

INFLUENCE OF ENVIRONMENT, DISTURBANCE, AND OWNERSHIP ON FOREST VEGETATION OF COASTAL OREGON

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Abstract. Information about how vegetation composition and structure vary quantitatively and spatially with physical environment, disturbance history, and land ownership is fundamental to regional conservation planning. However, current knowledge about patterns of vegetation variability across large regions that is spatially explicit (i.e., mapped) tends to be general and qualitative. We used spatial predictions from gradient models to examine the influence of environment, disturbance, and ownership on patterns of forest vegetation biodiversity across a large forested region, the 3-million-ha Oregon Coast Range (USA). Gradients in tree species composition were strongly associated with environment, especially climate, and insensitive to disturbance, probably because many dominant tree species are long-lived and persist throughout forest succession. In contrast, forest structure was strongly correlated with disturbance and only weakly with environmental gradients. Although forest structure differed among ownerships, differences were blurred by the presence of legacy trees that originated prior to current forest management regimes. Our multi-ownership perspective revealed biodiversity concerns and benefits not readily visible in single-ownership analyses, and all ownerships contributed to regional biodiversity values. Federal lands provided most of the late-successional and old-growth forest. State lands contained a range of forest ages and structures, including diverse young forest, abundant legacy dead wood, and much of the high-elevation true fir forest. Nonindustrial private lands provided diverse young forest and the greatest abundance of hardwood trees, including almost all of the foothill oak woodlands. Forest industry lands encompassed much early-successional forest, most of the mixed hardwood-conifer forest, and large amounts of legacy down wood. The detailed tree- and species-level data in the maps revealed regional trends that would be masked in traditional coarse-filter assessment. Although abundant, most early-successional forests originated after timber harvest and lacked legacy live and dead trees important as habitat and for other ecological functions. Many large-conifer forests that might be classified as old growth using a generalized forest cover map lacked structural features of old growth such as multilayered canopies or dead wood. Our findings suggest that regional conservation planning include all ownerships and land allocations, as well as fine-scale elements of vegetation composition and structure.

Key words: biodiversity indicators; disturbance effects; down wood; forest ownership; gradient analysis; hardwoods; land cover change; legacy trees; old growth; predictive vegetation mapping; regional conservation planning; snags.

INTRODUCTION

The conservation of biodiversity—the variety of life in an area—is globally recognized as a fundamental component of ecologically sustainable forest management (Santiago Declaration 1995). At broad geographic scales, distributions of ecological communities and patterns of land ownership and use are important considerations in conservation planning. Information about how vegetation composition and structure vary

quantitatively and spatially with land ownership and allocation, disturbance history, and physical environment is needed to assess current biodiversity distributions and to evaluate potential effects of land management policies on biodiversity.

At the bioregional scale, ownership patterns explain much of the variation in land management practices, current patterns of vegetation cover types, and trajectories of land cover change (Turner et al. 1996, Radeloff et al. 2001, Cohen et al. 2002, Stanfield et al. 2002, Black et al. 2003, Wimberly and Ohmann 2004). However, the unique contributions of different ownerships, especially private lands, to biodiversity values have rarely been explicitly examined in regional assessments (but see Crow et al. 1999, Lovett-Doust and Kuntz 2001).

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Applications of gap analysis, which uses GIS to assess the degree to which natural community types are represented in reserves (Burley 1988, Scott et al. 1993), thus far have not considered private lands. In most forested regions, seminatural managed forests comprise the predominant matrix in which reserves are embedded; these forests can contribute substantially to regional biodiversity while simultaneously producing commodity values (Noss and Harris 1986, Hunter 1991, Lindenmayer and Franklin 2002).

In addition, at regional and broader scales, biodiversity assessments have employed coarse-filter approaches (Nature Conservancy 1982) focused on plant communities that are broadly defined by dominant tree species or successional status, complemented by fine-filter approaches for Threatened or Endangered species. Broad-scale analyses have not considered within-community variability in species composition (Hunter 1991), nor structural elements such as canopy layering, dead wood, or large remnant trees. These fine-scale features of vegetation provide wildlife habitat and other ecological functions and can be viewed as structure-based biodiversity indicators (Lindenmayer et al. 2000). Because these vegetation elements are sensitive to many silvicultural practices, they are an important consideration in assessing the cumulative effects of forest management on biodiversity at the regional level. The failure of broad-scale biodiversity assessments to explicitly consider more detailed attributes of vegetation can be attributed simply to a lack of relevant vegetation data at this scale (Margules et al. 1994). Regional assessments have relied primarily on maps of vegetation cover types derived from satellite imagery. Consequently, although sample-based inventories provide detailed and quantitative information about the distribution of vegetation variability across large regions, current knowledge that is spatially explicit (i.e., mapped) tends to be general and qualitative.

To address these information needs, we undertook a study to quantify how vegetation composition and structure vary across a large, multi-ownership region, in response to environmental and disturbance factors. Specific objectives were to (1) quantify environmental and disturbance factors associated with regional-scale variation in vegetation; (2) determine the role of land ownership and forest management practices in explaining regional variation; (3) explore whether species composition and structural elements of vegetation respond similarly to environmental and disturbance factors; and (4) consider implications of our findings for biodiversity assessment and conservation planning. To address these objectives, we conducted several analyses of detailed maps of current (1996) and potential vegetation of the coastal province of Oregon. The vegetation maps were developed using the Gradient Nearest Neighbor (GNN) method for predictive vegetation mapping, which is described in detail in Ohmann and Gregory (2002). Our previous paper (Ohmann and

Gregory 2002) focuses primarily on the GNN method and presents little in the way of ecological interpretation. The current paper, building on the earlier work, presents more detailed, quantitative analyses of regional vegetation patterns based on the GNN maps, and particularly on the influence of land ownership and disturbance history on vegetation composition and structure.

The GNN-based maps contain unprecedented thematic and spatial detail on forest composition and structure at the tree and stand level, while encompassing a regional scale. We frame our analyses around selected vegetation attributes that represent both species- and structure-based measures of biodiversity. These attributes are of particular conservation interest in our region. Specifically, we describe regional gradients in species composition and potential vegetation types (Daubenmire 1968); stages of forest development, especially early- and late-successional forest; and tree-level elements, including large live and dead remnant trees and hardwoods. Whereas late-successional forest has been the focus of most policy attention in our region, the loss of structurally diverse young forest also is of concern (Hansen et al. 1991). Large live and dead remnant trees, or legacy trees, provide habitat and other ecological functions in younger forest (Neitlich and McCune 1997, Lindenmayer and Franklin 2002). The ecological roles of large dead wood in Pacific Northwest forests have been especially well documented (Harmon et al. 1986, Spies et al. 1988, Rose et al. 2001). Hardwood tree species provide important biodiversity values in the region's conifer-dominated forests (Neitlich and McCune 1997). Although our analyses focus on the forested portion of the coastal province of Oregon, many of our findings can be generalized to other regions, and our analytical approach is widely applicable to biodiversity assessments in general.

METHODS

Study area

The Oregon Coast Range encompasses ~29 000 km², about 80% of which is forested (Fig. 1). Elevations range from sea level to over 1000 m. The terrain is highly dissected, with steep slopes and high stream densities. Soils are predominantly well-drained Andisols and Inceptisols derived from a variety of parent materials, including marine sandstones and shales and basaltic volcanics. The overall climate is maritime, with mild wet winters and cool dry summers, but it varies geographically with proximity to the ocean, latitude, and orographic effects.

Gradients in woody plant species composition are associated primarily with a coastal-to-interior climatic gradient (Ohmann and Spies 1998). The temperate forests are dominated by coniferous trees, predominantly Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don), with Sitka spruce (*Picea sitchensis* (Bong.) Carr.)

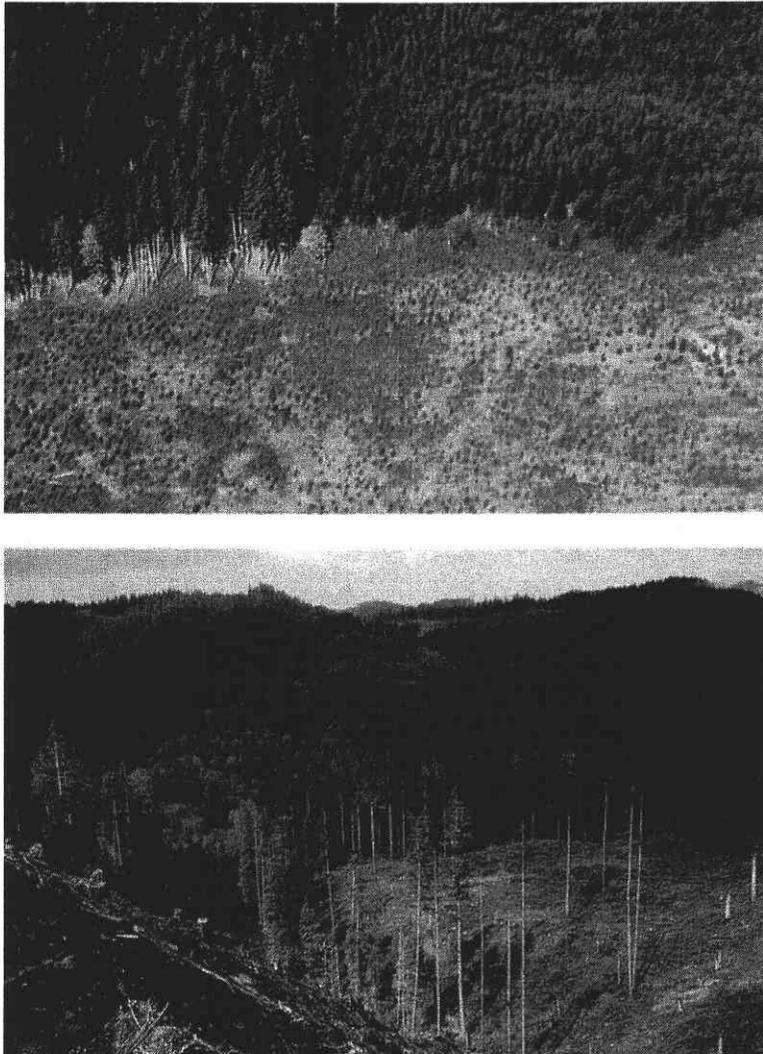


PLATE 1. Disturbance processes and physical environment interact to form complex patterns of forest vegetation in coastal Oregon (USA) landscapes. Forest management practices differ among land ownerships and can result in strong contrasts in forest condition. (Top) Forests managed intensively for wood production (foreground) typically lack structural diversity provided by large live and dead legacy trees from harvested stands. (Bottom) In some managed forests, legacy trees are retained during harvest operations to provide structural diversity and habitat. Hardwoods, another source of diversity in coastal forests, occur primarily in riparian areas, on disturbed sites (far hillside), or in oak woodlands along the margins of the Willamette Valley. Photo credits: T. Spies.

