$S E$	$S \cap E$	$E S$
Oregon	0.15	0.30	0.55
Half-state			
Western Oregon	0.09	0.35	0.56
Eastern Oregon	0.14	0.22	0.64
Subregion			
Coast	0.09	0.34	0.57
Western Cascades	0.07	0.30	0.63
Klamath	0.07	0.18	0.75
Eastern Cascades	0.11	0.24	0.65
Blue Mountains	0.14	0.17	0.69

† $S|E$ is variation explained by S not shared with E , $S \cap E$ is variation explained by S that is correlated with E , and $E|S$ is variation explained by E not shared with S .

with climate, primarily with *MAXTMP* and *MINTMP* in the western half of the state, was insufficient to raise questions about the primary importance of climate overall.

Our findings cannot be compared directly with previous studies because of differences in methods. Most investigators considered broad-scale climate only indirectly, by studying vegetation change along complex-gradients of elevation or latitude, and none explicitly examined relative contributions of regional (macroclimatic) and local (microclimatic) measures of temperature and moisture. Most studies emphasized local topography as an indirect measure of moisture stress through solar heating and desiccation from wind exposure. Plant evapotranspiration stress (blaring 1969, Zobel et al. 1976) is the measure of direct interest, but it is impractical to measure in regional studies.

Seasonal variability and extremes in climate were more important in explaining species gradients than were mean annual climatic conditions. In addition, the two dominant species gradients at the state scale were associated with continentality and growing season moisture stress, climatic gradients that integrate elements of both temperature and moisture. The importance of continentality in our study was consistent with del Moral and Watson's (1978) study that spanned an east-west gradient across the Cascade Range, although our study spanned a much wider latitudinal range. Species gradients across Oregon were much more strongly associated with moisture stress during the characteristic warm, dry summers than with winter conditions. This association was consistent with observed correspondence between growing season precipitation and temperature gradients and latitudinal vegetation gradients in the Appalachians (Cogbill and White 1991), the southern Rockies (Allen et al. 1991), and the northern California uplands (Parker 1994).

Topographic factors.—Topographic measures contributed slightly more to TVE in areas of greater climatic stress (Tables 8 and 9), as hypothesized, although subregional differences were most apparent in the stepwise CCAs (Table 8) and rather insubstantial in the partial CCAs (Table 9). Local and topographic factors explained the least variation in partial CCA in the Coast (Table 9), where climate is most mild, maritime, and wet. The Coast was the only geographic area where neither *SOLAR* nor *ASPECT* were significant in a stepwise model (Table 8). In the Eastern Cascades and Blue Mountains, *SLOPE* and especially *TREOCOV* explained more species variation than in the western subregions (Table 8). *TREOCOV* probably reflects a complex-gradient of disturbance, microsite environment, large-scale climate, net primary productivity, and other factors. However, we think the variable most strongly

TABLE 11. Alpha diversity (mean plot-scale species richness, $\bar{\alpha}$), gamma diversity (total species, S), and beta diversity ($\beta_w = [S/\bar{\alpha}] - 1$), and total variation (TV) from canonical correspondence analysis), by geographic area and vegetation layer. Alpha diversity differed significantly ($P < 0.01$) between half-states and among subregions for all vegetation layers.

Geographic area and vegetation layer	$\bar{\alpha}$	S	Beta diversity	
			β_w	TV
Oregon				
Woody	8.1	192	22.7	24.3
Trees	3.4	51	14.0	14.1
Shrubs	4.7	141	29.0	32.7
Half-state				
Western Oregon				
Woody	10.1	158	14.6	15.5
Trees	4.1	46	10.2	10.1
Shrubs	6.0	112	18.0	19.1
Eastern Oregon				
Woody	6.0	130	20.7	18.5
Trees	2.6	37	13.2	10.3
Shrubs	3.4	93	26.4	25.7
Subregion				
Coast				
Woody	8.5	97	10.4	9.7
Trees	3.3	28	7.5	6.6
Shrubs	5.2	69	12.3	11.1
Western Cascades				
Woody	10.8	119	10.4	9.3
Trees	4.5	34	6.6	6.0
Shrubs	6.4	85	12.3	12.2
Klamath				
Woody	11.3	124	10.0	10.6
Trees	4.7	37	6.9	7.4
Shrubs	6.6	87	12.2	13.2
Eastern Cascades				
Woody	5.9	99	15.8	12.6
Trees	2.7	30	10.1	7.1
Shrubs	3.2	69	20.6	18.7
Blue Mountains				
Woody	6.0	94	14.7	15.6
Trees	2.6	24	8.2	7.8
Shrubs	3.4	70	19.6	20.2

TABLE 12. Spearman's rank correlations of disturbance variables with elevation for 2443 field plots, by geographic area.

