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RELATIONSHIPS BETWEEN LANDSCAPE STRUCTURE AND BREEDING BIRDS IN THE OREGON COAST RANGE¹

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Abstract. Human-caused fragmentation of forests is increasing, yet the consequences of these landscape changes to vertebrate communities are poorly understood. Although bird community response to forest fragmentation caused by agricultural or urban development has been well studied, we have little understanding of these dynamics in landscapes undergoing intensive forest management, where late-seral forest stands are separated by younger forest stands of varying ages and are part of a spatially and temporally dynamic forest landscape.

We investigated the relationship between landscape structure and breeding bird abundance in the central Oregon Coast Range. We sampled vegetation and birds in 30 landscapes (250–300 ha) distributed equally among three basins. Landscapes represented a range in structure based on the proportion of the landscape in a late-seral forest condition and the spatial configuration of that forest condition within the landscape. We computed a variety of landscape metrics from digital vegetation cover maps for each landscape. Using analysis of variance and regression procedures, we quantified the independent effects of habitat area and configuration on 15 bird species associated with late-seral forest.

Species varied dramatically in the strength and nature of the relationship between abundance and several gradients in habitat area and configuration at the landscape scale. Landscape structure (composition and configuration) typically explained <50% of the variation in each species' abundance among the landscapes. Species' abundances were generally greater in the more heterogeneous landscapes; that is, they were associated with the more fragmented distribution of habitat. Only Winter Wrens showed evidence of association with the least fragmented landscapes.

These results must be interpreted within the scope and limitations of our study. In particular, the scale of our analysis was constrained by the lower and upper limits of resolution in our landscapes, as set by minimum patch size and landscape extent, respectively. Thus, our results do not preclude much stronger and different relationships at finer and/or coarser scales. In addition, our community-centered habitat classification scheme and artificially discrete representation of patch boundaries may not have captured the functionally meaningful heterogeneity for each species. Finally, our analysis was limited to relatively common and widespread diurnal breeding bird species. Species sensitive to habitat fragmentation at the scale of our analysis may have been rare already and therefore not subject to the parametrical statistical approach that we employed.

Key words: birds; fragmentation; habitat area; habitat configuration; habitat relationships; landscape pattern; Oregon Coast Range.

INTRODUCTION

A "landscape" is a heterogeneous land area composed of an interacting mosaic of patches, at any scale, relevant to the phenomenon (e.g., species) under consideration (McGarigal and Marks 1995). Landscapes are characterized by their spatial heterogeneity (i.e., patchiness) at a variety of scales (Forman and Godron 1986). Habitats are distributed within landscapes and their spatial patterns may exert a strong influence on the abundance, distribution, and dynamics of vertebrate populations inhabiting those landscapes (Wiens 1976, 1989a, b). The spatial configuration of a species' hab-

itat affects populations by influencing movement patterns of individuals, intra- and interspecific interactions among individuals, and exposure to factors associated with the juxtaposition of habitats (e.g., edge effects). Habitat fragmentation alters the spatial configuration of habitats, leading to population subdivision and the creation of a metapopulation structure, which can affect population stability or persistence (Gilpin and Hanski 1991). Habitat subdivision also can alter the stability of species interactions and opportunities for coexistence in both predator-prey and competitive systems (Kareiva 1990).

The hypothesis that landscape structure (i.e., the composition and spatial configuration of a landscape) plays an important role in the regulation of populations stems from a variety of sources, including island biogeography (MacArthur and Wilson 1967), metapopu-

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lation theory (Gilpin and Hanski 1991), patch dynamics theory (Pickett and White 1985), mathematical models on dispersal and spatially distributed populations (Kareiva 1990), and field studies on habitat fragmentation (Saunders et al. 1991). However, the basis for this conceptual framework is largely theoretical, and this hypothesis has not been rigorously challenged empirically (Kareiva 1990, Wiens 1992). There are few observational studies (e.g., Pokki 1981, Jennersten 1988, Quinn and Harrison 1988, Solbreck and Sillen-Tullberg 1990) and even fewer experimental studies (e.g., Hanski 1987, Kareiva 1987, Quinn and Robinson 1987, Quinn et al. 1989, Crist et al. 1992, Kadmon 1993) that demonstrate population responses to habitat configuration at the landscape scale. Moreover, these empirical studies have focused largely on plants and invertebrates in artificial laboratory systems or in small natural systems; it is unclear whether these empirical findings extend to vertebrates or to the large and spatially complex landscapes in which many vertebrates live. We are aware of few landscape-level studies on vertebrates (e.g., Wiens and Rotenberry 1985, Wiens et al. 1986 and 1987).

Support for the landscape structure hypothesis has come, in part, from field studies on forest fragmentation (Saunders et al. 1991). Studies from the eastern deciduous forest of North America indicate that the abundance of vertebrate species associated with forest interiors generally declines, whereas the abundance of those specializing on forest edges increases in response to forest fragmentation caused by agricultural development and urbanization (Whitcomb et al. 1981, Robbins et al. 1989, Terborgh 1989). Changes in vegetation, food resources, predation, brood parasitism, and competition have been noted as causes of the observed vertebrate community changes (Strelke and Dickson 1980, Kroodsma 1982, Brittingham and Temple 1983, Wilcove 1985, Noss 1988, Yahner and Scott 1988). The process of forest fragmentation, however, is not limited to urbanization and agricultural expansion; commercial timber management is the major cause of forest fragmentation in several regions of North America, including the Pacific Northwest (PNW) (Lehmkuhl and Ruggiero 1991). It is unclear whether the empirical findings on forest fragmentation from urban and agricultural landscapes extend to the spatially and temporally dynamic forest landscapes of the PNW. Furthermore, nearly all of the studies on fragmentation have employed a patch-centered sampling scheme in which independent forest patches, not landscapes, were sampled (e.g., Rosenberg and Raphael 1986, Lehmkuhl et al. 1991). Based on the relationship derived between species richness or abundance and a variety of "patch" characteristics, such as patch size and isolation, inferences often have been made about how "landscape" structure affects wildlife populations. Yet it is unclear whether relationships derived at the patch level can be

extrapolated to the landscape level (Wiens et al. 1987, 1993, Wiens 1989a, b).

Finally, landscape ecology is largely founded on the notion that landscape structure strongly influences ecological processes and, for example, vertebrate populations (Forman and Godron 1986, Urban et al. 1987, Turner 1989). Thus, quantifying landscape structure is a prerequisite to the study of landscape function and change. For this reason, much emphasis has been placed on developing methods to measure landscape structure (e.g., O'Neill et al. 1988, Li 1990, Turner 1990, Turner and Gardner 1991). While a number of investigators have quantified landscape structure in a variety of ecosystems (e.g., Krummel et al. 1987, Turner and Ruscher 1988, Gustafson and Parker 1992), few have examined the relationship between landscape structure and landscape function (e.g., Franklin and Forman 1987, Baker 1992 and 1993).

We initiated a research program to determine how changes in landscape structure (both composition and configuration) affect bird populations in the spatially and temporally dynamic forest landscape of the Oregon Coast Range. Because it was unclear whether existing theories would apply to this landscape, we chose a comparative mensurative experiment (Hurlbert 1984) designed to explore patterns in the relationship between landscape structure and bird populations. Specifically, we quantified the relationship between the extent and configuration of late-seral forest habitats and the abundances of several bird species associated with this forest type.

STUDY AREA

The study was conducted in the central Oregon Coast Range (Fig. 1) in Lobster Creek, Drift Creek, and Nestucca River basins. Drift Creek and Lobster Creek basins are located mainly in Lincoln and Benton Counties and drain into the Alsea River east of the Pacific Ocean near Waldport, Oregon. Nestucca River is located mainly in Tillamook County and drains directly into the Pacific Ocean near Pacific City. Elevation ranges from sea level to 968 m. Climate is maritime, characterized by mild, wet winters (October–June) and cool, dry summers (July–September). Annual precipitation ranges from 150 to 300 cm and occurs primarily during the winter months in the form of rain, with some snow at high elevations; temperatures during January and July average 2.4° and 16.6°C, respectively (Franklin and Dyrness 1973:71–72).

The study area is characterized by steep slopes and deeply cut drainages. The area is almost entirely forested and lies almost exclusively within the western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1973:70–108). The natural forest overstory is dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock, and red alder (*Alnus rubra*); western redcedar (*Thuja plicata*) and bigleaf maple (*Acer macrophyllum*) also are common. Understory

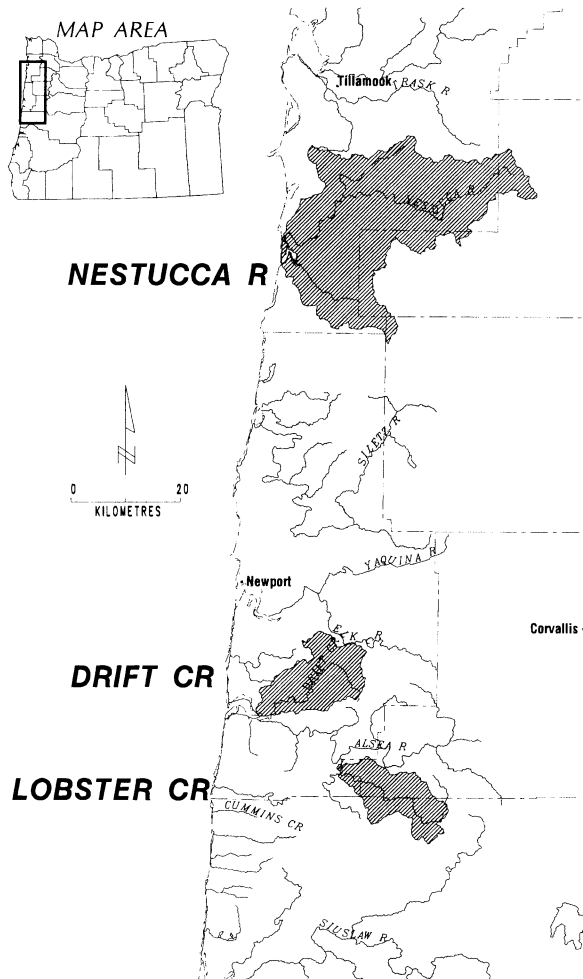


FIG. 1. Study area location.

vegetation is variable in composition and patchy in distribution; common species include salmonberry (*Rubus spectabilis*), vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), Oregon grapes (*Berberis* spp.), huckleberries (*Vaccinium* spp.), and swordfern (*Polystichum munitum*). Franklin and Dyness (1973:70–108) provide a more complete description of the vegetation.

The entire area experienced a catastrophic, stand-replacement fire in the mid-1800s and regenerated naturally (Spies and Cline 1988). Over the past 40 yr federal land managers have used the dispersed-patch or staggered-setting system of clear-cutting, which maximizes fragmentation of the late-seral forest (Franklin and Forman 1987); 10–20 ha patch cuts are interspersed with uncut forest areas of at least equal size (Smith 1986). As a result, the area currently possesses a bimodal age distribution. Mid-aged (40–100 yr) and older (> 140 yr) forest is poorly represented in the study area. For the purpose of this study, late-seral forest included large sawtimber (> 20% overstory cover composed of trees with a mean dbh > 53.3 cm, predominantly 120–140 yr old) as well as remnant old-

growth (> 20% overstory cover composed of trees with a mean dbh > 81.3 cm and multistory canopy, predominantly > 200 yr old) patches scattered irregularly throughout the large sawtimber. The study area contains some private lands (primarily industrial forestland), but is dominated by public lands administered by the USDA Forest Service and USDI Bureau of Land Management. In portions dominated by private ownership, the landscape consists largely of extensive, young (0–40 yr), even-aged, Douglas-fir plantations, although isolated, small patches of late-seral forest exist in some areas. In portions dominated by public ownership, the landscape consists of a matrix of late-seral, unmanaged forest dominated by Douglas-fir and red alder embedded with numerous small (8–25 ha), young, even-aged, Douglas-fir plantations. Consequently, a wide range of landscape structural conditions exists within the study area, particularly with respect to the extent and configuration of late-seral forest.

METHODS

Study design

We selected 10 landscapes in each of three basins (i.e., three replicates, $n = 30$ landscapes) based on the proportion of each landscape in a late-seral forest condition and the spatial configuration (i.e., relative fragmentation) of late-seral forest within the landscape (Fig. 2). This two-dimensional design ensured that we sampled a wide range of landscape structural conditions with respect to late-seral forest. Moreover, this design allowed us to separate the potentially confounding effects of habitat area and habitat configuration on the bird community.