prevalent near the coast and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) common in the Willamette Valley foothills. Hardwoods, especially red alder (*Alnus rubra* Bong.) and bigleaf maple (*Acer macrophyllum* Pursh), often dominate recently disturbed sites and riparian areas, and Oregon white oak (*Quercus garryana* Dougl. ex Hook.) is common near the Willamette Valley.

Forest management activities and fire suppression characterize current disturbance regimes in coastal Oregon forests (Cohen et al. 2002), although influences of historical wildfires are still visible (Impara 1997, Wimberly and Spies 2001). Forest management and vegetation conditions differ among the major ownerships in the region (see Plate 1, Fig. 1; Cohen et al. 2002,

Wimberly and Ohmann 2004, Johnson et al. 2007). Federal forests are managed under the Northwest Forest Plan, aimed at conserving late-successional forests and associated species (Forest Ecosystem Management Assessment Team 1993), and contain a mix of old and young forest. National Forests retain patterns created by decades of small harvest units staggered across the landscape, and much of the Bureau of Land Management (BLM) ownership occurs in a checkerboard pattern with private lands. State lands are managed for multiple timber, wildlife, aquatic, and recreation objectives. Forest industry lands occur in large blocks throughout the study area; these lands are intensively managed for timber production. Nonindustrial private forests are concentrated in the large river valleys and are managed

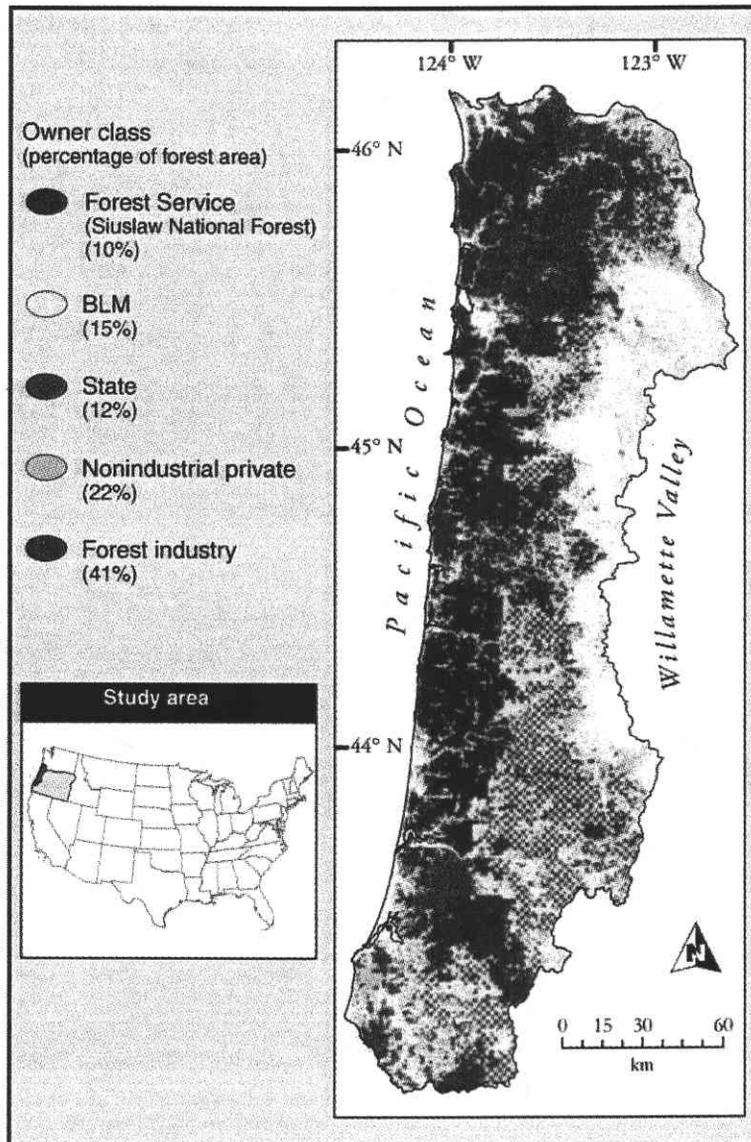


FIG. 1. Distribution of owner classes for forest land in the coastal Oregon study area (nonindustrial private subsumes small amounts of county, municipal, and tribal lands, national wildlife refuges and grasslands, and military lands).

less intensively for timber than industrial forests. Virtually all private forests have been harvested at least once and are less than 80 years old (unpublished Forest Inventory and Analysis [FIA] data).

Maps of vegetation composition and structure

We used vegetation maps developed with the Gradient Nearest Neighbor (GNN) method, which is described in detail in Ohmann and Gregory (2002). Briefly, the GNN method applies direct gradient analysis (canonical correspondence analysis [CCA]; ter Braak and Prentice 1988), and nearest-neighbor imputation (Van Deusen 1997) to ascribe detailed ground attributes of vegetation to each pixel or patch in a regional landscape. A multivariate gradient model

quantifies relations between ground and mapped data (rasters of explanatory variables) for the plot locations. For each mapped pixel, scores on the CCA axes are then calculated by applying model coefficients to the mapped explanatory variables. Measured and derived vegetation attributes of the ground plot that is nearest in multi-dimensional gradient space are then imputed to the pixel, and maps can be constructed for any of the vegetation attributes.

We constructed two CCA gradient models using the program CANOCO, version 4.5 (ter Braak and Smlauer 2002): one whose multivariate response variables were tree species ("species model") and one based on a combination of forest structure and species composition ("structure model"). Vegetation data used in model

TABLE 1. Explanatory variables used in Gradient Nearest Neighbor species and structure models.

Variable subset and code	Model		Definition
	Species	Structure	
Topography			
ELEV	†	†	elevation (m), from 30-m digital elevation model (DEM)
SLOPE	†	†	slope (%), from 30-m DEM
ASPECT	†	†	cosine transformation of aspect (degrees) (Beers et al. 1966), 0.0 (southwest) to 2.0 (northeast), from 30-m DEM
PRR		†	cumulative potential relative radiation during growing season based on hourly solar position, topography, and topographic shading (Pierce et al. 2005)
TP1150		†	topographic position index, calculated as difference between a cell's elevation and mean elevation of cells within a 150 m radius window
TP1450	†		topographic position index within a 450 m radius window
Climate			
ANNTMP	†	†	mean annual temperature (°C)
ANNFROST		†	mean no. days/yr when daily minimum temperature $\leq 0.0^\circ\text{C}$
SMRTP	†	†	moisture stress during growing season; ratio of mean temperature (°C) to mean precipitation (natural log, mm), May–Sep
CONTPRE	†	†	percentage of annual precipitation falling Jun–Aug
CVPRE	†	†	coefficient of variation of wettest (Dec) and driest (Jul) mean monthly precipitation
ANNSW	†	†	annual sum of total daily incident shortwave radiative flux (accounts for cloudiness) (MJ^2/d) (Thornton and Running 1999)
STRATUS	†	†	percentage of hours in July with cloud ceiling of marine stratus < 1524 m and visibility < 8 km
Landsat TM			
BRT		†	brightness axis from tasseled cap transformation (Kauth and Thomas 1976)
GRN		†	greenness axis from tasseled cap transformation
WET		†	wetness axis from tasseled cap transformation
ADGRN		†	absolute difference (Rubin 1990) of GRN; differences in values between pairs of neighboring cells are calculated and summed across a window of 13 total pixels
DIST		†	no. years since disturbance by clearcut harvest, from analysis of 1972–1995 Landsat TM data (Cohen et al. 2002)
Ownership			
FS		†	Forest Service
BLM		†	Bureau of Land Management
STATE		†	state
PNI		†	nonindustrial private
Location			
X	†	†	UTM easting (m)
Y	†	†	UTM northing (m)

† Variable used in the model.

development were from field plots installed in regional inventories (FIA, Current Vegetation Survey [CVS; Max et al. 1996], and a 1988 inventory of BLM lands), the Area Ecology Program of the USDA Forest Service, and one research study of old-growth forests (Spies 1991). The FIA and CVS plots were established on systematic grids. FIA plots, CVS plots on BLM lands, and CVS plots in National Forest wilderness areas were spaced every 5.5 km, and CVS plots on other National Forest lands every 2.7 km. The 1988 BLM inventory plots were established using a stratified random design. The Area Ecology and the old-growth study plot locations were selected subjectively without preconceived bias, primarily in older natural forest.