Geographic area	Spearman's rank correlation with <i>ELEV</i>	
	<i>AGE</i>	<i>CLEARCUT</i>
Oregon	0.40†	-0.42‡
Half-state		
Western Oregon	0.53‡	-0.38‡
Eastern Oregon	0.32†	-0.09§
Subregion		
Coast	-0.06§	0.05†
Western Cascades	0.49§	-0.41‡
Klamath	0.31†	-0.38‡
Eastern Cascades	0.41†	-0.06§
Blue Mountains	0.26†	-0.13§

† Variable included in stepwise model, not collinear with *ELEV* on axes 1 and 2 (see Fig. 6).

‡ Variable included in stepwise model, collinear with *ELEV* on axes 1 and 2 (see Fig. 6).

§ Variable not included in stepwise model, not collinear with *ELEV* on axes 1 and 2.

indicates local topographic moisture, and our grouping of *TREOCOV* with the disturbance variables in partial CCA may have obscured subregional differences in topographic effects. Water availability strongly influences leaf area index (LAI) in northwestern coniferous forests (Grier and Running 1977, Waring et al. 1978, Gholz 1982), and LAI probably is strongly correlated with our measure of canopy cover. In fact, *TREOCOV* may have better integrated microtopography, soils, and large-scale climatic factors that influence actual site moisture availability to plants than did *SOLAR* or *SLOPE*.

Our findings were consistent with Del Moral and Watson (1978), who found that topography more profoundly differentiated community composition on the eastern than on the western slopes of the Washington Cascades. They also attributed major contrasts in community structure between eastern and western Washington to variation in overstory dominance, an indirect expression of climatic and topographic moisture gradients. In eastern Oregon, moisture is more limiting and temperatures are colder and more variable, topography is often deeply dissected, and topographic effects would be expected to be more pronounced (del Moral and Watson 1978, Neilson et al. 1992).

In general, other gradient studies appear to emphasize greater topographic control over vegetation pattern than we observed in our study, probably because most addressed smaller geographic extents or prestratified their study areas by elevation or substrate before examining topographic effects (e.g., Whittaker 1960, Peet 1978, 1981, Allen and Peet 1990, Allen et al. 1991). Where as aspect and topographic position have been emphasized in other studies, slope accounted for more TVE than aspect or solar radiation in our study (Table 8). Inferring mechanisms is difficult, however, because

slope integrates many hydrological and geomorphic processes such as soil formation and movement (Swanson et al. 1988), seepage, shading, and snow movement. Flat sites are more likely to have deep, moist soils, although low slopes also can occur on dry, rocky ridgetops. Steep sites are more likely to be dry with shallow, rocky soils.

Disturbance.—Our findings on the influence of disturbance on regional species gradients were inconclusive for most geographic areas due to confounding of our explanatory variables, especially *CLEARCUT* with *ELEV* (Table 12). In western Oregon, where even-aged management predominates, the clear-cutting and elevation gradients were strongly collinear at the half-state scale and in the western Cascades and Klamath subregions (Table 12, Fig. 6). This confounding influenced the state-level analysis as well. *CLEARCUT* was not significant in eastern Oregon (Table 8), where selective harvesting is most commonly practiced and very few of our plots had been clear-cut (Fig. 4). The confounding of explanatory variables was due primarily to the non-random geographic distribution of federal and nonfederal land ownerships across Oregon's major environmental gradients, which was reflected in our sample of field plots. The systematic grid of FIA plots provided an unbiased sample of nonfederal lands, but these forests occur at lower elevations and are younger (Fig. 5) and more heavily disturbed by logging (Fig. 4) than federal lands. National Forest lands occur at higher elevations and the Ecology plots were almost all from older, natural stands (Figs. 4 and 5). The BLM lands span a range of ages and elevations, but the FIR plots were restricted to older stands in southwest Oregon.