We sampled the landscapes in a different basin each year between 1990 and 1992. Consequently, year and basin (replicates) were confounded; that is, we were unable to statistically separate the effects of year and basin in our analysis of the relationship between landscape structure and bird abundance. To estimate the potential significance of this confounding, we resampled a selection of late-seral forest patches in the Drift Creek basin each year and assessed annual variation in species' abundances (McGarigal 1993). Significant annual variation does not necessarily introduce any systematic bias into the analysis of variance (ANOVA) described below, because all landscape structural conditions were sampled each year; however, it does increase experimental error and therefore reduces the power to detect area and/or configuration effects. Significant annual variation does indicate a lack of temporal independence among the 30 landscapes that would violate the assumption of independent samples for the correlational analyses described below, in which each landscape was treated as an independent sample. For most species, the confounding was inconsequential; two species (Winter Wren and Chestnut-backed Chickadee, see Table 1 for scientific names), however,

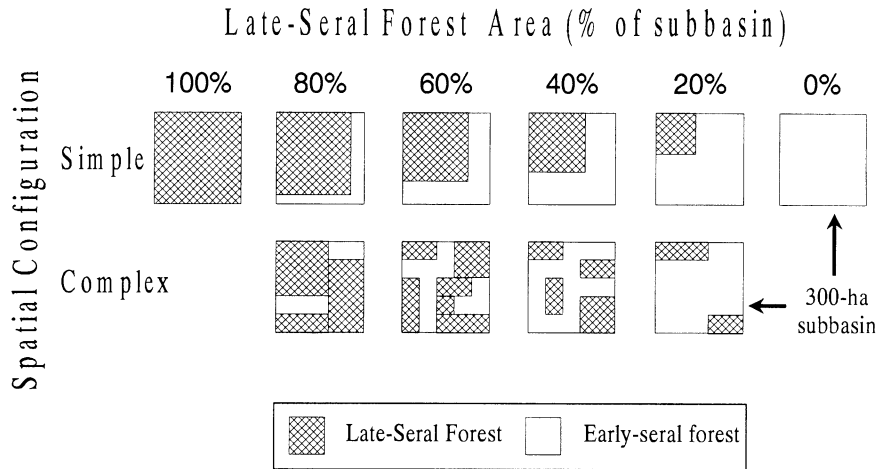


FIG. 2. Schematic of study design, representing 1 of 3 replicates, with each replicate in a separate basin. Late-seral forest includes all conifer-, mixed-, and hardwood-large sawtimber as defined in the Appendix; early-seral forest includes all other patch types defined in the Appendix.

experienced significant annual population fluctuations in Drift Creek basin during the period of study (McGarigal 1993). For these species, the significance tests associated with the correlational analyses reported below are used simply as aids in this exploratory analysis and not to suggest statistical rigor.

Each basin served as a complete block because the 10 landscapes within a basin were geographically separated from the other two basins, and all 10 landscape structural conditions were represented within each basin. Blocking factors cannot be tested in an ANOVA, yet we wished to assess the potential difference in bird abundances among the three geographic areas (basins) to evaluate the validity of treating all 30 landscapes as independent observations in the correlational analyses described below. Therefore, we randomly subsampled a selection of late-seral forest patches in each basin and assessed geographic variation in species' abundances (McGarigal 1993). Three species (Red-breasted Nuthatch, Varied Thrush, and Red Crossbill) demonstrated significant geographic variation in abundance at the patch level that could not be explained by annual variations (McGarigal 1993). For these species, the significance tests associated with the correlational analyses described below are not strictly valid.

We defined landscapes as 250–300 ha areas. Landscapes of this size represented a compromise between landscape size and sample size. Because populations of the species that we studied undoubtedly extend over much larger geographic areas, it would have been more ideal to sample larger landscapes, but because of logistic constraints, we would only have been able to sample a few landscapes, and the analysis would have been limited to a case study. We chose the largest landscape size that still provided sufficient sample size for multivariate analyses. Initially we chose watersheds as the basis for delineating landscapes, because much of the land management planning in the study area is con-

ducted on a watershed basis. Initial selection of watersheds was based on measurements of late-seral forest area and density of edge involving late-seral forest (as an index of spatial heterogeneity) from aerial photos (1988 and 1989 color infrared, 1:20 000). Priority was given to choosing watersheds that were of the proper extent (250–300 ha) and contained the necessary amount and configuration of late-seral forest (Fig. 2). However, because many watersheds did not meet these study design requirements, we usually (21 of 30 landscapes) deleted portions of single watersheds or combined portions of >1 watershed into landscapes for our purposes. It is important to note that we did not take a random sample of landscapes from the study area. Rather, we subjectively selected landscapes to represent gradients in late-seral forest area and configuration. Thus, although we gained power to evaluate the effects of habitat area and configuration on bird abundance (i.e., by guaranteeing a wide range of landscape structures), we forfeited some ability to directly characterize the entire study area on the basis of the empirical findings because our sample of landscapes may not have accurately represented the relative availability of landscape structures across the entire study area.

Bird sampling

We systematically located sample points in a uniform, grid-like fashion at 200-m intervals along transects spaced 400 m apart in each 250–300 ha landscape. The first transect and sample point were located randomly in each landscape. Based on an effective bird detection distance of 50 m, each sample point corresponded to an effective survey area of 0.785 ha, and the grid provided an $\approx 10\%$ uniform sample of the landscape area. At this sampling intensity, 32–38 sample points per landscape were required, depending on landscape size, for a total of 1046 sampling points. Because most species had greater effective detection distances,

TABLE 1. Number of detections and effective detection distance for bird species strongly associated with late-seral forest habitats in 30 300-ha landscapes in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990–1992. Species are ordered from most to least common based on total number of detections.

Acronym	Species (scientific name)	N_t^*	N_{new}^\dagger	$N_{\text{exact}}^\ddagger$	N_{50}^\S	% edge	Cdd¶	Edd#	SI**
WIWR	Winter Wren (<i>Troglodytes troglodytes</i>)	8291	7757	7060	3245	2.4	95	72	20
VATH	Varied Thrush (<i>Ixoreus naevius</i>)	5133	3960	1807	505	1.4	100	101	40
EVGR	Evening Grosbeak (<i>Coccothraustes vespertinus</i>)	3470	3164	1076	449	1.8	95	90	30
RECR	Red Crossbill (<i>Loxia curvirostra</i>)	2779	2547	881	457	9.9	95	72	20
CBCH	Chestnut-backed Chickadee (<i>Parus rufescens</i>)	2626	2596	2534	2142	5.7	50	49	10
BRCR	Brown Creeper (<i>Certhia americana</i>)	1164	1145	1045	801	0.8	55	54	10
HAFL	Hammond's Flycatcher (<i>Empidonax hammondii</i>)	984	897	763	341	0.9	90	79	25
WETA	Western Tanager (<i>Piranga ludoviciana</i>)	741	587	370	88	6.8	115	111	45
PIWO	Pileated Woodpecker (<i>Dryocopus pileatus</i>)	611	439	141	23	13.0	160	151	65
OSFL	Olive-sided Flycatcher (<i>Contopus borealis</i>)	540	306	175	33	42.4	175	149	65
RBNU	Red-breasted Nuthatch (<i>Sitta canadensis</i>)	481	430	257	88	2.3	100	97	40
GRJA	Gray Jay (<i>Perisoreus canadensis</i>)	418	385	329	191	3.7	85	72	20
WWPE	Western Wood-Pewee (<i>Contopus sordidulus</i>)	154	107	78	16	56.3	150	129	55
RTHA	Red-tailed Hawk (<i>Buteo jamaicensis</i>)	131	103	58	14	7.2	200	156	65
RBSA	Red-breasted Sapsucker (<i>Sphyrapicus ruber</i>)	129	118	68	22	9.1	130	94	35

* N_t = Total number of detections at all distances, including new and repeat detections of individuals from separate sampling points within a landscape.

† N_{new} = Total number of detections at all distances, including only detections of new individuals within a landscape during a visit.

‡ N_{exact} = Total number of detections, including new and repeat detections, with an exact estimate of detection distance.

§ N_{50} = Total number of detections within 50 m of a sampling point, including new and repeat detections of individuals from separate sampling points within a landscape.

|| % edge = Percent of detections within 50 m of a sampling point (N_{50}) that were within 10 m of a seral condition (i.e., induced) patch edge. See Appendix for definition of seral conditions.

¶ Cdd = 75% cumulative detection distance (m); 75% of detections with an exact estimate of detection distance (N_{exact}) were at this distance or less.

Edd = Effective detection distance (m) computed using the program DISTANCE (Buckland et al. 1993, Laake et al. 1993), based on detections with an exact estimate of detection distance (N_{exact}).

** SI = Sampling intensity (%); estimated percentage of each landscape sampled based on each species' effective detection distance (Edd) [from McGarigal 1993].

sampling intensity was actually much greater for most species (range 10–65%, Table 1).

We sampled diurnal breeding birds in the Drift Creek, Lobster Creek, and Nestucca River basins in 1990, 1991, and 1992, respectively. Each year, we sampled birds four times in each of the 10 landscapes at nearly regular intervals between 1 May and 12 July. We varied the order in which sampling points within a landscape were visited so that each point was surveyed at different times during the morning. Surveys were not conducted under conditions of dense, low-lying and widespread fog, winds exceeding 15 km/h, or rain heavier than a light drizzle. During each sample, observers visited all sampling points within the landscape on the same day. Surveys began 15–20 min before sunrise and ended within 4 h after sunrise. On each visit to a sample point, trained observers waited 2 min

to allow birds to resume normal activity and then recorded all birds detected (90.2% aurally, 1.0% visually, 8.8% both aurally and visually) at any distance during an 8-min sampling period (Reynolds et al. 1980, Scott and Ramsey 1981, Fuller and Langslow 1984, Verner 1988). Whenever possible (71.6% of total detections), observers noted the distance between bird and sample point when a bird was first detected. Because the same bird sometimes was heard at >1 station along a transect, observers noted for each detection whether the individual was a new or repeat detection. This was determined subjectively by keeping a mental image of bird locations along a transect for species with loud vocalizations or species that tend to move rapidly and have estimated home ranges encompassing the distance between two stations. Only new detections during the sample of a landscape were included in the analysis.

Our goal was to estimate relative bird abundance at the landscape level; therefore, bird abundances within each landscape were considered independent observations for purposes of analysis.

Visits were made by four observers in 1990 and 1992 and three observers in 1991; two observers were the same during all three years and three others were involved for one or two years each. During each year, each observer's effort was distributed equally among sample points over the four visits to eliminate any systematic observer bias (i.e., each observer visited each point once). However, in 1991, because there were only three observers, each observer visited some sampling points twice. We attempted to minimize observer variability by subjecting all observers to a 3–4 wk training period prior to the start of each breeding season.

Vegetation mapping

To map vegetation, we modified an existing vegetation classification scheme developed and widely used in western Oregon and Washington for wildlife-habitat relationships (Hall et al. 1985). We defined 27 patch types (see Appendix for complete definitions), including 5 nonforested patch types and 22 forested patch types; the latter varied on the basis of plant community (conifer, hardwood, mixed), seral condition (grass/forb, shrub, sapling, pole, small sawtimber, large sawtimber), and canopy closure (open, closed). These patch types correspond to broad habitat types that are widely recognized to be meaningful to a wide variety of wildlife in western Oregon and Washington (Bruce et al. 1985). Late-seral forest, as we defined it, included hardwood-, mixed-, and conifer-large sawtimber. In some landscapes, late-seral forest also included scattered remnant old-growth trees and patches. We defined minimum patch size as 0.785 ha and ≥ 50 m wide in the narrowest dimension. This minimum area corresponds roughly to the smallest estimated home range size of any bird species found in the study area (Brown 1985). The minimum width represents a somewhat arbitrary decision based on practical considerations to avoid mapping the numerous narrow stringers of discrete vegetation along small streams and roads. The implications of this choice of minimum patch size are discussed below under *Scope and limitations*.

Initially, we mapped vegetation patches in each landscape on aerial photos (1988–1989 color infrared, 1:20 000) using a stereoscope, then verified or remapped in the field (i.e., ground-truthed) 100% of each landscape. Vegetation cover maps of each landscape were then transformed into planimetrically corrected digital coverages using a second-order analytical stereoplotter (Carto AP190, Carto Instruments, Incorporated, P.O. Box 130, Vashon, Washington) with 6-power magnification binocular attachments. With these aerial photos, the analytical stereoplotter offered a potential resolution of < 1 m; however, given the error in

interpreting the exact location of “fuzzy” patch boundaries, we assumed a resolution of 20 m.

Data analysis

Fig. 3 portrays a schematic outline of the sequence of procedures employed in the data analysis.