Field data for the FIA and CVS inventory plots, used in both species and structure models, consisted of detailed measurements of live trees, standing and down dead wood, and understory vegetation. Field data for the Ecology, old-growth study, and 1988 BLM plots, used only in the species model, consisted of estimates of

relative abundance for tree species. Response variables in the species model were presence/absence of 34 tree species on 2600 plots. Response variables in the structure model for 763 plots were basal area by tree species and size class, volume of snags ≥ 50 cm diameter at breast height (dbh), volume of down wood ≥ 12.5 cm diameter at large end, and proportion of live tree basal area composed of hardwood species.

Explanatory variables were from rasters representing topography, solar radiation, climate, 1996 Landsat Thematic Mapper (TM) imagery, ownership, and geographic location (Table 1). A map quantifying occurrence of low stratus clouds was from unpublished data of C. Daly. Potential relative radiation was mapped by using methods of Pierce et al. (2005). All other climate variables were derived from Daymet rasters (Thornton et al. 1997) at 1-km resolution, based on 18 years of weather station data. We included *X* and *Y* in our models, despite their correlation with many of the other explanatory variables, to encourage selection of nearest-

neighbor plots that are closer in geographic space as well as in gradient space. Rasters for continuous variables were resampled by using bilinear interpolation, and ownership variables by using a majority filter, to a resolution of 1 ha for the species model and 30 m for the structure model.

Values for the explanatory variables were assigned to field plots by intersecting the variables with each plot's footprint, defined as a window of 13 pixels configured in a diamond pattern and anchored by the plot's X and Y coordinates. This shape approximates the plot's layout on the ground. Mean values were associated with each plot for continuous variables, and majority values for categorical variables.

The species and structure models each included all explanatory variables that were significant ($P < 0.01$), 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). Strongly collinear variables were excluded, although CCA is robust to multicollinearity (Palmer 1993).

The species and structure models apply to forest lands only. Spatial predictions from the models were made for the entire study area, and then a mask of nonforest from an independent source (unpublished data) was applied.

We assessed the accuracy of mapped vegetation classifications and continuous variables using cross-validation methods described in Ohmann and Gregory (2002). For vegetation variables of interest, this assessment involved comparing field-measured values with the GNN-based spatial predictions for the plot locations. We also evaluated how closely our predicted landscape proportions among vegetation classes compared with sample-based estimates from systematic plot inventories for the region.

Elements of vegetation biodiversity

Potential vegetation types.—We used spatial predictions from the species model to map five vegetation types. Each plot was classified into one of the vegetation types, and then a map was constructed based on the nearest-neighbor assignments of the plots. Plots were classified into a vegetation type based on the presence of plant associations, and of tree species that indicate particular physical environments, as recorded in the field. We interpret the vegetation classes as potential vegetation types (Daubenmire 1968) at the level of tree series. Series are defined by the tree species that dominate the site in the absence of disturbance, and the vegetation types are an integrated expression of multiple environmental factors that interact to influence tree species composition. Our classification and map does not include nonforest communities, rare community types such as forested wetlands or shore pine, or riparian forests.

Structural condition classes.—We used the spatial predictions from the structure model to map seven structural condition classes that describe stages of forest

TABLE 2. Variation explained by subsets of variables (see Table 1) in canonical correspondence analysis (CCA).

Variable subset	Model	
	Species	Structure
Topography	2.5	3.0
Climate	8.0	8.6
Disturbance		
Landsat TM	†	12.8
Ownership	†	5.5
Location	5.0	4.9
Full model	10.0	23.9

Notes: Each value represents an individual CCA using all variables in the subset. Values are the sum of all canonical eigenvalues as a percentage of all unconstrained eigenvalues (total inertia). Values are appropriately compared among variable subsets within models (columns), but not between models (rows).

† Not used.

development since stand-replacing disturbance. We defined old growth as stands with an old-growth habitat index (Spies et al. 2007) of ≥ 0.75 . The index is calculated from stand age, density of live trees ≥ 100 cm dbh, diameter diversity index (McComb et al. 2002), density of large snags (≥ 50 cm dbh and ≥ 15 m tall), and total down wood volume. Stands not qualifying as old growth were classified into a structural condition class based on quadratic mean diameter and crown cover.

Tree-level elements of vegetation structure.—We used spatial predictions from the structure model to map specific elements of vegetation structure important as wildlife habitat and to ecosystem function: large live and dead remnant trees from a previous stand removed by stand-replacing disturbance (usually clearcut harvest), large dead wood (standing snags and down wood), and hardwoods. A tree was defined as a remnant if it met either of these criteria: (1) plot has $< 40\%$ cover and tree is ≥ 50 cm dbh; or (2) plot has $\geq 40\%$ cover, plot quadratic mean diameter (QMD) is < 50 cm, and tree dbh is at least 50 cm greater than the plot QMD. This rule was applied to live trees, snags, and down wood.

Vegetation distribution by ownership and watershed

We quantified the distribution of vegetation variability among ownerships by intersecting the maps in GIS. Maps of land ownership (Fig. 1) were developed from GIS data obtained from land management agencies and other sources. Individual landowners were grouped into five classes that differ in their forest policies and management practices: Forest Service, BLM, state, nonindustrial private, and forest industry. In order to display geographic patterns that are discernable at the reduced sizes printed in this journal, we summarized the 30-m-pixel data for watersheds that are fifth-field hydrologic units within the USGS hierarchy. Watershed-level values for vegetation variables were calculated as the means of pixel-level values for all forested pixels from the structure model.

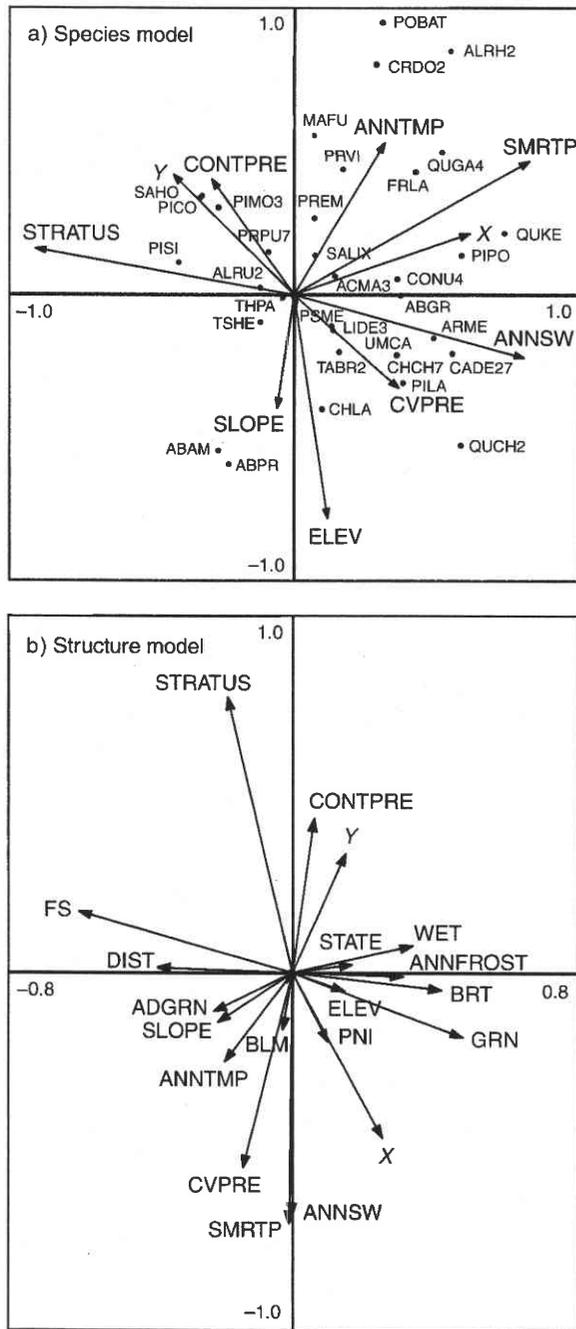


FIG. 2. Associations between vegetation and explanatory variables for the dominant gradients (axes 1 and 2) from canonical correspondence analysis (CCA). (Note that only axes 1 and 2 are shown here, whereas axes 1–8 were used in the GNM models.) Explanatory variables are shown as arrows. Arrow length and position show the correlation between the explanatory variable and the CCA axes. The correlation between an explanatory variable and each axis is determined by drawing a perpendicular line from the tip of the arrow to each axis. Smaller angles between arrows indicate stronger correlations between variables. (a) Explanatory variables (TPI450 and ASPECT not shown) and species centroids (dots) in the species model. Species codes and nomenclature are from the PLANTS database (USDA NRCS 2002): ABAM, *Abies amabilis*; ABGR,

RESULTS

Dominant ecological gradients in coastal Oregon

Quantitative accuracy evaluations for selected vegetation classes and variables from the species and structure models are in Appendices A–F. The prediction accuracy for individual continuous variables from the structure model varied (Appendix F). Accuracy generally was best for synthetic measures of the live tree canopy, such as quadratic mean diameter, stand age, canopy cover, and diameter diversity index. Accuracy was lowest for vegetation elements not directly measured by the Landsat sensor and that are only weakly correlated with overstory characteristics, such as down wood volume.