Disturbance and elevation were not confounded in the Coast subregion: *AGE* and *CLEARCUT* were uncorrelated with *ELEV* (Table 12) and gradients were not collinear (Fig. 6e). The Coast was the only subregion where private lands predominated (70% of the plots vs. 23-28% elsewhere), and where the mean elevations of federal and nonfederal plots did not differ. Clear-cutting was not strongly correlated with any of the first four CCA axes in the Coast. In partial CCA, only 2% of TVE was associated with *CLEARCUT* and uncorrelated with the other variables. Stand age was not significant in stepwise CCA (Table 8), and accounted for only 1% of TVE in partial CCA.

We attribute the small contribution of disturbance measures to explained species variation in the Coast to several factors. First, species presence-absence strongly influences regional-scale ordinations, where gradients are long and species constancy is low. Existing studies suggest that disturbance influences the relative abundances of species within a local area, but that few species are totally eliminated from a site by disturbance in general or by logging in particular (Ohmann and Bolsinger 1991, Ramey-Gassert and Runkle 1992, Halpern and Spies 1995). Furthermore, most early invaders on disturbed sites are herbaceous (Halpern and Spies

1995) and were not included in our study. In addition, the ubiquity of several long-lived, early-seral, shade-intolerant tree species in Oregon (e.g., *Pseudotsuga menziesii*) probably obscured some successional patterns in our analyses. Nevertheless, our findings in the Coast are consistent with Spies (1991) and Spies and Franklin (1991), who found that ecological differences among physiographic provinces were more important than stand age in explaining regional patterns of community composition in *Pseudotsuga menziesii* forests. Our finding in the Coast of the secondary association of disturbance factors with regional species gradients should not be confused with demonstrated effects of disturbance on other measures of biological diversity in forest ecosystems, such as vegetation structure and wildlife diversity (Hansen et al. 1991).

Across most of our Oregon study area, the confounding of explanatory variables prevented us from determining whether species gradients were influenced by elevation or by clear-cutting, or by both. In an ideal sample, field plots would be balanced across the multivariate and geographic space defined by stand age, disturbance history, and physical environment. However, very little of today's forest landscape at any elevation is in early-successional, natural forest (Hansen et al. 1991), and late-successional forests at low elevations are virtually nonexistent. Quantification of the role of disturbance relative to other environmental factors in controlling compositional gradients may be intractable using gradient analytical or other methods in regions where land ownership patterns and associated disturbance histories are confounded with environmental gradients. Chronosequence and experimental studies would be similarly challenged by the lack of available stands across the various gradients for sampling or treatment. Ultimately, research on disturbance and successional patterns needs to be based on longterm remeasurement of permanent plots from a design that is balanced across major disturbance and environmental gradients.

Geology.—More geologic variables were significant in stepwise CCA at broader geographic extents (Table 8), but overall contributions of geology to TVE were unrelated to geographic extent (Table 9). Four of the 14 geologic types were most strongly correlated with species gradients in stepwise CCA: ultramafic rock; mafic rock of the Pliocene and later; mafic pyroclastic rock, ash, ejecta, and vent deposits of the Pliocene and later; and depositional materials (Table 8, Fig. 6). However, multicollinearity between geologic and climatic variables precluded firm conclusions about associations of specific geologic types with species gradients in much of Oregon. Additional study is needed to separate effects of climate and geology, and to determine which properties of the parent materials influence community composition.

Geographic variation in environmental correlates of species gradients

The contrast in species-environment associations among geographic subregions was an important finding of our study. Despite the strong contrasts among subregions, we were able to synthesize patterns of vegetation and environment at the regional scale. Apparent contradictions in findings among landscape-scale vegetation studies thus can be attributed to real differences in species and ecological relations among places. Nevertheless, within-region variation in the environmental associations of species gradients in our study must be interpreted carefully, due to confounding of some of the explanatory variables in some geographic areas in our sample. In particular, disturbance gradients were confounded with elevation at the state level, in western Oregon, and in the western Cascades and Klamath subregions.