Bird abundance.—For each species, we calculated an index of abundance for each landscape to serve as the dependent variable in the analyses of bird-habitat relationships. We calculated the average number of bird detections (including both visual and aural detections of both sexes) per visit per station (i.e., sampling point within landscape) for each species, including detections at any distance from the station. We included detections of birds flying through or over the stand (5.2% of total detections) as well because we felt that these birds were probably using habitat within the landscape; excluding these detections did not change the results. Because we did not make any statistical comparisons among species, it was not necessary to compute density estimates for each species based on each species' effective detection distance, nor was it necessary to consider differences in detectability among species.

We did not adjust for potential differences in detectability among patch types for two reasons. First, birds were detected in more than one patch type from most stations, and it would have been impossible to adjust estimates for those stations. Second, we found little evidence that effective detection distances varied in relation to habitat area and configuration at the landscape scale. Specifically, of the 15 species associated with late-seral forest considered in this study (see *Results: Bird-habitat relationships*), 3 (Winter Wren, Varied Thrush, and Chestnut-backed Chickadee; see Table 1 for scientific names) had sufficient (> 30) detections in each landscape to compute a separate effective detection distance for each landscape and 3 (Evening Grosbeak, Brown Creeper, and Hammond's Flycatcher) required that we pool the detections across replicate landscapes in each landscape structural category (Fig. 2). Effective detection distances were computed using program DISTANCE (Buckland et al. 1993, Laake et al. 1993). We regressed late-seral forest area (%LAND) and 10 individual and three composite (principal components) indices of late-seral forest configuration (see *Methods: Data analysis: Vegetation patterns*) on each species' effective detection distance using simple linear regression models. Effective detection distance did not vary in relation to either habitat area or configuration at the landscape scale for the Winter Wren, Varied Thrush, Evening Grosbeak, Brown Creeper, and Hammond's Flycatcher ($P > 0.05$). Effective detection distance of the Chestnut-backed Chickadee increased slightly as late-seral forest area increased ($N = 30$, $P = 0.021$, $R^2 = 18\%$) and mean patch size increased ($N = 30$, $P = 0.037$, $R^2 = 15\%$). Thus, abundance estimates for this species were probably biased high in the least fragmented landscapes. Overall, however, we

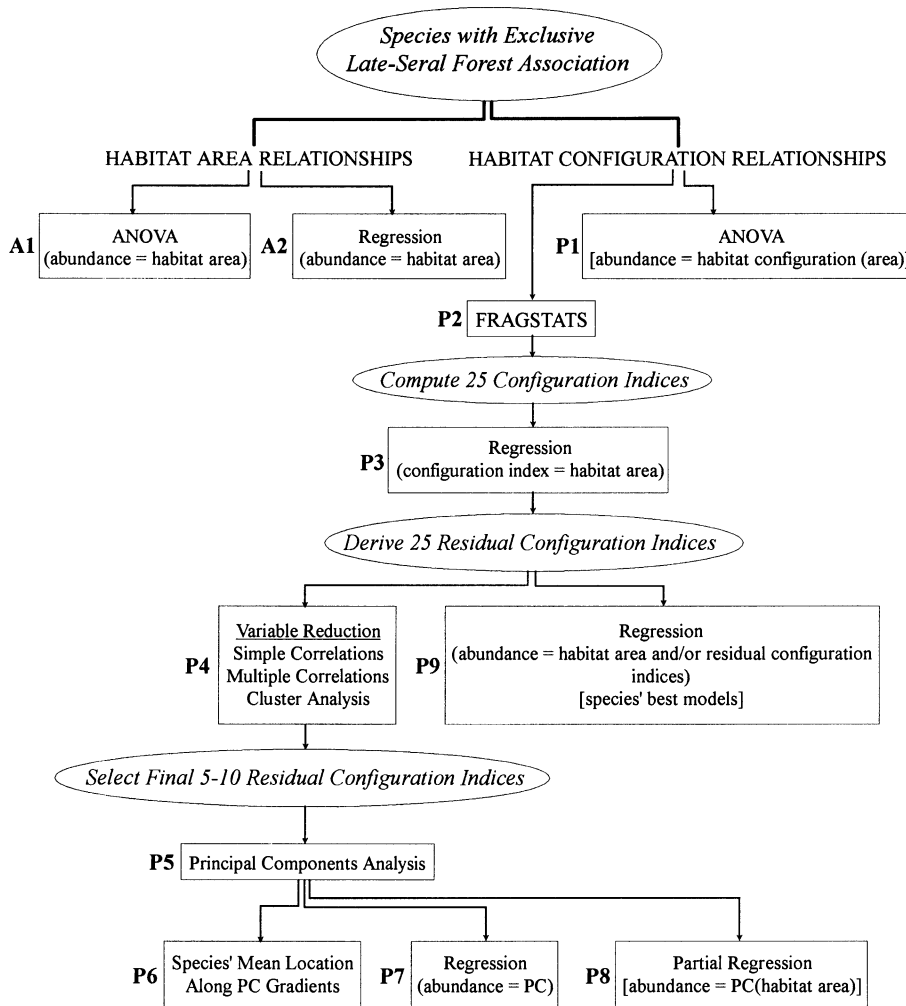


FIG. 3. Schematic outline of the sequence of procedures used to assess bird-habitat relationships (see text for details of procedures). Boxes represent statistical procedures and their alpha-number codes are cross-referenced with the discussion in the *Methods* section.

found little evidence that variation in effective detection distance among landscapes was affecting bird abundance estimates at the landscape scale and confounding our analyses. Finally, we felt confident that detectabilities within 50 m of the station did not vary among patch types. Thus, we also calculated the average number of bird detections per visit per area, including only detections within 50 m of the station. Preliminary analyses indicated that both abundance indices produced similar results, so we report only the results of analyses based on detections at any distance. Dependent variables were log-transformed to improve the distribution of the residuals in the analysis of variance (ANOVA) and regression analyses described below; subsequent analyses of the residuals indicated that normality and variance assumptions were adequately met in all cases.

Vegetation patterns.—We imported the digital vegetation map coverages of each landscape into the ARC/

INFO Geographic Information System and used the program FRAGSTATS (Fig. 3, P2; McGarigal and Marks 1995) to calculate the area and spatial configuration of late-seral forest (i.e., large sawtimber patch types pooled together) and each large sawtimber patch type (conifer-, mixed-, and hardwood-large sawtimber). We used the proportional abundance (%LAND; percent of landscape comprised by patch type) of late-seral forest and each large sawtimber patch type (hereafter, all referred to as patch types) in all analyses. The other patch types present in each landscape (shown pooled together as early-seral forest in Fig. 2) affected the configuration of late-seral forest only by affecting the contrast (see below) between each late-seral forest patch and its neighborhood.

For each patch type, 25 indices of landscape configuration were used that we considered appropriate for these landscapes (Table 2). These indices quantify different aspects of configuration, although many are re-

TABLE 2. Indices used to quantify the spatial extent and configuration of patch types in 30 300-ha landscapes in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990–1992.

Acronym	Index name (units)	Description*
%LAND†	Percent of landscape (%)	Percentage of the landscape composed of the corresponding patch type
LPI	Largest patch index (%)	Percentage of the landscape composed of the largest patch of the corresponding patch type
NP	Number of patches	Number of patches
PD	Patch density (no./100 ha)	Density of patches
MPS	Mean patch size (ha)	Average size of patch
PSSD	Patch size standard deviation (ha)	Absolute measure of patch size variability
PSCV	Patch size coefficient of variation (%)	Relative measure of patch size variability
TE	Total edge (m)	Total length of edge involving the corresponding patch type
ED	Edge density (m/ha)	Density of edge involving the corresponding patch type
CWED	Contrast-weighted edge density (m/ha)	Density of edge involving the corresponding patch type weighted by the degree of structural and floristic contrast between adjacent patches; equals ED when all edge is maximum contrast and approaches 0 when all edge is minimum contrast
MECI	Mean edge contrast index (%)	Mean patch edge contrast as a percent of maximum contrast; equals 100% when all edge is maximum contrast and approaches 0 when all edge is minimum contrast
AWMECI	Area-weighted mean edge contrast index (%)	Similar to mean patch edge contrast, but patch edge contrast weighted by patch area
TECI	Total edge contrast index (%)	Total edge contrast as a percent of maximum contrast; equals 100% when all edge is maximum contrast and approaches 0 when all edge is minimum contrast
MSI	Mean shape index	Mean patch shape complexity; equals 1 when all patches are circular and increases as patches become non-circular
AWMSI	Area-weighted mean shape index	Similar to mean shape index, but patch shape index weighted by patch area
LSI	Landscape shape index	Landscape shape complexity; equals 1 when the landscape consists of a single circular patch and increases as landscape shape becomes noncircular and the amount of internal edge increases
MPFD	Mean patch fractal dimension	Mean patch shape complexity; approaches 1 for simple geometric shapes (e.g., circle) and 2 for complex shapes
TCA	Total core area (ha)	Total amount of core area of the corresponding patch type; core areas were defined by eliminating a 100 m wide buffer along the perimeter of each patch
LCAS	Landscape core area similarity (%)	Percentage of the landscape composed of core area (as defined above) of the corresponding patch type
NCA	Number of core areas	Number of core areas, as defined above
CAD	Core area density (no./100 ha)	Density of core areas, as defined above
MCA	Mean core area (ha)	Average size of core area per patch, as defined above
MCAI	Mean core area index (%)	Average percentage of a patch that is core area, as defined above
TCAI	Total core area index (%)	Total percentage of the landscape that is core area, as defined above
CASD	Core area standard deviation (ha)	Absolute measure of core area variability, as defined above
CACV	Core area coefficient of variation (%)	Relative measure of core area variability, as defined above

* See McGarigal and Marks (1995) for a complete description and definition of each index.

† %LAND is equivalent to LSIM in McGarigal 1993.

dundant and simply represent alternative formulations of the same information. The landscape boundary was considered the patch edge for the purpose of calculating patch size, shape, and other metrics, even for those patches that continued beyond the landscape boundary. We computed several core area indices based on a specified edge width, which, for the purpose of this study, we defined as a 100 m wide buffer along the perimeter of each patch. This width represents a somewhat ar-

bitrary decision based, in part, on avian studies by Temple (1986) and local studies of microclimatic gradients along forest edges (Chen and Franklin 1990).

We computed several indices based on edge contrast. These metrics indirectly include information about the early-seral patches surrounding the target late-seral forest. Edge contrast was defined using weights ranging between 0 and 1, with increasing weights representing greater edge contrast. We defined edge contrast on the

basis of floristic and structural differences between adjacent patch types (see McGarigal 1993 for a more detailed explanation). Briefly, each change in seral condition along the sequence from grass/forb through large sawtimber (Appendix) received a weight of 0.2; each change in plant community along the sequence from hardwood to mixed to conifer received a weight of 0.05; and a change from an open- to closed-canopy condition received a weight of 0.05. Grass-forb and shrub conditions were always defined as open-canopy and small and large sawtimber conditions were always defined as closed canopy. Nonforest patch types were always considered open-canopied and a full plant community difference (weight = 0.1) with all other patch types. Seral condition difference among nonforest patch types or between nonforest and forest patch types depended on the height of the dominant vegetation in the nonforest patch type. The sum of seral condition, plant community, and canopy closure weights determined the overall weight for a particular edge. The decision to weight seral condition differences more than plant community and canopy closure differences was based partly on ecological considerations, but also on differences in the arbitrariness in delineating patch edges. Most seral condition differences represent induced edges (i.e., created through management activities); these edges were very discrete and thus objectively delineated. On the other hand, most plant community and canopy closure differences represent inherent edges (i.e., created through natural processes); these ecotones were usually "fuzzy" and thus difficult to delineate objectively.

Changes in habitat area and configuration were highly confounded in the 30 landscapes; that is, habitat area and configuration covaried in a somewhat predictable manner. To evaluate the independent relationships between habitat area and configuration and bird abundances, we used regression analysis to remove any significant empirical relationship between habitat area (%LAND) and each configuration index (Table 2) for each patch type (Fig. 3, P3). %LAND was regressed on each of the configuration indices using general linear and nonlinear (quadratic polynomials) models. Based on an analysis of the residuals, we used appropriate dependent variable transformations (\log_{10} or square root) to ensure that regression assumptions were met. Zero-intercept models were used for configuration indices that logically must pass through the origin when patch type area is 0. For each patch type, we included only landscapes in which the patch type was present. Thus, sample sizes for the regression analyses varied among patch types. We constructed models for each configuration index and patch type separately and selected the most logical model exhibiting the largest, significant R^2 , and best residual distribution. Using this process, we transformed the 25 original configuration indices into 25 new residual configuration indices for

each patch type representing variation in configuration independent of area.