In the species model, tree species gradients were most strongly associated with environmental variation; gradients were insensitive to disturbance history as reflected in the Landsat TM and ownership variables. Indeed, we were able to improve prediction accuracy for presence of individual tree species by excluding these variables from the model. Overall, climate variables explained the most variation in the species data, followed by geographic location and topography (Table 2). Climate variables would be even more important if elevation and solar radiation were classified as measures of climate rather than topography.

The dominant gradient (axis 1) in species composition was associated with a climate gradient from coastal maritime conditions to the drier, more variable climate farther inland and to the southeast (Fig. 2a), as expressed by STRATUS, SMRTP, and ANNSW (see Table 1). Coastal species *Picea sitchensis*, *Pinus contorta* Dougl. ex Loud. var. *contorta*, and *Salix hookeri* Barratt scored lowest on axis 1. Highest scoring were *Quercus kelloggii* Newb., *Pinus ponderosa* Dougl. ex Laws., *Q. chrysolepis* Liebm., and *Calocedrus decurrens* (Torr.) Florin—species that occur along interior valley margins in the southeastern part of the study area. Axis 2 was a gradient in elevation, mean annual temperature, and

A. grandis; ABPR, *A. procera*; ACMA3, *Acer macrophyllum*; ALRH2, *Alnus rhombifolia*; ALRU2, *A. rubra*; ARME, *Arbutus menziesii*; CADE27, *Calocedrus decurrens*; CHCH7, *Chrysolepis chrysophylla* (Hook) Hjelmqvist; CHLA, *Chamaecyparis lawsoniana* (A. Murr.) Parl.; CONU4, *Cornus nuttallii* Audubon; CRDO2, *Crataegus douglasii*; FRPU7, *Frangula purshiana* DC.; FRLA, *Fraxinus latifolia* Benth.; LIDE3, *Lithocarpus densiflorus* (Hook. & Arn.) Rehd.; MAFU, *Malus fusca* (Raf.) Schneid.; PISI, *Picea sitchensis*; PICO, *Pinus contorta*; PILA, *P. lambertiana* Dougl.; PIMO3, *P. monticola* Dougl. ex D. Don; PIPO, *P. ponderosa*; POBAT, *Populus balsamifera* ssp. *trichocarpa*; PREM, *Prunus emarginata* Dougl. ex Eaton; PRVI, *P. virginiana* L.; PSME, *Pseudotsuga menziesii*; QUGA4, *Quercus garryana*; QUCH2, *Q. chrysolepis*; QUKE, *Q. kelloggii*; SALIX, *Salix* L.; SAHO, *S. hookeriana*; TABR2, *Taxus brevifolia* Nutt.; THPL, *Thuja plicata*; TSHE, *Tsuga heterophylla*; UMCA, *Umbellularia californica* (Hook. & Arn.) Nutt. (b) Explanatory variables in the structure model (see Table 1) (ASPECT, TPI150, and PRR not shown).

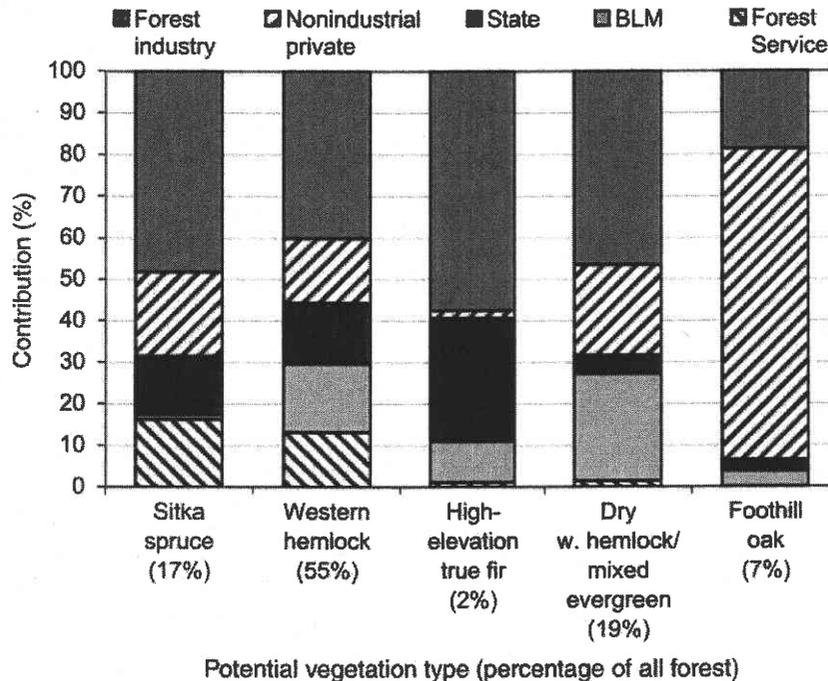


FIG. 3. Distribution of potential vegetation types among owner classes. Potential vegetation types are defined at the level of tree series, as follows. Sitka spruce forest: *Picea sitchensis* plant association, or *P. sitchensis* present. Western hemlock forest: *Abies grandis*, *Pseudotsuga menziesii*, *Lithocarpus densiflorus*, or *Tsuga heterophylla* plant association, and dry site indicators absent (*Abies grandis*, *Arbutus menziesii*, *Calocedrus decurrens*, *Chrysolepis chrysophylla*, *L. densiflorus*, *Pinus ponderosa*, *Quercus garryana*, *Q. chrysolepis*, *Q. kelloggii*, *Umbellularia californica*). High-elevation true fir forest: *Abies amabilis* or *A. procera* present. Dry western hemlock/mixed evergreen forest: *Abies grandis*, *P. menziesii*, *L. densiflorus*, or *T. heterophylla* plant association and dry site indicators present (*Abies grandis*, *Arbutus menziesii*, *Calocedrus decurrens*, *Chrysolepis chrysophylla*, *L. densiflorus*, *Pinus ponderosa*, *Quercus garryana*, *Q. chrysolepis*, *Q. kelloggii*, *Umbellularia californica*). Foothill oak woodlands: *Quercus* plant association, or *Q. garryana* or *Q. kelloggii* present.

summer moisture stress (SMRTP). Lowest scoring species were true firs found at high elevations in the Coast Range, *Abies procera* Rehd. and *A. amabilis* Dougl. ex Forbes. Highest scores were for *Populus balsamifera* L., *Alnus rhombifolia* Nutt., and *Crataegus douglasii* Lindl., which are shade-intolerant, broadleaf, deciduous species found in riparian and disturbed habitats in the Willamette Valley.

In contrast to species gradients, variation in forest structure (based on live tree size and density and dead wood biomass) was most strongly associated with disturbance history (Fig. 2b). The Landsat variables explained more variation (13%) than any of the other variable subsets, followed by climate (9%; Table 2). Although Forest Service ownership was strongly correlated with axis 1 (Fig. 2b), ownership variables alone explained only 6% of total variation in forest structure. Location and topography had the least explanatory power. The dominant gradient (axis 1) in the structure model was from older stands of large trees with dense canopies on Forest Service lands (low scores) to young stands of small trees (high scores; Fig. 2b). Young scoring species on axis 1 were large size-classes of *Tsuga heterophylla*, *Picea sitchensis*, and *Pseudotsuga menziesii*. Highest scores on axis 1 were for *Abies procera* and *A.*

amabilis, *Q. kelloggii*, and *Arbutus menziesii* Pursh. Axis 2 was a coastal-to-interior climate gradient that captured the species component of the response variables; it was similar to axis 1 in the species model.

Distribution of potential vegetation types and structural conditions

Western hemlock forest was the most widely distributed vegetation type (55% of all forest), and high-elevation true fir forest (2%) and foothill oak woodlands (7%) were least common (Fig. 3). The vegetation types were unevenly distributed across owner classes. Except for foothill oak woodlands, about one-third of each vegetation type was publicly owned. In contrast, 94% of the foothill oak woodlands were privately owned, primarily by nonindustrial private owners (Fig. 3) in the Willamette Valley foothills (Fig. 4).

Sparse- and open-canopy forests ($\leq 40\%$ cover) comprised 14% of the forest landscape (Fig. 5). These open-canopy forests were created by clearcutting rather than by natural disturbance, and were heavily concentrated (83%) on private lands and in watersheds predominantly in private ownership (Figs. 1 and 6a). Stands of $\geq 40\%$ cover and quadratic mean diameter (QMD) < 50 cm (sapling/pole and small/medium

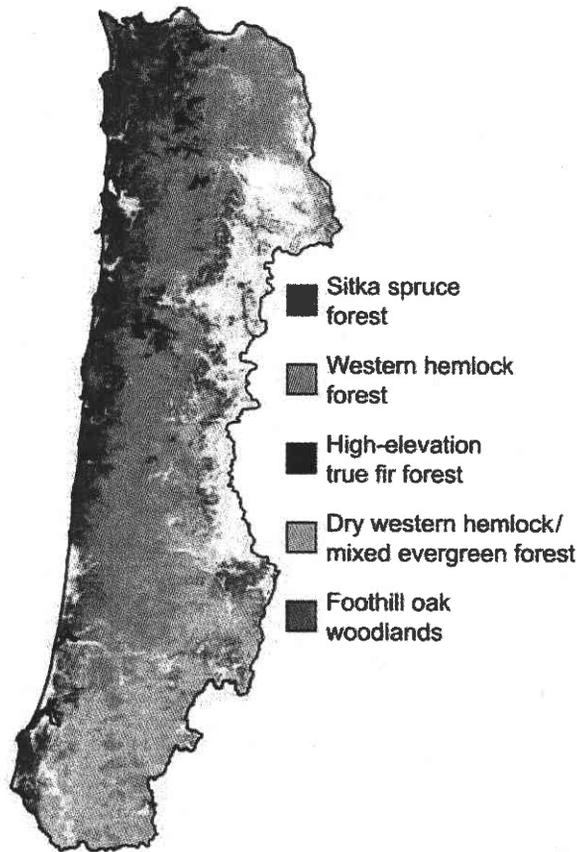


FIG. 4. Geographic distribution of potential vegetation types (see Fig. 3 for definitions).

classes) predominated, comprising 71% of all forest (Fig. 5). These young- to middle-aged forests were concentrated (68%) on private lands and in watersheds in the north and in the Willamette Valley foothills (Figs. 1 and 6b). Stands of $\geq 40\%$ cover and QMD ≥ 50 cm, mature forests that did not qualify as old growth, were a smaller part (16%) of the forest landscape. Sixty-eight percent of the large tree and 89% of the very large tree structural conditions were on public lands (Figs. 1 and 5), primarily in coastal watersheds dominated by Forest Service ownership (Figs. 1 and 6c). Old-growth forests were a very small fraction (1%) of the current landscape; they were located primarily on BLM and Forest Service lands (Figs. 1 and 5) in the southern half of the study area (Fig. 6d).