The greatest contrast in Oregon's forest vegetation was between the maritime, moist climate of the Coast and western Cascades and the drier, continental climate of the eastern Cascades and Blue Mountains. The Klamath subregion was intermediate in character, reflecting the subregion's central nature to forest flora of the western United States from both historical and climate perspectives (Whittaker 1960). Chief among the within-region differences was the greater importance of moisture in explaining species variation in eastern Oregon. Continentality measures (*CVPRE*, *CONTPRE*, *MINTMP*, *CVTMP*) were more important in explaining compositional gradients in western Oregon, especially in the Coast subregion, than in eastern Oregon (Table 8, Fig. 6). Western Oregon encompasses the influence of the Pacific Ocean, and the orographic effects of the Coast Range with the Willamette Valley in its rain shadow. Indeed, the influence of climate in general was especially strong in the Coast subregion, where elevation, temperature, and precipitation variables contributed 60% of TVE in CCA with variance partitioning (Table 9), and 78% of TVE in stepwise CCA (Table 8). The observed shifts in environmental correlates with geographic location also corroborated relations between major forest zones and primary environmental constraints hypothesized by Franklin and Dyrness (1973:50).

In general, vegetation was more complex and spatial pattern was finer grained in eastern than in western Oregon. Beta diversity was greater in eastern Oregon for both tree and shrub layers (Table 11), as was similarly observed by del Moral and Watson (1978), and more species were rare (Fig. 10). This finer scale pattern of variation in vegetation in eastern Oregon was corroborated in the geographic pattern of residuals (Fig. 9) and by the greater contribution of local measures of slope and canopy cover to explained variation (Table 8). In contrast to other studies (e.g., Whittaker 1960, del Moral and Watson 1978), however, our results

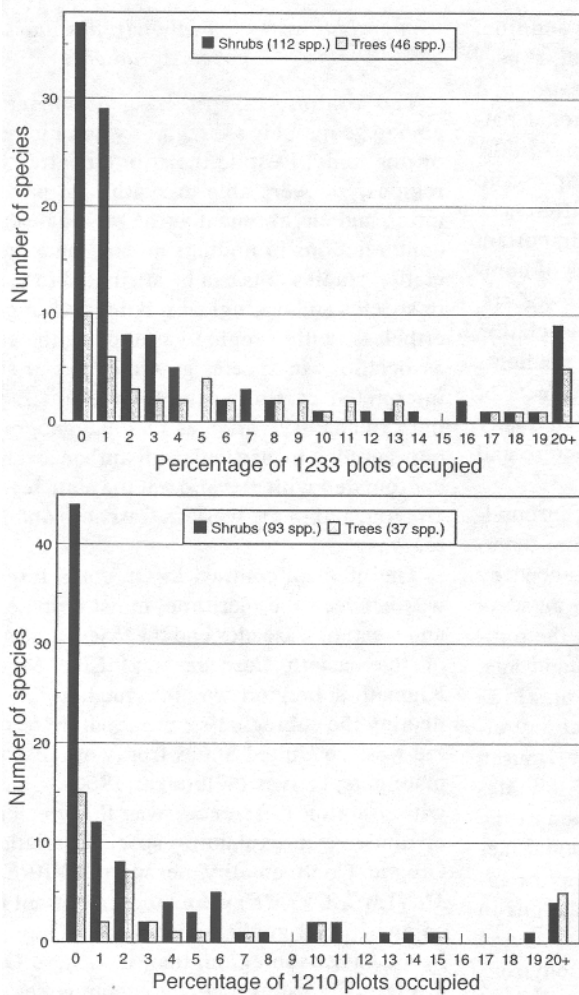


FIG. 10. Frequency of tree and shrub species by constancy (percentage of plots occupied) in western (top) and eastern (bottom) Oregon.

showed that alpha and gamma diversity were greater in western than in eastern Oregon (Table 11), probably because we excluded the species-rich herbaceous layer. In addition, we sampled a much longer latitudinal gradient than did del Moral and Watson, and western Oregon is hotter and drier than western Washington.