To summarize the set of 25 residual configuration indices for each patch type into a more parsimonious set of variables, we used a combination of techniques, including: (1) Pearson product-moment correlations between each pair of indices; (2) multiple correlations between each index and all others; (3) cluster analysis using the Unweighted Pair-Group Average fusion strategy (Sneath and Sokal 1973) based on Pearson product-moment correlations between each pair of indices; and (4) principal components analysis (PCA). For all techniques, we included only landscapes in which the corresponding patch type was present. We used the first three procedures to eliminate redundant variables (Fig. 3, P4). The choice of an index within a group of redundant indices was based on personal preference and interpretability. We reduced the set of 25 residual configuration indices to 10 final variables for each patch type that quantified somewhat different aspects of configuration. The final number of variables, in part, reflected our desire to maintain roughly a 3:1 ratio of observations-to-variables in the PCA. We used PCA to summarize the 10 final residual configuration indices into 3-4 new principal components representing independent gradients in configuration for each patch type (Fig. 3, P5). The final principal components were rotated using the Varimax method and were interpreted using the component loadings (i.e., correlations between the principal component and each original variable). We did not test component loadings for statistical significance; instead, we based our interpretations on the largest loadings (generally $r > 0.75$) for each component. We judged the usefulness of the final principal components using the broken-stick criterion (Jackson 1993) and final communalities for each variable. The broken-stick criterion involves comparing the eigenvalue or relative percent variance accounted for by each principal component with that expected under the broken-stick distribution (i.e., based on random data). Components with eigenvalues greater than expected are judged meaningful. Final communalities represent the percent of variation in each original variable accounted for by the retained principal components.

Bird-habitat relationships.—To identify species closely associated with late-seral forest, we compared the distribution of detections among patch types to that expected based on the distribution of sampling effort among patch types. First, we compared observed and expected distributions among seral condition classes (grass/forb, shrub, sapling, pole, and large sawtimber); there were not enough small sawtimber patches to include this seral condition. We considered all bird detections ≤ 50 m from a station; we excluded detections at greater distances because of the subjectivity in estimating exact bird locations and patch associations at distances > 50 m. For each detection within 50 m, we

recorded the seral condition of the bird's location; birds within 10 m of a seral condition edge were recorded as such (i.e., they were not associated with either patch type). For each species, we summed the number of detections in each seral condition class across all sampling points ($n = 1046$) and calculated the proportion in each type, as well as the percentage of total observations in induced edge habitat (i.e., ≤ 10 m from seral condition edge). Note that we did not allocate each detection to 1 of the 27 specific patch types because we were not confident that all bird observers could consistently differentiate among patch types. However, we were confident that seral conditions could be consistently and objectively differentiated by all observers. To determine the expected distribution, we calculated the area of each seral condition within a 50-m radius circle around each sampling point. Thus, a sampling point located ≥ 50 m from an induced edge contributed 0.785 ha of the corresponding seral condition, whereas a sampling point located < 50 m from an induced edge contributed area to each seral condition proportional to its representation on the plot. We summed the area of each seral condition across all sampling points ($n = 1046$) and calculated the proportion of the total area sampled (815.17 ha, excluding small sawtimber and nonforested patch types) in each seral condition. We did not account for seral condition edges (i.e., the area within 10 m of an induced edge) in these area calculations, but this should not bias the proportional abundance of each seral condition. Indeed, results were similar when we excluded all sampling points containing a seral condition edge within 50 m.

We compared observed and expected distributions both graphically and objectively using 95% simultaneous Bonferroni confidence intervals (Neu et al. 1974, Byers and Steinhorst 1984). However, because the individual bird detections used to calculate the observed distribution did not represent independent observations (e.g., the same birds were likely detected on subsequent visits to sample points), the significance tests associated with the confidence intervals are not valid. Thus, we used the confidence intervals as an aid and not to suggest statistical rigor. Adequate expected cell values (> 1) were achieved for species with > 48 total detections, although we evaluated species with as few as 20 detections.

Second, because associations with seral conditions may mask stronger associations with specific plant communities (e.g., conifer-dominated habitats vs. hardwood-dominated habitats), we also compared observed and expected distributions among specific patch types. Because bird detections within 50 m were not recorded to specific patch type, for the reasons discussed above, we included only sampling points ≥ 50 m from a patch edge. Thus, each 50-m radius plot consisted of a single patch type and all detections within 50 m could be associated with a specific patch type. Fifty-nine percent (613/1046) of the sampling points representing 12 for-

ested patch types were included in the analysis; the 3 shrub types were combined into a single class, and the remaining 8 forested patch types were not adequately sampled. We compared observed and expected distributions as described above. Because we were interested in identifying species exclusively associated with large sawtimber or a specific plant community within large sawtimber, we used this analysis to filter out species that seemed, on first examination, to exclusively select the large sawtimber seral condition (i.e., late-seral forest), but upon scrutiny actually selected a particular plant community type in both the pole and sawtimber seral conditions; the detailed results of this analysis are not included in this paper.

In addition, for species with exclusive selection for the large sawtimber seral condition, we regressed the area of each large sawtimber patch type (conifer-, hardwood-, and mixed-large sawtimber) on the abundance index for each species separately using general linear and nonlinear (quadratic polynomials) models. We included all 30 landscapes in the analysis, regardless of whether the corresponding patch type was present or absent from the landscape, and treated all 30 landscapes as independent observations.

From these analyses, we identified 15 species strongly associated with late-seral forest habitats (either late-seral forest as a class or one of the individual large sawtimber patch types) or the juxtaposition of late-seral forest and early-seral, open-canopied habitats and that were sufficiently abundant and widely distributed for statistical analyses; all subsequent analyses were restricted to these species. For these species, we assessed the effects of habitat area and configuration on each species' abundance using three-way ANOVA (3 basins by 6 levels of area by 1 or 2 levels of configuration depending on area, $n = 30$) with basin as a block and configuration nested within area (Fig. 3, A1 and P1). Although we categorized both area and configuration variables for purposes of this ANOVA study design (Fig. 2), we did this in part to ensure representation of the full range of these inherently continuous gradients in landscape structure. Moreover, the ANOVA design treated configuration as a simple dichotomous variable defined on the basis of edge density (i.e., high or low density), yet we recognized that configuration consists of many aspects. Therefore, we also assessed the relationship between habitat area and configuration and bird abundance using correlational procedures, as follows.

To determine the strength and nature of the relationship between *habitat area* and bird abundance, we used regression analysis (Fig. 3, A2). The area (%LAND) of the corresponding patch type (either late-seral forest as a class or the individual large sawtimber patch types) was regressed on each species' abundance index separately using general linear and nonlinear (quadratic polynomials) models. We included all 30 landscapes in the analysis, regardless of whether the

corresponding patch type was present or absent from the landscape, and treated all 30 landscapes as independent observations. The results were similar when only landscapes with non-zero values of the independent variable ($n \geq 27$) were included in the analysis.

To determine the strength and nature of the relationship between *habitat configuration* and bird abundance, we used four techniques. For all techniques, we included only landscapes in which the corresponding patch type was present and treated those landscapes as independent observations. First, we calculated each species' weighted average location along each of the retained standardized principal components for the corresponding patch type (Fig. 3, P6). We used each species' index of abundance to weight each landscape's standardized principal component score. The weighted average location represents the species' average association or location along the landscape configuration gradient represented by the principal component. We also constructed a 95% confidence interval (CI) about the mean. If the CI did not include zero (i.e., the average landscape condition), we concluded that the species was associated with landscape configurations significantly different from the average landscape configuration along the corresponding principal component gradient. Recall that the area effect was removed from the configuration indices; that is, after removing the relationship with area, the residual configuration indices represent the departure in landscape configuration from expected for the amount of patch type present in a landscape. Therefore, a species with a location significantly different from the average used landscapes in which the corresponding patch type was distributed more or less heterogeneously (depending on the direction of the difference) than the average configuration, regardless of whether the patch type comprised 20 or 80% of the landscape.

Second, we determined the relationship between each corresponding principal component and each species' abundance using simple linear regression (Fig. 3, P7). The principal component scores for the corresponding patch type were regressed on each species' abundance index separately.

Third, we determined the relationship between each corresponding principal component and each species' abundance after accounting for any relationship with habitat area using partial regression analysis (Fig. 3, P8). The principal component scores and habitat area (%LAND) for the corresponding patch type were regressed on each species' abundance index separately. The partial F statistic and associated partial R^2 for the principal component variable measure the additional explanatory contribution of the configuration gradient after habitat area has been taken into account. Even though the empirical, and often nonlinear, relationship between area and configuration was removed from each configuration index univariately, this did not preclude multiple linear correlations between the principal com-

ponent variables and habitat area, because the principal components represented linear combinations of all the configuration variables. We conducted partial regression analyses only for species with significant habitat area relationships.

Last, we evaluated the relationship between each species' abundance and a combination of habitat area (%LAND) and individual residual configuration indices using multiple linear regression (Fig. 3, P9). Specifically, we used stepwise selection and maximum R^2 methods to identify the "best" simple or multiple linear regression model. In general, we identified the model with the largest R^2 in which all component variables had significant ($P < 0.1$) partial F statistics.

RESULTS

Bird abundance

We recorded 82 704 detections representing 89 species during four visits to 1046 sampling stations distributed among the 30 landscapes. Thirty-three percent ($n = 27 652$) of these detections were of the 15 species associated with late-seral forest addressed in this paper (Table 1). Eighty-nine percent ($n = 24 541$) of these detections were of new individuals and therefore included in this analysis. Number of detections varied greatly among species, in part because of differences in abundance, but also because of differences in effective detection distances (Table 1).

Landscape configuration

By design, the configuration of late-seral forest varied greatly among the 30 landscapes (Table 3). Most indices of late-seral forest configuration had coefficients of variation $>50\%$ (mean = 76%), indicating that gradients in many aspects of configuration were represented in these landscapes. Three principal components for late-seral forest were judged meaningful by the broken-stick criterion and accounted for 78% of the variation in the original data set containing the final 10 residual configuration indices (Table 4). The first principal component (PC1) represented a gradient in *patch shape and edge contrast*. Landscapes positively associated with PC1 contained late-seral forest distributed in patches with more complex shapes, greater edge density, less core area, and greater edge contrast than the average landscape for the particular amount of late-seral forest present. The second principal component (PC2) represented an independent gradient in *patch density*. Landscapes positively associated with PC2 contained late-seral forest fragmented into more patches than the average landscape for the particular amount of late-seral forest present. The third principal component (PC3) represented an independent gradient in *patch size*. Landscapes positively associated with PC3 contained late-seral forest distributed in smaller patches than the average landscape for the particular amount of late-seral forest present. These three PC's represent

TABLE 3. Summary statistics on late-seral forest area and configuration for 29 300-ha landscapes in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990–1992. Only indices included in the final principal components analysis for late-seral forest or one of the large sawtimber patch types (Table 4) are included.

Index*	Units	Min	Max	Mean	CV
Percent of landscape	%	0.7	100.0	51.9	56
Patch density	no./100 ha	0.3	2.1	0.6	74
Mean patch size	ha	2.1	281.3	124.6	73
Patch size coefficient of variation	%	0.0	172.0	31.0	174
Mean patch fractal dimension	none	1.19	1.37	1.27	3
Core area density	no./100 ha	0.0	1.7	0.7	65
Core area coefficient of variation	%	0.0	195.4	37.7	171
Mean core area index	%	0.0	76.6	40.7	58
Total core area index	%	0.0	76.6	44.0	48
Landscape core area similarity	%	0.0	76.6	28.0	83
Largest patch index	%	0.7	100.0	49.6	61
Edge density	m/ha	1.1	39.3	19.5	58
Contrast-weighted edge density	m/ha	0.6	25.4	10.8	65
Total edge contrast index	%	2.3	92.6	36.3	51

* See Table 2 for description of each index.

dominant gradients of variation in the configuration of late-seral forest (i.e., fragmentation) among the 29 landscapes containing late-seral forest. Final communalities indicate that most of the residual configuration indices were well accounted for by the three PC's; notable exceptions were total edge contrast index and patch size variability. The relative percent variance measure indicates that landscape configuration cannot be described adequately by a single gradient because each gradient alone accounts for only 20–30% of the variance.