Distribution of tree-level structural elements

Live remnant trees were most abundant overall on nonindustrial private lands, but remnant trees were larger and of greatest volume on BLM lands (Table 3). Live remnants were present most often (24% of forest area) on nonindustrial private and least often (7%) on forest industry lands. Although mean densities of live remnants were similar among ownerships, remnant trees comprised a greater proportion of all live trees on nonindustrial private lands (7%) than on other ownerships.

The volumes of both large snags and large down wood increased with forest stand development, as represented by the structural condition classes (Fig. 7). Within forest stands, down wood volume was several times greater than snag volume, with these differences most pronounced in young to middle-aged forest (Fig. 7) and on forest industry lands (Table 4). Large dead wood was most abundant overall on public ownerships, particu-

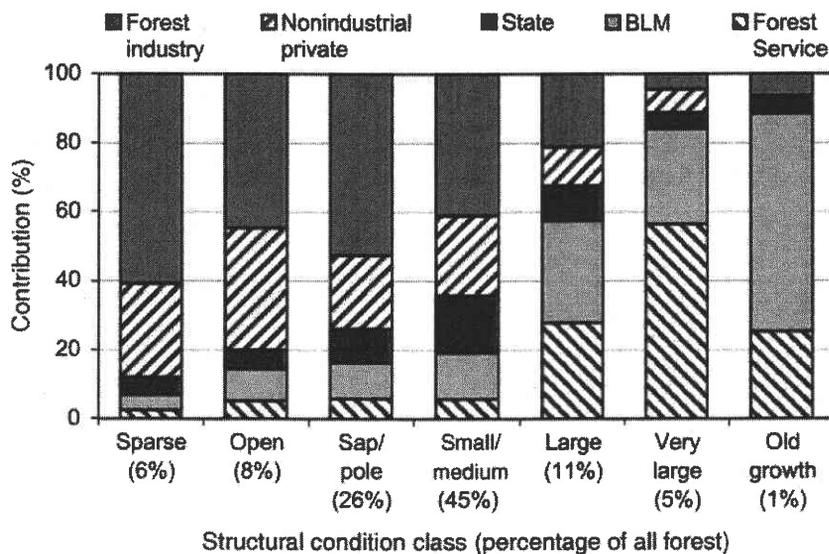


FIG. 5. Distribution of structural condition classes among owner classes: sparse, $< 10\%$ cover; open, $10\text{--}39\%$ cover; sapling/pole (sap/pole), $\geq 40\%$ cover, $2.5\text{--}24.9$ cm quadratic mean diameter (QMD); small/medium, $\geq 40\%$ cover, $25.0\text{--}49.9$ cm QMD; large, $\geq 40\%$ cover, $50.0\text{--}74.9$ cm QMD; very large, ≥ 75 cm QMD; old growth, old-growth habitat index ≥ 0.75 .

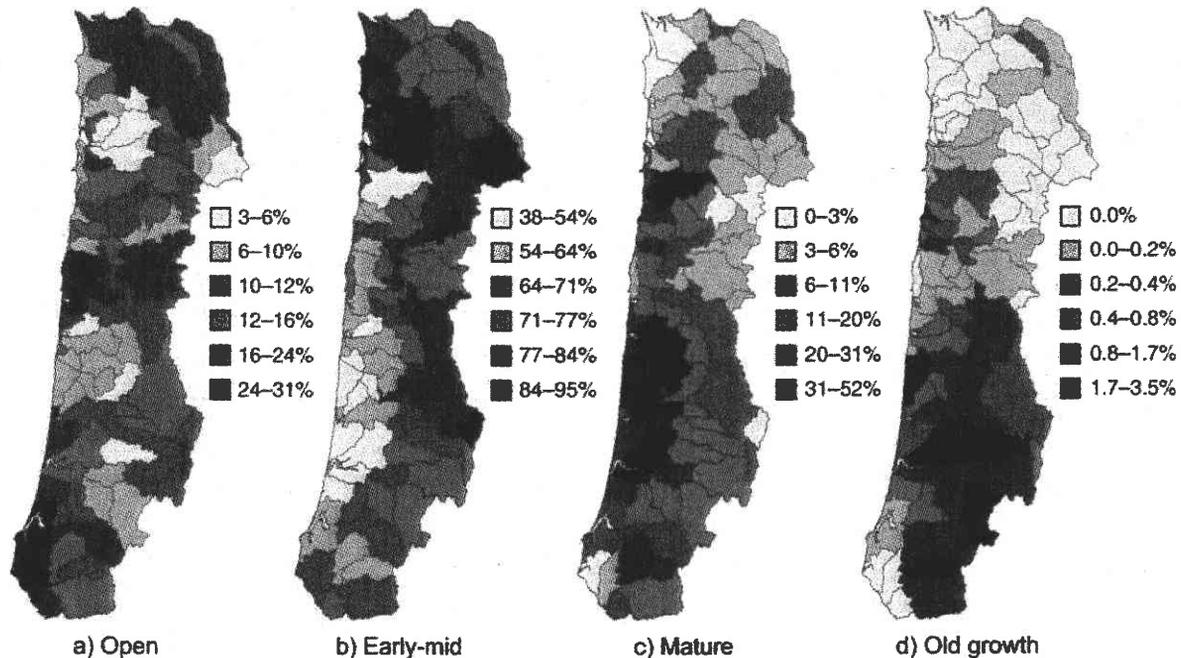


FIG. 6. Abundance of structural condition classes in watersheds as a percentage of forest area. Percentage values were divided into classes by using the Jenks natural breaks function (Jenks 1967). (a) Open forest (<40% cover). (b) Early- to mid-successional forest (≥40% cover, 2.5–49.9 cm quadratic mean diameter [QMD]). (c) Mature forest (≥40% cover, ≥50 cm QMD). (d) Old growth (old-growth habitat index ≥0.75).

larly state and Forest Service lands, with snags most plentiful on Forest Service lands and down wood on state lands (Table 4). Large snags and down wood were least abundant overall on private ownerships, especially nonindustrial private lands. Large dead wood was most abundant in watersheds encompassing Forest Service or state land, and watersheds in the southeastern part of the study area containing mixtures of BLM and forest industry lands (Figs. 1, 8). Large remnant snags were most plentiful on state lands and least so on non-

industrial private lands (Table 3). Remnant down wood was most plentiful on state and forest industry lands and least abundant on Forest Service lands (Table 3).

Hardwoods composed over a third of total tree basal area on nonindustrial private lands, much more than on any other ownership (Table 4). These landowners also owned the greatest area of hardwood-dominated (≥65% of basal area) forest, but most of the mixed conifer–hardwood (20–64% hardwood) area was owned by forest industry (Table 4). As a percentage of total forest

TABLE 3. Abundance of live and dead remnant (legacy) trees in early- and mid-successional forests (<40% cover, or ≥40% cover and <50 cm quadratic mean diameter [QMD]), by owner class.

Remnant tree attribute	Forest Service	BLM	State	Nonindustrial private	Forest industry
Remnant live trees					
Area with ≥0.5 trees/ha (%)	14.5	12.7	8.4	23.7	7.2
Mean density (trees/ha)	0.8	1.0	0.9	2.0	0.9
Mean volume (m ³ /ha)	12.4	17.4	13.8	13.3	11.2
Percentage of all live trees†	3.5	3.9	3.2	7.1	3.2
Remnant snags					
Mean density (trees/ha)	1.3	1.4	2.0	0.8	1.5
Mean volume (m ³ /ha)	4.8	8.5	13.2	3.5	7.3
Percentage of all snags†	17.4	15.6	28.9	15.8	23.7
Remnant down wood					
Mean volume (m ³ /ha)	18.6	51.0	89.4	23.6	72.7
Percentage of all down wood†	7.8	17.0	29.0	17.4	30.0

Note: A tree is defined as a remnant if either (1) plot is <40% cover and tree is ≥50 cm dbh; or (2) plot is ≥40% cover, QMD is <50 cm, and tree dbh is at least 50 cm greater than the QMD.

† Values in these rows represent the percentage of all live trees, snags, or down wood in the owner class that are remnant.