Collectively, our results supported the notion that where regional climate is more stressful for plant life—overly cold, hot, or dry—species respond to smaller scale variations in substrate, topography, and biotic interactions (Neilson et al. 1992). However, these fine-scale factors were poorly captured by our explanatory variables. Vast portions of the mid-elevation Coast and Cascade ranges, where the CCA model performed well more consistently (Fig. 9), are within the core of the biome where climate is benign and most fine-scale resource variation is within a given species' range of tolerance (Neilson et al. 1992). In these areas the CCA models, weighted heavily toward regional climate variables, performed better than at the periphery. Gradient

methods yield lower TVEs (Table 6), and presumably larger residuals, under conditions of high beta diversity such as we encountered in eastern Oregon.

Sampling effects and unexplained variation in CCA

Several characteristics of CCA and our data affected our levels of explained variation and interpretation of results. Chief among these was the confounding of TVE with sample size (numbers of plots and species) (Table 6). We propose the following mechanism behind the sample-size effect. Greater numbers of plots sample increasing numbers of species as more rare species are encountered. Rare species are those with small geographic ranges, narrow habitat specificity, or small, nondominant population sizes (Rabinowitz 1981). The rare species increase total variation in the species-by-plot data matrix, but their presence is unlikely to be explained by environmental variables, and TVE thus decreases. The species-area relation and the positive relation between species distribution and abundance account for this sampling effect (Hanski et al. 1993). Current models of regional species distribution (Levins 1969, Brown 1984, Collins and Glenn 1991, Brown 1995) predict that most species are locally distributed and regionally rare. Studies of vegetation (Whittaker 1960, del Moral and Watson 1978) and other taxa have shown that species with more extensive distributions tend to be more locally abundant than species with more restricted distributions (Hanski et al. 1993). Because locally rare species are more difficult to detect than locally abundant species, the number of sites at which a species is found with some fixed scheme of sampling is a monotonically increasing function of the average abundance of the species (Hanski et al. 1993). The shapes of our species frequency distributions were consistent with these models (Fig. 10). Species rarity also increased with geographic extent in our study: at the subregion scale, 28–44% of species had constancies of < 1%, but 50% of species were this rare at the state scale.

The sample-size effect limited our ability to compare CCAs among geographic extents and locations with different sample sizes, led us to present TVEs as proportions rather than actual amounts, and led us to emphasize the direction rather than magnitude of TVE differences. The sample-size effect also calls into question the comparison of TVEs among studies. Our TVEs fell on the low end of the 10–50% range that is typical of gradient analyses (Gauch 1982, Palmer 1993), but this may be attributable to our substantially longer gradients and sample sizes. Sampling issues as they pertain to CCA merit further investigation, especially in regional studies of long gradients.

Several aspects of our sample design and data contributed to our unexplained variation and limited our conclusions. Of primary importance was the confounding of land ownership patterns, and associated disturbance histories, with major environmental gradients in

Oregon. Also, our estimates of species diversity were influenced by sample size (number of plots) and plot size (Magurran 1988) to an unknown degree (Table 11). Diversity comparisons also were complicated by the different areal extents of the subregions. Other sampling effects and sources of error can be attributed to the scale of the field plots (plot size) relative to the spatial resolution of the explanatory variables, misregistration of the plot locations to the mapped explanatory variables, errors in the climate models and other mapped data, and errors in the field-recorded data. Although our purpose was to infer regional-scale pattern, observations of community composition were from plots of predetermined size, shape, and distribution. These traits varied among the component data sets (Table 2), but we had no reason to suspect the differences would bias our results. Plot size was not associated with CCA axes 1-4 in any geographic area.

We doubt that sampling or data quality had any substantive effects on our overall findings, other than limiting conclusions about clear-cutting associations with regional species gradients to the Coast subregion. The indirect gradient analyses corroborated conclusions from the direct gradient analyses on the important environmental controls of regional species gradients. The species variation explained by spatial position that was uncorrelated with environmental measures (Table 10) can be considered a synthetic descriptor of unmeasured underlying processes (Borcard et al. 1992). Our results suggested that omitted explanatory factors were potentially most important in eastern Oregon and to a lesser degree at broader geographic extents (Table 10). In the drier habitats of eastern Oregon, measures of fine-scale environment such as understory light and moisture conditions probably would explain additional variation. At the state scale, unmeasured historical factors such as evolutionary processes and species dispersal and migration probably contributed to spatial pattern in the species data. Future advances in the spatial representation of environmental measures thought to control regional species gradients, and advances in the understanding of sampling issues as they pertain to CCA, will improve regional gradient analyses.