The results of PCA for the conifer and mixed large sawtimber patch types were comparable (Table 4). In both cases, the interpretations of the retained PC's are slightly different as judged by the component loadings. Edge contrast was separated out as a distinct and independent gradient for both patch types, indicating that the degree of structural and floristic contrast between these patch types and the surrounding landscape varies strongly among landscapes, although the edge contrast gradient for the mixed large sawtimber patch type was not deemed significant by the broken-stick criterion. The other PC's represent gradients in other aspects of configuration; each represents a gradient in which the corresponding large sawtimber patch type is distributed more or less heterogeneously than the average landscape for the amount of sawtimber present. Otherwise, the performance of PCA for these two patch types as judged by the relative percent variance measure and final communalities was similar to that described above for late-seral forest.

Bird-habitat relationships

Species associated with late-seral forest.—Twelve bird species exhibited strong and exclusive “selection” for late-seral forest based on the analyses of use vs. availability (Table 5). All of these species, however, were detected in two or more seral conditions, and some (e.g., Winter Wren) were relatively common in

younger seral conditions, even though they demonstrated exclusive statistical selection for late-seral conditions. In addition to these 12 species, 3 other less common but widely distributed species (Olive-sided Flycatcher, Red-tailed Hawk, and Western Wood-Pewee) seemed to be associated with late-seral forest, yet were detected too infrequently (< 20 times) within 50 m of a station (excluding detections within 10 m of an induced edge) to analyze (Table 1). Nevertheless, the limited detections within 50 m for these species coupled with field observations associated with the more distant detections suggested that these species were associated with the juxtaposition of late-seral forest and early-seral, open-canopied habitats. Moreover, these 3 species were each present in more than 23 of the 30 landscapes. Therefore, we included these 3 species in all subsequent analyses. Several additional species seemed to be strongly associated with late-seral forest, but were detected too infrequently (e.g., Spotted Owl, Vaux's Swift, Bald Eagle) to warrant conclusions regarding habitat associations, or were absent from too many (> 12) landscapes to analyze using ANOVA or regression (e.g., Downy Woodpecker, Pine Siskin, and Ruffed Grouse). In addition, 2 species (Hermit Warbler and Pacific-slope Flycatcher) demonstrated exclusive “selection” for the large sawtimber seral condition, but examination at a finer resolution (i.e., specific patch types) revealed that these species actually selected particular plant communities (conifer- and hardwood-dominated, respectively) in both the pole and large sawtimber seral conditions. Similarly, 2 species (Golden-crowned Kinglet and Hairy Woodpecker) exhibited “selection” for large sawtimber, but showed “selection” for other seral conditions as well. These species were excluded from subsequent analyses.

Thus, we identified 15 species that were strongly associated with late-seral forest habitats or the juxtaposition of late-seral forest and early-seral, open-canopied habitats, and that were sufficiently abundant and

TABLE 4. Principal components derived from a set of residual configuration indices (i.e., correlation with habitat area has been removed, see *Methods: Data analysis: Vegetation patterns* for details) for late-seral forest and two large sawtimber patch types in 30 300-ha landscapes in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990–1992. Component loadings $> \pm 0.69$ are in boldface type.

Patch type*	Principal components				Final communality (%)†
	PC1	PC2	PC3	PC4	
Expected eigenvalue‡	2.93	1.93	1.43	1.10	
Late-seral forest					
Observed eigenvalue	3.32	2.33	2.18		
% variance	33.2	23.3	21.8		
Cum. % variance	33.2	56.5	78.3		
Component loadings§					
TCAI	-0.86	-0.16	-0.36		88.7
MPFD	0.85	-0.05	0.05		72.6
ED	0.81	0.34	0.05		77.0
TECI	0.76	-0.12	0.17		61.6
MCAI	-0.64	-0.46	-0.55		91.5
PD	-0.04	0.89	0.09		79.4
CAD	0.26	0.84	0.01		77.6
PSCV	-0.12	0.58	0.55		65.0
MPS	-0.17	-0.29	-0.84		82.0
LPI	-0.36	0.23	-0.84		87.7
Conifer-large sawtimber					
Eigenvalue	2.95	2.62	1.80		
% variance	29.5	26.2	18.0		
Cum. % variance	29.5	55.7	73.7		
Component loadings§					
PSCV	0.90	0.01	0.10		82.7
ED	0.81	0.46	0.01		86.9
PD	0.79	0.03	0.09		63.6
MPS	-0.63	-0.52	-0.14		68.3
LCAS	-0.39	-0.88	0.10		93.1
TCAI	-0.12	-0.85	0.03		74.6
MPFD	-0.22	0.69	0.33		63.1
CAD	0.34	0.39	-0.12		28.5
TECI	-0.07	0.08	0.95		90.7
CWED	0.35	-0.07	0.86		85.7
Mixed-large sawtimber					
Eigenvalue	2.26	2.05	2.04	1.85	
% variance	22.6	20.5	20.4	18.5	
Cum. % variance	22.6	43.1	63.5	82.0	
Component loadings§					
CWED	0.95	0.08	-0.02	0.06	91.3
TECI	0.85	-0.36	0.00	0.06	85.1
ED	0.10	0.89	0.23	0.14	86.9
TCAI	0.46	-0.74	-0.09	0.12	78.4
PSCV	0.01	0.16	0.89	0.23	86.9
PD	0.15	0.30	0.79	0.01	73.7
CAD	0.42	0.32	-0.73	0.06	81.8
MPS	0.18	-0.12	-0.04	-0.90	85.2
CACV	0.38	-0.06	0.11	0.75	72.4
MPFD	-0.18	0.59	-0.10	-0.62	77.8

* See Appendix for definition of each patch type. Late-seral forest, $n = 29$ landscapes; conifer-large sawtimber, $n = 27$ landscapes; mixed-large sawtimber, $n = 27$ landscapes.

† Final communalities equal the percent of variation in each variable accounted for by the retained principal components.

‡ Expected eigenvalue based on the broken-stick distribution (i.e., random data) (Jackson 1993). Principal components with observed eigenvalue $>$ expected eigenvalue are considered meaningful.

§ Component loadings equal the correlations between each variable and the principal component; see Table 2 for description of each index and appropriate units.

widely distributed for subsequent statistical analyses. Variation in abundance among landscapes for 3 of these species was more strongly related to the abundance of a specific large sawtimber patch type than to the abundance of late-seral forest as a class. Pileated Wood-

peckers and Red-breasted Nuthatches were more closely related to changes in conifer large sawtimber area, and Western Tanagers were more closely related to changes in mixed large sawtimber. Therefore, all bird-habitat relationship analyses for these 3 species were

TABLE 5. Distribution of bird detections (observed) and sampling effort (expected) among five seral condition classes in 30 300-ha landscapes in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990–1992. Data represent total area in each seral condition within 50 m of a sampling point ($n = 1046$ sampling points distributed among 30 landscapes) and birds detected within 50 m of a sampling point during four visits to each point.*

Species‡ distributions	Seral condition†					Total
	Grass/forb	Shrub	Sapling	Pole	Large saw	
Expected distribution						
Area sampled (ha)	34.45	16.92	54.40	297.83	411.58	815.17
Percent	4.2	2.1	6.7	36.5	50.5	100
Observed distribution						
Brown Creeper						
No. detections	1	0	1	7	786	795
Percent	0.1	0.00	0.1	0.9	98.9	100
Standard residuals*§	-5.63	-4.07	-7.14	-16.63	+19.20	
Winter Wren						
No. detections	6	7	18	830	2297	3158
Percent	0.2	0.2	0.6	26.3	72.7	100
Standard residuals§	-11.04	-7.24	-13.27	-9.54	+17.59	
Evening Grosbeak						
No. detections	1	0	1	22	417	441
Percent	0.2	0.0	0.2	5.0	94.6	100
Standard residuals§	-4.09	-3.03	-5.24	-10.96	+13.02	
Hammond's Flycatcher						
No. detections	1	0	1	8	320	330
Percent	0.3	0.0	0.3	2.4	97.0	100
Standard residuals§	-3.47	-2.62	-4.48	-10.25	+11.88	
Chestnut-backed Chickadee						
No. detections	9	3	44	572	1386	2014
Percent	0.5	0.2	2.2	28.4	68.8	100
Standard residuals§	-8.25	-6.01	-7.79	-6.04	+11.58	
Varied Thrush						
No. detections	0	0	1	76	420	497
Percent	0.0	0.0	0.2	15.3	84.5	100
Standard residuals§	-4.58	-3.22	-5.58	-7.84	+10.67	
Red Crossbill						
No. detections	0	0	5	48	359	412
Percent	0.0	0.0	1.2	11.7	87.1	100
Standard residuals§	-4.17	-2.93	-4.29	-8.36	+10.47	
Gray Jay						
No. detections	0	0	0	27	157	184
Percent	0.0	0.0	0.0	14.7	85.3	100
Standard residuals§	-2.79	-1.96	-3.50	-4.91	+6.65	
Red-breasted Nuthatch						
No. detections	0	0	0	6	80	86
Percent	0.0	0.0	0.0	7.0	93.0	100
Standard residuals§	-1.91	-13.4	-2.40	-4.53	+5.55	
Western Tanager						
No. detections	1	3	3	11	63	81
Percent	1.2	3.7	3.7	13.6	77.8	100
Standard residuals§	-1.31	+1.02	-1.03	-3.42	+3.46	
Red-breasted Sapsucker						
No. detections	0	0	0	2	18	20
Percent	0.0	0.0	0.0	10.0	90.0	100
Standard residuals§	-0.92	-0.65	-1.15	-1.96	+2.49	
Pileated Woodpecker						
No. detections	0	0	1	2	17	20
Percent	0.0	0.0	5.0	10.0	85.0	100
Standard residuals§	-0.92	-0.65	-0.29	-1.96	+2.17	

* Only species with ≥ 20 detections and demonstrating exclusive selection for large sawtimber are included here. Seral conditions used significantly more or less than expected based on 95% simultaneous Bonferroni confidence intervals are in boldface type; however, note that any category with zero observed use is always found to be significantly different than expected. Species are ordered relative to the strength of their selection for large sawtimber as judged by the magnitude of the standardized residuals.

† See Appendix for definition of seral conditions.

‡ Scientific names in Table 1.

§ Standardized residuals = (observed - expected)/ $\sqrt{\text{expected}}$.

conducted using the corresponding large sawtimber patch type.

Habitat area.—The relationship between habitat area and species' abundances within landscapes varied dramatically among the 15 species associated with late-seral forest. Based on the ANOVA, 5 species (Gray Jay, Brown Creeper, Winter Wren, Varied Thrush, and Chestnut-backed Chickadee) were strongly affected by changes in habitat area ($P \leq 0.007$), 5 species (Evening Grosbeak, Hammond's Flycatcher, Pileated Woodpecker, Western Wood-Pewee, and Red-breasted Nuthatch) were moderately affected ($0.011 \leq P \leq 0.092$), and 5 species (Red Crossbill, Red-breasted Sapsucker, Western Tanager, Olive-sided Flycatcher, and Red-tailed Hawk) were virtually unaffected ($P \geq 0.212$). Based on the regression analysis, the percent of variation in species' abundances accounted for by changes in late-seral forest area ranged from 0 to 63%. Species divided logically into three groups based on the strength of this relationship. Roughly 50–60% of the variation among landscapes in Gray Jay, Brown Creeper, Winter Wren, and Varied Thrush abundance was explained by the extent of late-seral forest. Only the Gray Jay had a significantly nonlinear relationship. Roughly 20–30% of the variation in Pileated Woodpecker, Evening Grosbeak, Red-breasted Nuthatch, Hammond's Flycatcher, Chestnut-backed Chickadee, and Western Tanager abundance was explained by the abundance of late-seral forest. Virtually none ($\leq 3\%$) of the variation in Red Crossbill, Western Wood-Pewee, Olive-sided Flycatcher, Red-breasted Sapsucker, and Red-tailed Hawk abundance was explained by late-seral forest area. Note that the results from the ANOVA and regression approaches are fairly consistent, with the exception of two species (Western Tanager and Western Wood-Pewee).