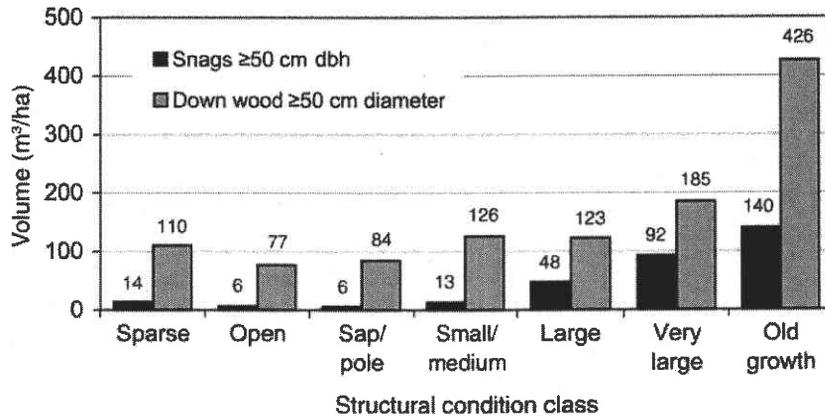


FIG. 7. Volume of large snags and large down wood by structural condition class. See Fig. 5 for definitions of structural condition classes.

owned, hardwood and mixed forests were by far more predominant on nonindustrial private lands than on any other ownership. Over the entire study area, 75% of the hardwood forest and 64% of the mixed forest was privately owned. Hardwoods were most abundant in the northeastern watersheds that encompass the Willamette Valley foothills (Fig. 9), which are primarily in non-industrial private ownership (Fig. 1).

DISCUSSION

Disturbance and environmental influences on forest composition and structure

The weak association we observed between tree species composition and disturbance is consistent with other studies in the Pacific Northwest (Spies 1991, Ohmann and Spies 1998, Wimberly and Spies 2001, Wimberly and Ohmann 2004). Species presence-absence strongly influences regional ordinations, in which gradients are long and species turnover is high. Disturbance can affect the relative abundances of tree species on a site by influencing rates of tree establishment, mortality, and growth, but changes in community composition arising from these individual-tree-level processes operate relatively slowly, and rarely result in elimination of a species from a site. In coastal Oregon, several ubiquitous and long-lived conifer species can persist through all stages of forest development, further blurring the effects of disturbance on community composition. The degree to which this finding can be

generalized to other forested regions will depend upon the particular autecology and life-history characteristics of the species being considered, the nature of the disturbance, and the successional dynamics of the communities (Roberts and Gilliam 1995).

The strong link between forest structure and disturbance was expected. The Landsat TM variables directly measure the upper forest canopy, and thus are correlated with time since stand-replacing disturbance and stage of development. However, ownership variables by themselves had relatively weak explanatory power for forest structure (Table 2). Because each owner class encompasses forests of all stages of development, the Landsat TM data were needed to predict specific locations of forest conditions within ownerships. Nevertheless, the Forest Service ownership was strongly correlated with axis 1 (Fig. 2b), and we found pronounced differences in forest structure among owner classes (Tables 3 and 4, Fig. 5). The contrast in forest structure among ownerships was somewhat less than expected because of the influence of large live and dead legacy trees from previous, late-successional forests. Forest management regimes that are considered characteristic of the owner classes have been practiced for only a few decades at most, and legacy trees have been diminished but not erased from the current landscape by current forest management practices.

Ownership variables were not used in the species model, and accounted for a relatively small amount of

TABLE 4. Abundance of hardwood tree species, large snags, and large down wood by owner class.

Vegetation attribute	Forest Service	BLM	State	Nonindustrial private	Forest industry
Mean hardwood basal area proportion	17	17	21	37	17
Area (1000 ha) of hardwood forest†	16 (7)	20 (6)	19 (7)	102 (21)	61 (7)
Area (1000 ha) of mixed conifer-hardwood forest‡	48 (20)	64 (20)	81 (30)	150 (31)	198 (21)
Mean volume of snags ≥ 50 cm dbh (m ³ /ha)	56.6	32.7	22.4	6.1	10.5
Mean volume of down wood ≥ 50 cm diameter at large end (m ³ /ha)	142.5	130.5	184.6	43.2	120.0

† Hardwood tree species compose $\geq 65\%$ of total tree basal area; values in parentheses show the percentage of ownership.

‡ Hardwood tree species compose 20–64% of total tree basal area; values in parentheses show the percentage of ownership.

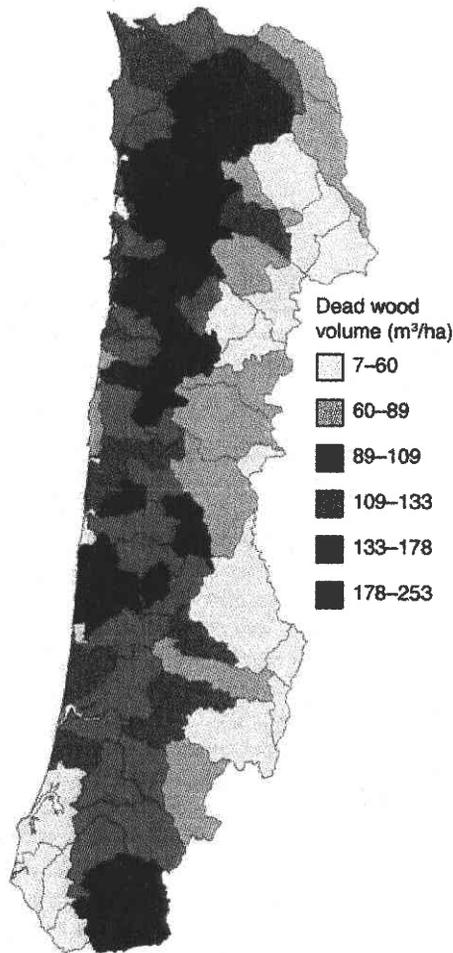


FIG. 8. Volume (m^3/ha) of large dead wood (snags ≥ 50 cm dbh and down wood ≥ 50 cm diameter at large end) in watersheds. Volume values were divided into classes by using the Jenks natural breaks function (Jenks 1967).

the total inertia in the structure model (6%) relative to Landsat TM variables (13%) (Table 2). When ownership variables were excluded from the model, spatial predictions were patterned very similarly but less variation was explained, so we elected to retain ownership variables in the structure model. Because of the relatively low importance of ownership in the structure model, and because plots from a given ownership can be assigned as nearest neighbors for pixels of any ownership, we concluded that the relationships between ownership and structural elements of vegetation biodiversity reflected real differences and were not just an artifact of including ownership in the model.

Regional patterns of key elements of vegetation biodiversity

Hardwoods.—The area of hardwood forest in coastal Oregon has increased overall since the 1930s (Wimberly and Ohmann 2004), but it is unknown how current hardwood abundance compares with the longer-term,

historical range of variability. Unlike other biodiversity elements emphasized in this paper, most hardwoods were on private lands, and on nonindustrial lands in particular (Table 4). Nonindustrial forests are concentrated in environments that favor hardwoods: lower elevations, woodland and riparian habitats of the Willamette Valley foothills, and valley bottoms of large rivers and streams. In addition, most of these hardwoods are shade-intolerant, early-successional species associated with disturbance, and private forests have been more heavily disturbed by timber management activities than public forests. Many of the hardwoods on nonindustrial private lands are remnants (Table 3) from harvesting disturbance. On nonindustrial private forests, more live trees (including hardwoods) are left uncut, and efforts to control hardwoods are less thorough. Much of the total area of hardwood forest was on heavily disturbed forest industry lands, despite intensive management favoring conifers.

Late-successional forest.—Our findings validate concerns over the loss of late-successional forest and

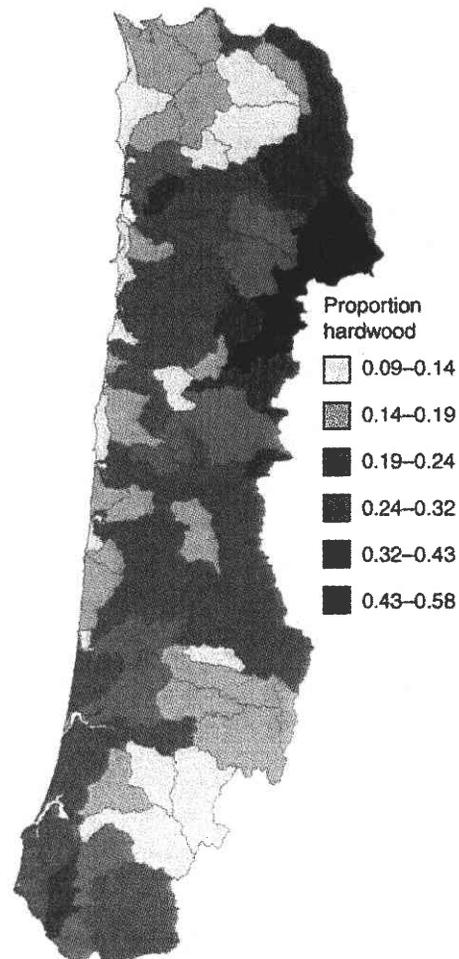


FIG. 9. Mean hardwood proportion of total tree basal area in watersheds. Proportion values were divided into classes by using the Jenks natural breaks function (Jenks 1967).

associated species. Older forests were a very small component of the current landscape relative to historical amounts: large-conifer forest (QMD ≥ 50 cm) has declined dramatically, from 42% of the Coast Range in 1936 (Wimberly and Ohmann 2004) to 17% in 1996, and the 1936 area already was below the historical range of 52% to 85% of the landscape (Wimberly et al. 2000). Stands of QMD ≥ 75 cm that lacked other old-growth characteristics comprised only 5% of current forest area. Only 1% of the landscape, or $\sim 15,000$ ha, met a definition of old growth that takes into account several age and structural characteristics. Application of different definitions of old growth would yield different estimates, but these estimates still would not make up more than a small fraction of Coast Range forests.