CONCLUSIONS

Our study was the first systematic quantification, synthesis, and mapping of vegetation-environment gradients across a large, contiguous region of the western United States based on field plot data. The study examined associations of both local- and regional-scale environmental factors with regional species gradients across forest land of all land ownerships. Regional patterns of variation in species composition were complex and multidimensional. Environmental correlates of species gradients, species diversity patterns, and the spatial patterning of plant communities varied with geographic extent and location.

Our findings supported a conceptual model of mul-

tiscaled controls on vegetation distribution, and the related notion that local community structure is the result of both regional- and local-scale processes. Broad-scale climate was the primary control on regional species gradients: climatic factors were the strongest associates of community gradients across the range of geographic extents we examined. At the state scale, the two dominant gradients reflected climatic regimes that integrate temperature and moisture factors: continentality and moisture stress during the growing season. Geology, topography, and disturbance factors were secondary in explaining species variation across all of our geographic extents and locations. Local topographic factors (slope and tree canopy cover, an indirect measure of site moisture) explained slightly more variation at smaller geographic extents and in areas of less equable climate. Spatial structure in our species data that was uncorrelated with explanatory variables suggested that fine-scale understory environment and unmeasured historical factors may have influenced present-day community patterns.

Our gradient study was the first to examine associations between human disturbance and species gradients using plot data at the regional scale. However, the confounding of land ownership patterns and their associated disturbance histories with elevation gradients across much of Oregon, and in our sample, rendered our findings inconclusive in all but the Coast subregion. In the Coast, clear-cutting accounted for only 2% of explained variation in partial canonical correspondence analysis (CCA). Stand age was not significant in stepwise CCA, and accounted for only 1% of explained variation in partial CCA. Ordinations of long, regional gradients are influenced more by species presence than by abundance, and few woody species are totally eliminated or introduced to sites by clear-cutting. Quantifying the role of disturbance in regional species gradients may be intractable in regions where geographic patterns of ownership and environment are confounded. Further research on successional patterns should be based on long-term remeasurement of permanent plots from a design that is balanced across regional disturbance and environmental gradients.

Within Oregon and for the range of geographic extents we examined, variation in environmental correlates of species gradients was more strongly associated with geographic location than with geographic extent. The most striking contrast in vegetation within our region was between the wet, maritime climate of the Coast and western Cascades subregions in northwest Oregon, and the dry, variable, continental climate of eastern Oregon. The Klamath subregion was intermediate in character. Our environmental measures, which were heavily weighted to climate, more successfully explained patterns of community composition in western than in eastern Oregon. In the benign climate of western Oregon, topographic effects were minimal and geographic patterns of variation in gradients were

coarse grained. In the drier and less equable climate of eastern Oregon, both climatic and topographic moisture were substantially more important in explaining compositional gradients, local measures of slope and tree canopy cover assumed greater importance, beta diversity was greater, more species were rare, and geographic patterns of variation in community composition and environment were more fine grained.

Despite strong ecological contrasts within the region, we were able to synthesize species-environment relations at the regional scale. These findings suggested that apparent conflicts among local vegetation studies can be explained by real ecological differences among places. Indeed, our regional study provides a broader context for considering gradient and classification studies conducted at smaller, landscape scales within the region.

We demonstrated the tremendous potential for quantifying and mapping regional ecological patterns through multivariate and geographic analysis of large plot-scale data sets and geographic data. Regional gradient studies can provide the quantitative, ecological basis for stratifying regions into relatively homogeneous subregions for finer scale modeling and analysis, as well as for developing regional strategies for conserving biological diversity, for predicting and planning for the effects of global climate change, and for the inventory and monitoring of forest vegetation at broad geographic scales. Although there are several important limitations to direct gradient analyses based on regional, plot-scale databases, such findings provide a strong quantitative and empirical basis for generating hypotheses about regional ecological pattern and process for further study with complementary approaches, such as regional experiments, retrospective studies, and paleoecological studies.

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