Habitat configuration.—Based on the ANOVA, only 2 of 15 species (Olive-sided Flycatcher and Western Wood-Pewee) associated with late-seral forest were affected ($P < 0.043$) by habitat configuration when evaluated as a simple dichotomous variable nested within four levels of habitat area (20, 40, 60, and 80% of landscape area in late-seral forest); both species were more abundant in the more fragmented landscapes. However, 8 species occupied landscapes that were more heterogeneous or fragmented than the average landscape configuration as defined by the first principal component gradient (Figs. 4 and 5). The exact nature of the gradient (i.e., the specific aspects of habitat configuration represented) varied among patch types (Table 4), but all represented a gradient from a relatively simple configuration of habitat (i.e., less fragmented) to a relatively complex configuration of habitat (i.e., more fragmented). Four of these species (Red-breasted Sapsucker, Western Wood-Pewee, Olive-sided Flycatcher, and Red-tailed Hawk) distinctly occupied landscapes that were more fragmented than the average landscape condition (Figs. 4 and 5), although the per-

centage of variation in each species' abundance among landscapes accounted for by this configuration gradient was low ($R^2 \leq 19\%$, Table 6) based on simple linear regression analysis. These species were not affected by habitat area. Conversely, the other 4 species (Gray Jay, Pileated Woodpecker, Red-breasted Nuthatch, and Western Tanager) also occupied landscapes that were more fragmented than the average landscape configuration (Figs. 4 and 5), yet variation in abundance among landscapes was not related to variation along this configuration gradient alone (Table 6) based on simple linear regression analysis. However, variation along this configuration gradient was at least mildly significant ($P < 0.097$) for 3 of these species (Gray Jay, Pileated Woodpecker, and Western Tanager) when habitat area relationships were taken into account first (Table 7).

Seven species occupied landscapes that were different from the average landscape configuration along the second principal component gradient (Figs. 4 and 5). Again, the nature of the gradient varied among patch types (Table 4). Four of these species (Western Wood-Pewee, Red-tailed Hawk, Pileated Woodpecker, and Red-breasted Nuthatch) occupied landscapes that were more fragmented than the average landscape condition (Figs. 4 and 5); however, only variation in Pileated Woodpecker abundance among landscapes was related to variation along this configuration gradient either with (Table 7) or without (Table 6) first taking habitat area into account, although the percent of variation accounted for was low in both cases ($R^2 = 15$ and 27% , respectively). The other 3 species (Gray Jay, Brown Creeper, and Hammond's Flycatcher) occupied landscapes that were less fragmented than the average landscape condition (Figs. 4 and 5), although only the Brown Creeper had a significant simple linear relationship between abundance and this principal component (Table 6) and none had significant partial correlations (Table 7). Thus, in contrast to the first principal component, habitat configuration defined by the second principal component did not have strong and consistent effects on abundance.

Seven species occupied landscapes that were more heterogeneous or fragmented than the average landscape condition as defined by the third principal component gradient (Figs. 4 and 5); all 7 species were associated with landscapes in which the late-seral forest was distributed in patches of smaller size than the average landscape. Simple linear regression results supported this finding for 4 of these species (Western Wood-Pewee, Red-tailed Hawk, Brown Creeper, and Hammond's Flycatcher), although the percent of variation accounted for by this patch size gradient was low ($R^2 \leq 17\%$, Table 6). Moreover, the latter 2 species did not have significant partial correlations (Table 7), indicating that mean patch size was not important after habitat area was considered. The other 3 species (Gray Jay, Olive-sided Flycatcher, and Red-breasted Sap-

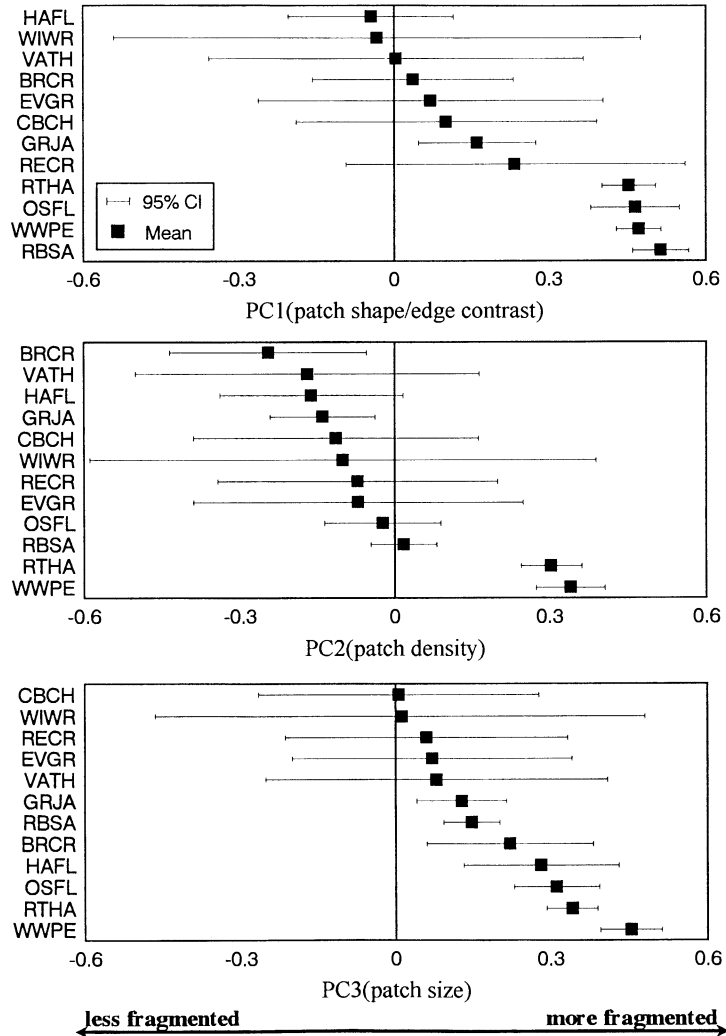


FIG. 4. Weighted average location (and 95% confidence interval) of bird species associated with late-seral forest along the first three principal component gradients representing the spatial configuration of late-seral forest in 29 300-ha landscapes in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990–1992. Data represent birds detected at any distance during four visits to 32–38 sampling points within each landscape. Weighted averages were based on relative abundance in each landscape. See Table 1 for the common and scientific names corresponding to bird acronyms, and Table 4 for definitions of each principal component.

sucker) did not have simple linear relationships either with (Table 7) or without (Table 6) first taking habitat area into account. Two other species (Winter Wren and Western Tanager) had significant partial correlations (Table 7) even though their weighted average landscape condition did not differ from the average (Figs. 4 and 5). Fifteen percent of the variation in Winter Wren abundance among landscapes was explained by the patch size gradient after taking habitat area into account. Winter Wrens were associated with less fragmented landscapes (i.e., those with larger patch sizes than average). Thirteen percent of the variation in Western Tanager abundance among landscapes was explained by a gradient in patch density and patch size variability after taking into account mixed large saw-

timber area. Western Tanagers were associated with the more fragmented landscapes.

In a separate analytical approach, the “best” combination of habitat area and residual configuration indices for each species explained between 26 and 68% of the variation in abundance among landscapes (Table 8). Three species did not exhibit any significant habitat configuration relationships after habitat area was taken into account. Conversely, 4 species exhibited significant relationships with habitat configuration only. Both habitat area and habitat configuration contributed to the other 8 species, although habitat area was the most significant explanatory variable in all cases. Individual residual configuration indices explained an additional 11–28% of the variation in species’ abundances among

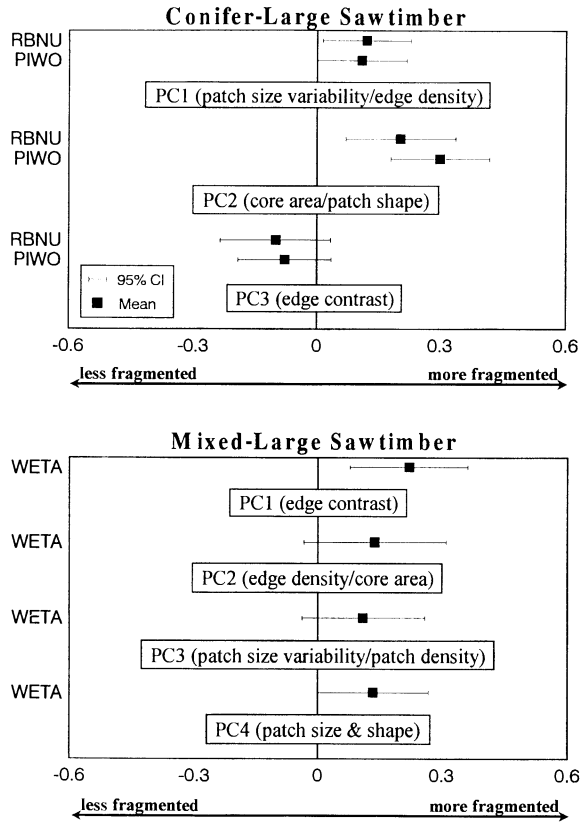


FIG. 5. Weighted average location (and 95% confidence interval) of bird species strongly associated with conifer- and mixed-large sawtimber along the first 3–4 principal component gradients representing the spatial configuration of conifer- (top) and mixed- (bottom) large sawtimber in 27 300-ha landscapes in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990–1992. Data represent birds detected at any distance during four visits to 32–38 sampling points within each landscape. Weighted averages were based on relative abundance in each landscape. See Table 1 for the common and scientific names corresponding to bird acronyms, and Table 4 for definitions of each principal component.

landscapes after accounting for habitat area. Fourteen residual configuration indices were selected in one or more of the final models.

The results of these different analytical procedures led to differing conclusions regarding the relationship between habitat configuration and species' abundances. For example, only 2 of 15 species associated with late-seral forest were affected by the configuration of late-seral forest within levels of late-seral forest abundance, based on an analysis of variance. However, 10 of 15 species associated with late-seral forest habitats, on the average, occupied landscapes that differed from the average landscape condition with respect to one or more gradients in habitat configuration, based on their weighted average location along the principal component gradients (Figs. 4 and 5). Yet of the 22 significant ($P < 0.060$) associations identified using this ap-

proach, including all species and principal components, only 11 were significant ($P < 0.065$) based on simple linear regression analysis of the relationship between bird abundance and each configuration gradient (Table 6); the R^2 values ranged from 12 to 27%. Moreover, of the 12 significant ($P < 0.060$) associations based on weighted average locations along principal components for species with significant area relationships, only five were significant ($P < 0.068$) when the relationship between habitat area and abundance was first taken into account using partial regression analysis (Table 7). Finally, 12 of 15 species associated with late-seral forest habitats had significant partial correlations with 1 or more of the original residual configuration indices either with or without first taking into account habitat area (Table 8).

DISCUSSION

The relationship between late-seral forest area and bird abundance varied dramatically among species. In particular, the abundances of 5 species were largely unaffected by late-seral forest area, even though these species were generally always found in association with this patch type. Thus, even species exhibiting a definitive association with a particular habitat type at the patch level had a great deal of variation in abundance among landscapes that could not be explained by habitat area alone. Much of the explanatory power was apparently lost when translating patch-level habitat associations to population abundance at the landscape level. These results suggest that caution should be exercised when attempting to extrapolate bird-habitat relationships derived at one scale to other scales; factors affecting the selection of habitats by an individual at the patch scale may affect population abundance at the landscape scale differently (Wiens et al. 1987 and 1993, Wiens 1989a, b).

Like habitat area, the relationship between late-seral forest configuration and bird abundance varied dramatically among species. Not surprisingly, the strongest configuration effects were for species associated with the juxtaposition of late-seral and early-seral habitats. But even for these few species, the percentage of variation in abundance among landscapes attributable to habitat configuration was moderate ($R^2 = 30\text{--}50\%$). For species with significant habitat area effects, habitat configuration explained an additional 0–28% of the variance, and without exception habitat area was more important than habitat configuration. Thus, with the exception of a few "edge" species, variation in abundance among landscapes was more strongly related to changes in habitat area; habitat configuration was of secondary importance.

The relationship between landscape configuration and bird abundance was complex and difficult to assess because of the variety of ways in which landscape configuration can be expressed and because of the variety of analytical approaches available. Our analyses dem-

TABLE 6. Simple linear regressions between each principal component (see Table 4 for the definition of each component) and the abundance of each bird species associated with late-seral forest or one of the large sawtimber patch types in 30 300-ha landscapes in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990–1992.*

Patch type† Species‡	PC1			PC2			PC3		
	b_1	R^2	P	b_1	R^2	P	b_1	R^2	P
Late-seral forest									
Gray Jay	+	6%	.202	–	5%	.265	+	4%	.321
Brown Creeper	+	0%	.783	–	17%	.026	+	15%	.036
Winter Wren	–	2%	.432	–	21%	.013	+	0%	.822
Varied Thrush	–	0%	.990	–	22%	.011	+	5%	.253
Evening Grosbeak	+	1%	.536	–	1%	.562	+	2%	.474
Hammond's Flycatcher	–	1%	.701	–	6%	.217	+	17%	.025
Chestnut-backed Chickadee	+	8%	.141	–	9%	.105	+	0%	.869
Red Crossbill	+	2%	.422	–	0%	.770	+	0%	.724
Western Wood-Pewee	+	13%	.050	+	7%	.176	+	12%	.065
Olive-sided Flycatcher	+	17%	.027	–	0%	.882	+	7%	.160
Red-tailed Hawk	+	19%	.019	+	8%	.135	+	11%	.086
Red-breasted Sapsucker	+	16%	.031	+	0%	.938	+	1%	.553
Conifer-large sawtimber									
Pileated Woodpecker	+	4%	.317	+	27%	.006	–	2%	.483
Red-breasted Nuthatch	+	4%	.334	+	10%	.108	–	2%	.437
Mixed-large sawtimber									
Western Tanager§	+	9%	.131	+	3%	.359	+	2%	.456

* Linear model: $\log_{10}(\text{abundance}) = b_0 + b_1(\text{principal component})$. Data represent birds detected at any distance during four visits to 32–38 sampling points within each landscape. Species are ordered in decreasing magnitude of the strength of the correlation between abundance and habitat area, based on simple linear regression (see *Methods: Data analysis: Bird-habitat relationships* for details); significant ($P < 0.10$) relationships are in boldface type.