Structurally diverse young forest and legacy trees.—Early-successional forest in our study area developed following clearcutting and lacked the structural complexity of forest originating after natural disturbance (Cohen et al. 2002). Although young, open-canopy forests (<40% cover) comprised 14% of the landscape (Fig. 5), only 4% of this area contained live remnant trees. Dead wood volumes were lowest in early- to mid-successional forest and increased with forest development (Fig. 7), with a very slight U-shaped pattern, in contrast to the pronounced U-shaped pattern observed in natural forests (Spies et al. 1988).

Patterns of variation of remnant trees and large dead wood among the owner classes were complex (Table 3), undoubtedly reflecting multiple interacting environmental, disturbance, and historical factors. The low abundance of live remnant trees and snags on forest industry lands probably can be explained by the high intensity of timber management. The moderately high levels of down wood in industrial forests (Tables 3 and 4) may be due to these forests' high productivity, along with the low utilization standards of early logging operations and the fact that many areas recently supported late-successional forest. The very large amounts of remnant snags and down wood on state lands can be attributed to the extensive Tillamook burns of the 1930s–1950s; this northern Coast Range land is now mostly in state ownership (Figs. 1, 8). Much of the area burned was late-successional forest with high standing volumes; much of the burned area was not salvage-logged, and standing dead trees often were felled and left on site. Although Forest Service lands had high levels of large dead wood overall (Table 4), relatively little of it was legacy compared with that in other ownerships (Table 3). Much of the Siuslaw National Forest is middle-aged forest on sites that burned repeatedly prior to establishment, consuming much of the pre-existing dead and down wood (Wimberly and Spies 2001).

*Implications for ecological assessment
and conservation planning*

Spatial predictions from the gradient models were of excellent reliability at the scale of our $\sim 29,000$ -km²

region (Appendix E), and moderately accurate for specific sites (Ohmann and Gregory 2002; Appendices A–D and F). Accuracy probably falls somewhere in between these scales for the owner classes (2335–9381 km²) and fifth-field hydrologic units (~ 300 km² average) used for analysis and display in this paper. Therefore, the vegetation summaries are appropriately used for broad-scale ecological analyses and for informing planning and policy decisions at regional and sub-regional scales, but not for making tactical or project-level decisions. In a multi-scale framework for ecological research and management, the data can be aggregated and generalized to address questions at province to continental extents, as well as provide context for more detailed studies at local sites.

Although the spatial detail provided by the GNN maps is valuable for a host of other applications (e.g., Spies et al. 2007), many of the regional, multi-ownership analyses we present in this paper could be conducted aspatially, i.e., based on the field plots alone. However, sample-based estimates have inherent limitations that are overcome through use of spatially complete predictions based on the same plots. Most importantly, sample sizes from regional inventories often are insufficient to characterize the vegetation of smaller landscapes, watersheds, or other strata of interest. For example, the fifth-field hydrologic units we used in this paper to illustrate geographic patterns (Figs. 6, 8, and 9) contained an average of only 17 plots, and almost half (41%) contained <10 plots. Even though within-region variability in vegetation could be quantified based on this sample, the distribution of variation among smaller landscapes or watersheds—both spatially and statistically—could not be depicted reliably. Although we do not present quantitative analyses of subregional, watershed-scale variation in this paper, our illustrations of geographic patterns (Figs. 4, 6, 8, and 9) would not be possible based on plots alone.

Although we lack independent data for assessing GNN map accuracy at the watershed scale, we have much more confidence in the GNN maps than in the plot-based estimates at this scale. Even at the scale of the larger fourth-field hydrologic units (subbasins), which contained an average of 58 plots, GNN- and plot-based estimates for vegetation variables used in this paper often differed by more than 30% (data not presented). Although the GNN- and plot-based estimates are quite similar at the scale of the entire region (Appendix E), it could be argued that for smaller geographic areas, the GNN-based estimates probably are better than the plot-based estimates since GNN results in a complete enumeration.

Another advantage of GNN-based analyses over plot-based estimates is that the GNN models can utilize data from plots that are not systematically or randomly distributed, and thus not valid for estimation purposes. Large numbers of these plot data sets exist in most regions, and can greatly contribute to more robust

spatial predictions. For example, 1557 of the 2600 plots used in our species model were selected using methods that disqualified them from statistical estimation.

The strong association between tree species and environment revealed by our study supports the need to consider regional environmental gradients in conservation plans for forest plant communities. Although ownership lacked predictive power in the species model, the sorting of vegetation types among ownerships suggests that ownership should not be neglected in conservation planning in our study area. For example, foothill oak woodlands occurred almost exclusively on nonindustrial private lands (Fig. 3). High-elevation true fir forest, although common in federally owned reserves throughout most of the Pacific Northwest and elsewhere (Scott et al. 2001), was rare in the Coast Range and very little was federally owned (Fig. 3). Although plant communities and their distribution among ownerships and land allocations will differ in other regions, environmental gradients can be expected to be strongly associated with species gradients in most places.

It should be emphasized that our finding of a weak relationship between disturbance and regional gradients in tree species does not apply to other taxa, nor to ecosystems not sampled in our study, such as grasslands or wetlands. Additional research is needed to determine how other taxa respond to the environmental and disturbance gradients in our region and elsewhere, and the degree to which particular tree species- or structure-based measures might successfully serve as indices for other taxa (Flather et al. 1997, Lindenmayer et al. 2000).

Our findings argue compellingly for considering ownership and associated disturbance regimes in the management and conservation of forest structural conditions. Contrasts in forest structure among ownerships in the Coast Range have increased dramatically over the past few decades (Wimberly and Ohmann 2004), and this trend is expected to continue (Johnson et al. 2007). Changes in forest structure have been much more strongly associated with ownership than with environmental differences (Wimberly and Ohmann 2004).

Clearly, forest composition and structure must be addressed in an integrated fashion, rather than independently, in landscape management and conservation planning. Vegetation composition and structure, environment, ownership, and disturbance interact in complex ways that can be expected to vary with location. Unfortunately, few regional studies similar to ours in other ecoregions are available for comparison, as most have examined effects of human disturbance on land cover change, and in particular the conversion of forest to other land uses (e.g., Turner et al. 1996) or disturbance effects on landscape pattern (e.g., Mladenoff et al. 1993, Crow et al. 1999). Nevertheless, it can be generalized that management effects on both the composition and structure of forest vegetation need to be examined as an interaction between disturbance and

the innate biological and physical properties of the ecosystem (Gilliam and Roberts 1995).

The multi-ownership perspective of our analyses revealed biodiversity concerns and benefits that might not be readily visible in analyses of single ownerships. In multi-ownership regions consisting of natural and managed forest, all lands contribute to regional biodiversity. In coastal Oregon, federal lands provide most of the late-successional and old-growth forest. State lands contain a wide range of forest ages and structures, including diverse young forest, ample large legacy wood, and most of the public component of high-elevation true fir forest. Nonindustrial private lands provide diverse young forest and the greatest abundance of hardwood trees, including almost all of the foothill oak woodlands. Forest industry lands encompass much early-successional forest, most of the mixed hardwood-conifer forest, large amounts of legacy down wood, and more than half of the high-elevation true fir forest. The unique biodiversity characteristics of the ownerships argue for an approach to regional conservation planning that includes all ownerships and that is not limited to reserves or federal lands.

The detailed nature of the GNN vegetation maps allowed us to examine several biodiversity elements for the first time at a regional scale. Some of our key findings from analyses of the tree-, stand-, and species-level data would be masked in a traditional coarse-filter analysis. For example, although early-successional forests are abundant in the Coast Range, they mostly lack structural features such as legacy trees. Many large-conifer forests that might be classified as old growth using a generalized forest cover map lack other structural characteristics of old growth such as multilayered canopies or dead wood. The detailed vegetation maps also provide the basis for simulating landscape trajectories to predict future conditions (Johnson et al. 2007) and evaluating the effects of silvicultural treatments and forest policies on vegetation, aquatic, and wildlife biodiversity (Burnett et al. 2007, Spies et al. 2007), as well as on commodity values (Johnson et al. 2007).