† See Appendix for definition of each patch type. Late-seral forest, $n = 29$ landscapes; conifer-large sawtimber, $n = 27$ landscapes; mixed-large sawtimber, $n = 27$ landscapes.

‡ Scientific names in Table 1.

§ PC4: coefficient = +; $R^2 = 4\%$; $P = 0.334$.

TABLE 7. Partial linear regressions between each principal component (see Table 4 for the definition of each component) and the abundance of each bird species associated with late-seral forest or one of the large sawtimber patch types, after accounting for any relationship between habitat area and bird abundance, in 30 300-ha landscapes in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990–1992.*

Patch type† Species‡	PC1			PC2			PC3		
	b_2	pR^2 (%)	P	b_2	pR^2 (%)	P	b_2	pR^2 (%)	P
Late-seral forest									
Gray Jay*§	+	11	.097	+	0	.818	–	1	.600
Brown Creeper	+	0	.997	–	3	.403	+	2	.495
Winter Wren	–	8	.139	–	6	.206	–	15	.040
Varied Thrush	–	1	.720	–	7	.171	–	1	.612
Evening Grosbeak	+	1	.625	+	2	.424	–	1	.549
Hammond's Flycatcher	–	2	.527	–	0	.835	+	7	.165
Chestnut-backed Chickadee	+	8	.150	–	2	.480	–	4	.309
Conifer-large sawtimber									
Pileated Woodpecker	+	12	.088	+	15	.053	–	2	.450
Red-breasted Nuthatch	+	8	.154	+	3	.424	–	3	.427
Mixed-large sawtimber									
Western Tanager	+	17	.038	+	3	.412	+	13	.068

* Linear model: $\log_{10}(\text{abundance}) = b_0 + b_1(\% \text{area}) + b_2(\text{principal component})$. Data represent birds detected at any distance during four visits to 32–38 sampling points within each landscape. Only species with a significant relationship between abundance and habitat area are included. Species are ordered in decreasing magnitude of the strength of the correlation between bird abundance and habitat area, based on simple linear regression (see *Methods: Data analysis: Bird-habitat relationships* for details); significant ($P < 0.10$) relationships are in boldface type.

† See Appendix for definition of each patch type. Late-seral forest, $n = 29$ landscapes; conifer-large sawtimber, $n = 27$ landscapes; mixed-large sawtimber, $n = 27$ landscapes.

‡ Scientific names in Table 1.

§ Nonlinear model: $\log_{10}(\text{abundance}) = b_0 + b_1(\% \text{area}) + b_3(\% \text{area})^2 + b_2(\text{principal component})$.

|| PC4: $b_2 = +$, $pR^2 = 1\%$, $P = 0.729$.

TABLE 8. Multiple linear regressions between the "best" and parsimonious combination of habitat area and residual habitat configuration indices and the abundance of bird species for species associated with late-seral forest or one of the large sawtimber patch types in 30 300-ha landscapes in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990–1992.*

Patch type† Species‡	Variable§	b	pR ² (%)	P	Full model	
					R ² (%)	P
Late-seral forest						
Gray Jay	%LAND	+	0	.882	68	<.001
	(%LAND) ²	+	8	.165		
Brown Creeper	LCAS	–	17	.030	55	<.001
	%LAND	+	55	<.001		
Winter Wren	MCA	+	23	.009	62	<.001
	%LAND	+	55	<.001		
Varied Thrush	%LAND	+	47	<.001	47	<.001
Evening Grosbeak	%LAND	+	30	.002	30	.002
Hammond's Flycatcher	%LAND	+	26	.007	38	.007
	MPFD	–	18	.027		
	TECI	+	11	.088		
Chestnut-backed Chickadee	%LAND	+	38	<.001	40	.004
	MPS	+	23	.011		
	MCAI	–	19	.022		
Red Crossbill	%LAND	+	22	.017	33	.042
	MPFD	+	21	.019		
	PSCV	+	19	.026		
	MPS	+	18	.029		
Western Wood-Pewee	MECI	+	38	<.001	51	<.001
	CACV	+	28	.004		
Olive-sided Flycatcher	MECI	+	39	<.001	39	<.001
Red-tailed Hawk	TCAI	–	36	<.001	50	<.001
	CACV	+	20	.017		
Red-breasted Sapsucker	TECI	+	26	.004	26	.004
Conifer-large sawtimber						
Pileated Woodpecker	%LAND	+	41	<.001	52	<.001
	ED	+	28	.005		
Red-breasted Nuthatch	%LAND	+	24	.012	33	.008
	ED	+	16	.045		
Mixed-large sawtimber						
Western Tanager	%LAND	+	26	.009	43	.004
	CWED	+	23	.015		
	PSCV	+	16	.049		

* Data represent birds detected at any distance during four visits to 32–38 sampling points within each landscape. Species are ordered in decreasing magnitude of the strength of the correlation between bird abundance and habitat area, based on simple linear regression (see *Methods: Data analysis: Bird-habitat relationships* for details).

† See Appendix for definition of each patch type. Late-seral forest, $n = 29$ landscapes; conifer-large sawtimber, $n = 27$ landscapes; mixed-large sawtimber, $n = 27$ landscapes.

‡ Scientific names in Table 1.

§ See Table 2 for a description of each variable, but note that the relationship with habitat area (%LAND) has been removed from each configuration index (see *Methods: Data analysis: Vegetation patterns* for details).

onstrate that the choice of methods can strongly influence conclusions regarding the effects of habitat configuration on bird abundance. Results based on the analysis of variance were the least powerful (i.e., the least likely to detect significant relationships). Based on this approach, only 2 species (Western Wood-Pewee and Olive-sided Flycatcher) were affected by the configuration of late-seral forest. Both species were more abundant in landscapes containing more fragmented configurations of late-seral forest involving high-contrast edges. This conclusion was consistently supported by the correlational analyses. There was consistent evidence from three correlational procedures that 5 of the remaining 13 species were responsive to habitat configuration. All 5 species (Western Tanager, Red-breasted Sapsucker, Red-tailed Hawk, Pileated Woodpecker,

and Gray Jay) were associated with more heterogeneous or fragmented habitat configurations. Based on field observations, Western Tanagers and Red-breasted Sapsuckers seemed to be associated with high-contrast edges involving hardwoods in mixed or hardwood-dominated large sawtimber stands. Red-tailed Hawks, Pileated Woodpeckers, and Gray Jays seemed to be responsive to several aspects of configuration, including patch shapes, core area, edge density, and edge contrast. There was consistent evidence from two correlational procedures that 2 of the remaining 8 species (Red-breasted Nuthatch and Winter Wren) were responsive to habitat configuration. Red-breasted Nuthatch had a weak and positive correlation with conifer-large sawtimber edge density. Winter Wren was the only species that demonstrated a weak association with

less fragmented landscapes. After accounting for habitat area, mean patch size and mean core area size explained an additional 15–23% of the variation in Winter Wren abundance among landscapes. Rosenberg and Raphael (1986) and Lehmkuhl et al. (1991) also found Winter Wren to be one of the few species associated with less fragmented landscapes in the Pacific Northwest. Of the remaining species, 2 (Brown Creeper and Hammond's Flycatcher) had weak and inconsistent relationships, 3 (Varied Thrush, Chestnut-backed Chickadee, and Red Crossbill) had support from only one analytical approach, and 1 (Evening Grosbeak) had no evidence at all of any relationship with habitat configuration.

Contrary to the idea that habitat fragmentation is detrimental to species that specialize on a particular habitat, most species that exhibited significant relationships with habitat configuration in our study were associated with the more fragmented distribution of habitat (although see *Scope and limitations*). Similarly, it is increasingly assumed by researchers and managers that landscape structure plays a dominant role in the regulation of wildlife populations (e.g., Turner 1989, Kareiva 1990, Saunders et al. 1991, Dunning et al. 1992). Our results suggest that landscape structure at the scale of small 300-ha watersheds in the central Oregon Coast Range may have only a moderate effect on bird abundance. Of the 15 resident breeding bird species that we studied, landscape structure (i.e., habitat area and configuration) typically explained less than half of the variation in abundance among landscapes. Hence, although landscape structure was demonstrably related to several species' abundances, we cannot conclude that it was a dominant factor given the large amount of unexplained variation. Our findings are consistent with the few other studies from the PNW region.

Rosenberg and Raphael (1986) and Lehmkuhl et al. (1991) investigated the relationship between breeding bird communities in late-seral (mean dbh > 26 cm) and old-growth (mean dbh > 81 cm and multistory canopy) forest patches, respectively, and various measures of fragmentation of the surrounding landscapes in northwestern California and western Washington, respectively. They sampled forest patches from landscapes similar in structure to those we sampled. Although they did not sample whole landscapes, they also failed to detect or detected only weak relationships between species' abundance and landscape structure, and found most species with significant relationships to be positively correlated with gradients of increasing habitat fragmentation.

The magnitudes of the relationships between landscape structure and bird abundance that we found undoubtedly reflect the limitations of our study (see *Scope and limitations*), but also may reflect the spatio-temporal vegetation dynamics and regional landscape context of the central Oregon Coast Range. Most of the

expectations about bird population response to habitat fragmentation stem from studies on forest fragmentation caused by urbanization and agricultural development, particularly in the eastern deciduous forest of North America. In this form of fragmentation, forest tracts are progressively reduced to smaller and more isolated patches embedded within a relatively permanent (barring reforestation) matrix of nonforest. The landscape structure becomes relatively static. Forest patches adjoin nonforest habitat and remain isolated from similar forest patches for long periods of time. From a forest-dwelling animal's perspective, forest fragments presumably become embedded in a matrix of largely unsuitable habitat that inhibits the movement of animals among isolated forest patches, depending on the species habitat selectivity and vagility. However, commercial timber management is the major anthropogenic cause of forest fragmentation in the PNW (Lehmkuhl and Ruggiero 1991). Commercial timber management alters landscape structure by changing the areal extent and spatial distribution of plant communities and seral stages across the landscape, and this occurs on a backdrop of a natural patch mosaic created by changing landforms and natural disturbances (Swanson et al. 1988). In this scenario, the natural landscape is a spatially and temporally dynamic mosaic of forest patches (i.e., shifting mosaic) due to natural disturbances (e.g., fire and windthrow) and forest regrowth, and it is the scale and structure of this mosaic that is dramatically altered by timber management activities (Swanson et al. 1990). Vertebrate population dynamics in forests being fragmented by timber management activities are likely to differ from those in forests being fragmented by urbanization and agricultural development. Sharp forest/nonforest edges are transient in managed forest landscapes because of forest regrowth, and regenerating plantations do not function as non-habitat for many species (e.g., Table 5), but rather as habitat of variable quality and permeability to animal movements. Late-seral forest patches may never be truly isolated or may be isolated for only a brief period of years. Moreover, vertebrate populations in the PNW have evolved in a naturally heterogeneous landscape and may have evolved strategies for coping with the interspecific interactions (e.g., competition and predation) associated with fragmented habitats. For these reasons, it seems unlikely that the empirical findings on forest fragmentation from urban or agricultural landscapes extend to the dynamic forest landscapes of the PNW and elsewhere (Hejl 1992). Indeed, it seems likely that vertebrate response to habitat fragmentation would be less pronounced.

Most of the empirical studies on fragmentation, primarily from the eastern deciduous forest, have been conducted in landscapes in which the human-caused fragmentation process has progressed steadily for a long period of time (200 yr in many areas) and has reached a state in which forest cover represents a re-

gionally rare cover type and forest patches represent truly isolated fragments. In contrast, in the central Oregon Coast Range (and other areas in the PNW) late-seral forest still represents the matrix cover type. Large regional source populations of species associated with the matrix habitat type may be able to offset any local habitat configuration-related effects because local bird abundance patterns are produced not only by local processes or events, but also by the dynamics of regional populations or events elsewhere in the species' range (Wiens 1981, Vaisanen et al. 1986, Haila et al. 1987, Ricklefs 1987, Wiens 1989b). That broad-scale processes act to constrain or influence finer scale phenomena is one of the key principles of hierarchy theory (Allen and Star 1982) and "supply-side" ecology (Roughgarden et al. 1987). Densities of forest-dwelling, long-distance migratory birds in forest patches in Connecticut were significantly and positively correlated with regional forest abundance (Askins and Philbrick 1987, Askins et al. 1987). The authors suggested that local bird abundance was influenced by the proximity and size of potential source populations from the regional landscape. In our study area, if mechanisms are operating on species associated with late-seral forest to reduce population abundance in fragmented landscapes, immigration from large regional source populations may be sufficient to offset any tendency for local population declines. This would be particularly likely for vagile species such as birds that can disperse over large distances easily.

Our findings are generally supported by other avian studies conducted in forest-dominated landscapes. For example, Welsh and Healy (1993) found that the abundances of most breeding bird species associated with late-seral forests in New Hampshire were not different between small (64 ha), unmanaged areas (100% sawtimber forest; mean dbh > 25.4 cm, > 80 yr) and similar-sized areas that had 40% of their area in young forest stands (mean dbh < 25.4 cm, < 70 yr). In a similar study in Missouri Ozark forests, Thompson et al. (1992) sampled breeding birds in small (200 ha), unmanaged areas (100% pole-sawtimber forest, > 20 yr) and similar-sized areas that had 20% of their area in young forest stands (< 20 yr). Of 9 forest-interior, neotropical migrants, 3 were more abundant in the managed landscapes, 3 were equally abundant in both landscapes, and 3 were more abundant in the unmanaged landscapes. In southeastern Wyoming, Keller and Anderson (1992) sampled breeding birds in small (20–100 ha), old-growth (undefined) areas and similar-sized (25–45 ha) areas that had 20–50% of the old-growth vegetation removed in small (1–3 ha) patch cuts or 100-m wide strip cuts. Of the 16 species studied, only 2 species were consistently affected by fragmentation. In eastern Maine, Derleth et al. (1989) sampled breeding birds in second-growth forest stands (>35 yr old) and stands containing small (1–8 ha) clearcuts. Most species were more abundant in the treatment stands.

Although we are unaware of comparable studies involving larger sampled landscapes, the limited evidence gathered so far for these forest landscapes suggests that we should not blindly accept the landscape structure hypothesis described in the introduction. Habitat configuration and subdivision undoubtedly play a role in regulating population abundance, distribution, and dynamics, but the magnitude and nature of this role may vary geographically and over time in relation to changes in regional habitat conditions and other factors, and probably varies among species in relation to habitat selectivity, vagility, and scale.

SCOPE AND LIMITATIONS

The scope of this study was restricted in several ways. These limitations identify additional research needs that should be examined before applying our results in a management context. First, the scale of our investigation placed upper and lower limits of resolution on our ability to detect habitat configurations and assess bird-habitat relationships (Wiens 1989a). The extent of our landscapes was roughly 300 ha; this defined the upper limit of resolution. Populations of the species we investigated undoubtedly extend over much larger areas and are subject to demographic influences operating over correspondingly larger areas. The maximum potential number of individuals present in our 300-ha landscapes varies among species, but probably ranges from <1 (e.g., Spotted Owl) to several hundred (e.g., Swainson's Thrush) under ideal habitat conditions. Each landscape is nested within a larger regional landscape context and this context will influence the internal landscape dynamics to some degree (Wiens 1989a, b). Thus, the bird species we analyzed may be responsive to variations in habitat area and configuration at a coarser scale than we investigated. The moderate relationships we detected do not preclude much stronger landscape structural relationships at coarser scales.

We defined minimum patch size as 0.785 ha and ≥ 50 m in the narrowest dimension; this defined the lower limit of resolution. Therefore, our results do not preclude stronger landscape structural relationships at finer resolutions. Patchiness occurs at many scales and patches can be defined in hierarchical fashion at progressively finer and finer scales (Kotliar and Wiens 1990). Because landscape metrics are not invariant to scale (Turner et al. 1989), changing the minimum patch size would have significant effects on measures of landscape structure for specific patch types. A mixed-large sawtimber patch, for example, could be broken into progressively smaller and more numerous conifer and hardwood patches, and various indices of configuration could change dramatically and unpredictably. However, reducing minimum patch size would probably not affect metrics for the large sawtimber class; except for scattered individual trees or very narrow riparian leaf strips, sawtimber patches < 0.785 ha rarely occurred

within the study area. Similarly, increasing minimum patch size to 2 ha would have had no effect on the large sawtimber metrics because the smallest large sawtimber patch we sampled was 2.06 ha (Table 3).

Second, the analysis presented in this paper largely was limited to a single scale. We quantified the relationship between landscape structure and bird abundance at the landscape (among-patch) scale of 300-ha watersheds. As the studies by Wiens and Rotenberry on shrubsteppe birds (Wiens and Rotenberry 1981, Wiens 1985 and 1986, Rotenberry 1986, Wiens et al. 1987) and other studies (e.g., Gutzwiller and Anderson 1987, Hengeveld 1987, Morris 1987) demonstrate, habitat selection occurs at multiple scales, and habitat associations often vary among scales of investigation or analysis. We are unable to infer about habitat associations at finer or coarser scales from this analysis alone.

Third, we classified habitat from a community-centered perspective. That is, we defined 27 patch types on the basis of factors (e.g., seral condition, plant community, canopy closure) believed to be important to a wide variety of wildlife in western Oregon and Washington. These factors may or may not be important from an organism-centered perspective. Other habitat features (e.g., snags, vertical foliage diversity, available water) not effectively captured in this simple classification scheme might be more important in governing the abundance and spatial distribution patterns of any particular species. We could redefine patches by combining patch types that are functionally equivalent from an organism-centered perspective, but we would still be constrained by the original patch type map unless we remapped each landscape for each species using a species-specific habitat classification scheme. We avoided this problem by focusing our analysis on those species strongly associated with a single patch type as we originally defined them. Moreover, vegetation patches were somewhat arbitrarily and subjectively made discrete during the cover mapping and digitization process. Plant community differences were in many cases not abrupt. Thus, the final patch mosaics represented over-simplified representations of the actual spatial heterogeneity present in these landscapes. By focusing our analysis on large sawtimber, we minimized this problem because most sawtimber patch edges were induced by timber management activities and therefore were relatively discrete and objectively delineated.

These three limitations are inherent to all landscape ecological investigations and deal with the issue of "measured heterogeneity" vs. "functional heterogeneity" (Kolasa and Rollo 1991). The scheme used to classify landscapes coupled with the scale of investigation and analysis determines measured heterogeneity because the quantifiable configurations are constrained by these decisions. Measured heterogeneity may or may not correspond to something functionally meaningful to a particular species (Wiens 1989a, b, Kolasa

and Rollo 1991). Thus, results based on measured heterogeneity may lead to erroneous conclusions. We did not know a priori what the functionally relevant scales and habitat types were for each species in our study area. Thus, we selected a scale and classification scheme that stood the "best" chance of allowing us to detect functionally meaningful configurations for some species and yet also were meaningful from a land management perspective. Although these limitations are important to consider when interpreting these results, we are not aware of other published attempts to investigate empirical relationships in the field between vertebrate populations and landscape structure at equal or greater extents using a replicated sampling design.

Fourth, our analysis was limited to diurnal birds during the breeding season. Nocturnal birds were not considered in this analysis, nor did we assess temporal patterns (e.g., seasonal or yearly changes) in the relationship between bird abundance and landscape structure. We sampled birds in each landscape during a single year only because of constraints on available logistic resources. Bird populations and habitat associations are known to fluctuate both seasonally and annually to some degree in some cases (Rice et al. 1980, Marcot 1985, Wiens 1989b). Although our resurvey results indicated that annual variation was not significant for most species, the confounding of year and basin in our study design undoubtedly added unexplained variation to the data set, making landscape structural relationships more difficult to detect.

Fifth, we assessed bird abundance only. We did not assess measures of fitness because of the difficulty in doing so at the scale of our investigation. It seems likely that, in response to changes in habitat quality at the landscape level, functional responses would precede numerical responses. Abundance, as determined by counts of singing or calling birds, may not be a good indicator of habitat quality (Van Horne 1983, Wiens 1989b). Individual fitness could have varied in relation to landscape structure without changing overall abundance and we would not have detected it.

Finally, for statistical reasons, our analysis was limited to relatively common and widespread species. Rare and uncommon species (e.g., Spotted Owl, Vaux's Swift) or those with patchy distributions in the study area (e.g., Downy Woodpecker, Marbled Murrelet) could not be analyzed using parametric statistical procedures because of violations of assumptions associated with these procedures. Yet these species could very well be the ones most sensitive to landscape structure (Terborgh and Winter 1980, Pimm et al. 1988).

Given these limitations, the many potential sources of error in measuring bird abundance, and the natural stochastic variation in wildlife populations, it is not too surprising that we did not detect stronger relationships. Our study provides empirical evidence that landscape structure at the scale of 300-ha watersheds is probably important to several bird species in the central Oregon

Coast Range. Moreover, our study illustrates some of the difficulties in extrapolating relationships developed at the patch level to the landscape level. Even though several species had strong patch-level habitat associations, this did not translate into strong explanatory relationships between abundance and the total area and configuration of that habitat type at the landscape level. Thus, modeling population abundances within landscapes based on simple patch-type associations could produce erroneous results. In addition, our analyses demonstrate the potential limitations of using a single statistical procedure to evaluate landscape ecological relationships. We suggest that, when possible, investigators use several analytical approaches and use the consistency in results among approaches to gauge confidence in the conclusions. Thus, our study both serves as a lesson on the limitations of avian field studies at the landscape scale and provides an empirical basis, in part, for understanding the relationship between landscape structure and bird abundances. Finally, our study demonstrates that landscape ecological relationships can and should be studied in the field to test theoretical concepts. Given the increasing role of landscape ecology in conservation biology and land management, we must build a stronger empirical basis for understanding landscape ecological relationships.

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APPENDIX

Patch type classification system (modified from Hall et al. 1985:17–31) used to classify vegetation in 30 300-ha landscapes in Drift Creek, Lobster Creek, and Nestucca River basins in Benton, Lincoln, and Tillamook Counties, Oregon, 1990–1992.

Patch type	Definition
Plant community: All patches have a designated plant community.	
Nonforested	Areas that do not support forest vegetation because of natural or human-induced conditions
Water	Open water (e.g., ponds, lakes)
Herbaceous wetlands	Bogs, marshes, and meadows dominated by herbaceous plants and having a site potential for minimal shrub cover (<60% woody cover); generally dominated by rushes, sedges, and grasses
Hardwood/shrubby wetlands	Wetlands dominated by woody vegetation with woody crown cover >60%; commonly dominated by alder, bigleaf maple, willows, or Oregon ash
Grass-forb dry hillsides	Grasslands with <40% woody cover; mainly caused by humans who control the tree or shrub vegetation to maintain the area in permanent pasture
Brush fields	Brush-dominated areas that will remain in brush unless some sort of disturbance alters the site and makes tree growth possible
Forested	Areas that support forest vegetation
Hardwood community	>70% hardwood (red alder) composition
Conifer community	>70% conifer composition
Conifer-hardwood community	<70% hardwood or conifer composition
Seral condition: All forested plant communities have a designated seral condition.	
Grass-forb	Shrubs*: <40% crown cover; <1.5 m mean height Trees*: <20% crown cover; <3 m mean height; <2.5 cm mean dbh†
Shrub	Shrubs: >40% crown cover any height Trees: <20% crown cover; <3 m mean height; <2.5 cm mean dbh
Sapling	Trees: >20% crown cover Conifers: >3 m mean height; 2.5–10.1 cm mean dbh
Pole condition	Hardwoods: 3–15 m mean height; 2.5–10.1 cm mean dbh Trees: >20% crown cover Conifers: >3 m mean height; 10.2–30.4 cm mean dbh
Small sawtimber	Hardwoods: 3–15 m mean height; 10.2–30.4 cm mean dbh Trees: >20% cover; 30.5–53.2 cm mean dbh
Large sawtimber	Trees: >20% cover; >53.2 cm mean dbh
Canopy closure: All forested plant communities with sapling and pole seral condition have a designated canopy closure condition.	
Open canopy	20–70% tree crown cover
Closed canopy	70–100% tree crown cover

* Shrubs and trees were distinguished on the basis of the characteristic life form associated with each species and not on the basis of plant size.

† dbh = diameter at breast height.