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LITERATURE CITED

- Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. *Journal of Forestry* 64:691-692.
- Black, A. E., P. Morgan, and P. F. Hessburg. 2003. Social and biophysical correlates of change in forest landscapes of the Interior Columbia Basin, USA. *Ecological Applications* 13: 51-67.
- Burley, F. W. 1988. Monitoring biological diversity for setting priorities in conservation. Pages 227-230 in E. O. Wilson,

- editor. Biodiversity. National Academy Press, Washington, D.C., USA.
- Burnett, K. M., G. H. Reeves, D. J. Miller, S. Clarke, K. Vance-Borland, and K. Christiansen. 2007. Distribution of salmon-habitat potential relative to landscape characteristics and implications for conservation. *Ecological Applications* 17:66–80.
- Cohen, W. B., T. A. Spies, R. J. Alig, D. R. Oetter, T. K. Maier-Sperger, and M. Fiorella. 2002. Characterizing 23 years (1972–95) of stand replacement disturbance in western Oregon forests with Landsat imagery. *Ecosystems* 5:122–137.
- Crow, T. R., G. E. Host, and D. J. Mladenoff. 1999. Ownership and ecosystem as sources of spatial heterogeneity in a forested landscape, Wisconsin, USA. *Landscape Ecology* 14:449–463.
- Daubenmire, R. F. 1968. Plant communities. Harper-Row, New York, New York, USA.
- Flather, C. H., K. R. Wilson, D. J. Dean, and W. C. McComb. 1997. Identifying gaps in conservation networks: of indicators and uncertainty in geographic analysis. *Ecological Applications* 7:531–452.
- Forest Ecosystem Management Assessment Team. 1993. Forest ecosystem management: an ecological, economic, and social assessment. Joint publication of the U.S. Forest Service, National Marine Fisheries Service, Bureau of Land Management, U.S. Fish and Wildlife Service, National Park Service, and U.S. Environmental Protection Agency, Washington, D.C., USA.
- Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests. *BioScience* 41:382–392.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133–302.
- Hunter, M. L., Jr. 1991. Coping with ignorance: the coarse-filter strategy for maintaining biodiversity. Pages 266–281 in K. A. Kohm, editor. *Balancing on the brink of extinction*. Island Press, Covelo, California, USA.
- Impara, P. C. 1997. Spatial and temporal patterns of fire in the forests of the Central Oregon Coast Range. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Jenks, G. F. 1967. The data model concept in statistical mapping. *International Yearbook of Cartography* 7:186–190.
- Johnson, K. N., P. Bettinger, J. D. Kline, T. A. Spies, M. Lennette, G. Lettman, B. Garber-Yonts, and T. Larsen. 2007. Simulating forest structure, timber production, and socioeconomic effects in a multi-owner province. *Ecological Applications* 17:34–47.
- Kauth, R. J., and G. S. Thomas. 1976. The tasseled cap—a graphic description of the spectral-temporal development of agricultural crops as seen by Landsat. Pages 4B-41–4B-50 in *Proceedings of the symposium on machine processing of remotely sensed data*. Purdue University, West Lafayette, Indiana, USA.
- Lindenmayer, D. B., and J. F. Franklin. 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington, D.C., USA.
- Lindenmayer, D. B., C. R. Margules, and D. B. Botkin. 2000. Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology* 14:941–950.
- Lovett-Doust, J., and K. Kuntz. 2001. Land ownership and other landscape-level effects on biodiversity in southern Ontario's Niagara Escarpment Biosphere Reserve. *Landscape Ecology* 16:743–755.
- Margules, C. R., I. D. Cresswell, and A. O. Nicholls. 1994. A scientific basis for establishing networks of protected areas. Pages 327–350 in P. L. Forey, C. J. Humphries, and R. I. Vane-Wright, editors. *Systematics and conservation evaluation*. Clarendon Press, Oxford, UK.
- Max, T. A., H. T. Schreuder, J. W. Hazard, D. O. Oswald, J. Teply, and J. Alegria. 1996. The Pacific Northwest Region vegetation inventory and monitoring system. Research Paper PNW-RP-493. USDA Forest Service Pacific Northwest Research Station, Portland, Oregon, USA.
- McComb, W. C., M. T. McGrath, T. A. Spies, and D. Vesely. 2002. Models for mapping potential habitat at landscape scales: an example using northern spotted owls. *Forest Science* 48:203–216.
- Mladenoff, D. J., M. A. White, J. Pastor, and T. R. Crow. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. *Ecological Applications* 3:294–306.
- Nature Conservancy. 1982. Natural Heritage Program operations manual. The Nature Conservancy, Arlington, Virginia, USA.
- Neitlich, P. N., and B. McCune. 1997. Hotspots of epiphytic lichen diversity in two young managed forests. *Conservation Biology* 11:172–182.
- Noss, R. F., and L. D. Harris. 1986. Nodes, networks, and MUMs: preserving diversity at all scales. *Environmental Management* 10:299–309.
- Ohmann, J. L., and M. J. Gregory. 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest neighbor imputation in coastal Oregon, USA. *Canadian Journal of Forest Research* 32:725–741.
- Ohmann, J. L., and T. A. Spies. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. *Ecological Monographs* 68:151–182.
- Palmer, M. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* 74:2215–2230.
- Pierce, K. B., T. R. Lookingbill, and D. L. Urban. 2005. A simple method for estimating potential relative radiation (PRR) for landscape-scale vegetation analysis. *Landscape Ecology* 20:137–147.
- Radeloff, V. C., R. B. Hammer, P. R. Voss, A. E. Hagen, D. R. Field, and D. J. Mladenoff. 2001. Human demographic trends and landscape level forest management in the north-west Wisconsin Pine Barrens. *Forest Science* 47:229–241.
- Roberts, M. R., and F. S. Gilliam. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. *Ecological Applications* 5:969–977.
- Rose, C. L., B. G. Marcot, T. K. Mellen, J. L. Ohmann, K. L. Waddell, D. L. Lindley, and B. Schreiber. 2001. Decaying wood in Pacific Northwest forests: concepts and tools for habitat management. Pages 580–612 in D. H. Johnson and T. A. O'Neil, managing directors. *Wildlife-habitat relationships in Oregon and Washington*. Oregon State University Press, Corvallis, Oregon, USA.
- Rubin, T. 1990. Analysis of radar texture with variograms and other simplified descriptors. Pages 185–195 in *Proceedings, image processing '89*. Sparks, Nevada. American Society for Photogrammetry and Remote Sensing, Falls Church, Virginia, USA.
- Santiago Declaration. 1995. The Montreal process: criteria and indicators for the conservation and sustainable management of temperate and boreal forests. Canadian Forest Service, Hull, Quebec, Canada.
- Scott, J. M., F. Davis, B. Csuti, R. Noss, B. Butterfield, C. Groves, H. Anderson, S. Caicco, F. D'erchia, T. C. Edwards, Jr., J. Ulliman, and R. G. Wright. 1993. Gap analysis: a geographic approach to protection of biological diversity. *Wildlife Monographs* 123:1–41.
- Scott, J. M., F. W. Davis, R. G. McGhie, R. G. Wright, C. Groves, and J. Estes. 2001. Nature reserves: do they capture the full range of America's biological diversity? *Ecological Applications* 11:999–1007.

- Spies, T. A. 1991. Plant species diversity and occurrence in young, mature, and old-growth Douglas-fir stands in western Oregon and Washington. Pages 111–121 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. General Technical Report PNW-GTR-285. U.S. Department of Agriculture, Forest Service Pacific Northwest Research Station, Portland, Oregon, USA.
- Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69:1689–1702.
- Spies, T. A., B. C. McComb, R. S. H. Kennedy, M. T. McGrath, K. Olsen, and R. J. Pabst. 2007. Potential effects of forest policies on terrestrial biodiversity in a multi-ownership province. *Ecological Applications* 17:48–65.
- Stanfield, B. J., J. C. Bliss, and T. A. Spies. 2002. Land ownership and landscape structure: a spatial analysis of sixty-six Oregon (USA) Coast Range watersheds. *Landscape Ecology* 17:685–697.
- ter Braak, C. J. F., and I. C. Prentice. 1988. A theory of gradient analysis. *Advances in Ecological Research* 18:271–313.
- ter Braak, C. J. F., and P. Smilauer. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, New York, USA.
- Thornton, P. E., and S. W. Running. 1999. An improved algorithm for estimating incident daily solar radiation from measurements of temperature, humidity, and precipitation. *Agricultural and Forest Meteorology* 93:211–228.
- Thornton, P. E., S. W. Running, and M. A. White. 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *Journal of Hydrology* 190: 214–251.
- Turner, M. G., D. N. Wear, and R. O. Flamm. 1996. Land ownership and land-cover change in the Southern Appalachian Highlands and the Olympic Peninsula. *Ecological Applications* 6:1150–1172.
- USDA NRCS. 2002. The PLANTS database, version 3.5. National Plant Data Center, Baton Rouge, Louisiana, USA. (www.plants.usda.gov)
- Van Deusen, P. C. 1997. Annual forest inventory statistical concepts with emphasis on multiple imputation. *Canadian Journal of Forest Research* 27:379–384.
- Wimberly, M. C., and J. L. Ohmann. 2004. A multi-scale assessment of human and environmental constraints on forest land cover change on the Oregon (USA) coast range. *Landscape Ecology* 19:631–646.
- Wimberly, M. C., and T. A. Spies. 2001. Influences of environment and disturbance on forest patterns in coastal Oregon watersheds. *Ecology* 82:1443–1459.
- Wimberly, M. C., T. A. Spies, C. J. Long, and C. Whitlock. 2000. Simulating historical variability in the amount of old forests in the Oregon Coast Range. *Conservation Biology* 14: 167–180.

APPENDIX A

Error matrix for potential vegetation types from the Gradient Nearest Neighbor model (*Ecological Archives* A017-001-A1).

APPENDIX B

Kappa coefficients of agreement for potential vegetation types from the Gradient Nearest Neighbor species model (*Ecological Archives* A017-001-A2).

APPENDIX C

Error matrix for vegetation classes from the Gradient Nearest Neighbor structure model (*Ecological Archives* A017-001-A3).

APPENDIX D

Kappa coefficients of agreement for vegetation classes from the Gradient Nearest Neighbor structure model (*Ecological Archives* A017-001-A4).

APPENDIX E

Comparison of forest area predicted from the Gradient Nearest Neighbor structure model and estimated from systematic grids of field plots for vegetation classes, large snags, and large down wood (*Ecological Archives* A017-001-A5).

APPENDIX F

Comparison of predictions from the Gradient Nearest Neighbor structure model with ground observations for several measures of forest composition and structure (*Ecological Archives* A017-001-A6).