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Chapter 12: Ecological Processes Linking Forest Structure and Avian Diversity in Western Oregon

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INTRODUCTION

Ecologists have long debated the factors that may influence patterns of faunal diversity. Recent studies have found that landscape, regional, and continental-scale features explain some of the variation in bird diversity (Terborgh 1989, Huff and Raley 1991, Currie 1991). Yet, studies considering multiple spatial scales have found that many bird species are most strongly correlated with habitat features within forest stands (e.g., Lehmkuhl et al. 1991, McGarrigal, personal communication), especially forest structural complexity (see Cody 1985). Structurally complex forests are thought to provide relatively more habitat niches and, thus, support high animal species diversity (James 1971, Urban and Smith 1989).

In natural coniferous forests of the Pacific Northwest (PNW) United States, structural complexity is bimodally distributed over the course of succession, being relatively high in the early and late-seral stages (Spies et al. 1988). This is because structural features such as large trees, snags, and fallen logs often survive canopy-replacement disturbances, and hence are incorporated into early successional forests. These features then decay and structural complexity decreases, until large trees are recruited in the old-growth stage. Animal diversity in PNW forests is also thought to

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be relatively high both early and late in succession (Harris 1984). Ecologists generally assume this follows from the patterns of structural complexity and habitat niche diversity (Hansen et al. 1991).

Forest management practices have provided a test of this hypothesis. Traditional clearcutting removes structural legacy, and recently harvested plantations are relatively homogeneous in structure. As predicted, bird diversity has been found to be lower in closed-canopy plantations than in natural closed-canopy forests (Hansen et al. in review). Consequently, many forest managers are now retaining canopy trees, snags, and fallen trees in harvest units to maintain suitable habitats for native organisms. Initial studies show a positive relation between animal richness and structural retention (Hansen and Hounihan in press). This provides support for the "Habitat Niche" hypothesis that forest structural complexity strongly influences vertebrate species diversity.

Studies in recent clearcuts, however, suggest factors in addition to habitat niche diversity may influence animal diversity. Hansen et al. (in review) found that clearcut sites with no large live or dead trees supported levels of bird diversity comparable to those in mature forests. This observation led us to a novel hypothesis that the level of energy available to consumers is higher in open-canopy than in closed-canopy stands. We predict that relatively more of the net primary production (NPP) in open-canopy, hardwood-dominated stands is fixed as palatable leaves, fruits, and seeds, and that this higher level of energy available to consumers supports higher levels of animal diversity. Closed-canopy, conifer stands, in contrast, are predicted to fix relatively more energy as wood and unpalatable conifer needles, have less energy available to consumers, and thus support lower levels of animal diversity. In support of this hypothesis, Turner and Long (1975) found that the production of understorey plants and leaves of trees was about 48% higher in 20- to 30-year-old (relatively open-canopy) stands than in 40- to 70-year-old stands (closed-canopy).

A third hypothesis on factors controlling bird diversity involves nest predation. Previous studies of bird response to canopy density indicated that the abundances of some ground and shrub-nesting birds are dramatically lower in harvest units with a few canopy trees (1-5 per ha) than in units with no canopy trees (Hansen and Hounihan in press). These same species are also more abundant in the centres of clearcuts than near forest edges (Hansen et al. in prep.). These findings raise the hypothesis that nest predation is higher in sites where predators can use canopy trees as perches for locating the nests of prey species (Vega 1993).

Here we report the results of a coordinated set of studies on the effects of stand energetics, structural complexity, and predation rates on bird diversity (Figure 1). Specific hypotheses were:

H_o: Taxonomic diversity of birds is not influenced by the level of net primary productivity consumable by animals, by the structural complexity of the vegetation, nor by nest predation rates.

H_1: In PNW coniferous forests, the energy available to consumers is inversely related to canopy density (Figure 2a) because relatively more energy is fixed as wood and unpalatable conifer needles in closed-canopy stands than in open-canopy stands. Taxonomic diversity of birds is positively related to energy availability because greater resource partitioning is possible (Figure 2b). Consequently, bird diversity will be negatively related to canopy tree density (Figure 2c).

H_2: The vertical and horizontal complexity of vegetation structure is highest at some intermediate canopy density (Figure 3a) because more canopy layers and variation in canopy layers are possible. Animal diversity increases with structural complexity (Figure 3b) because of the greater diversity of habitat niches. Consequently, animal diversity will be highest under intermediate canopy densities (Figure 3c).

H_3: Detection of bird nests by predators is highest under intermediate canopy densities (Figure 4a). Bird reproduction and diversity are inversely related to rates of nest predation (Figure 4b), hence bird reproduction and diversity show the response to canopy density depicted in Figure 4c.

Primary results on nest predation rates and bird response to habitat features of stands are reported in Vega (1993). Here we summarize those results, and also examine the Energy and Habitat Niche hypotheses.

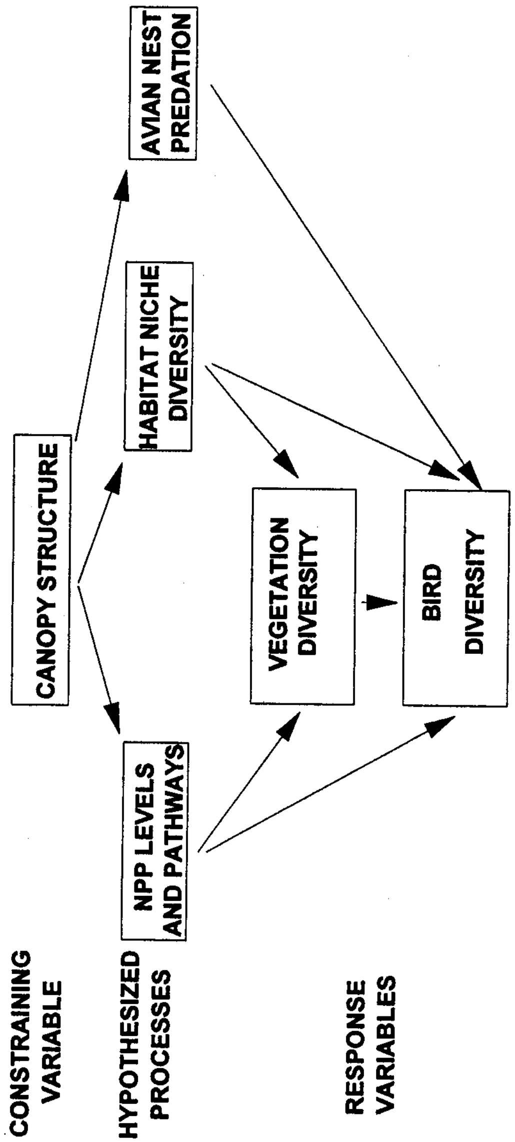

Figure 1. Driving variables, hypothesized pathways, and response variables examined in this study.

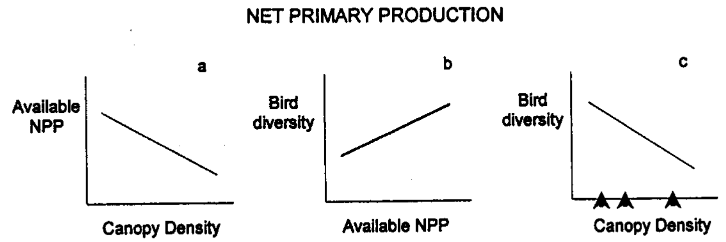

Figure 2. Hypothesized relationships between: (a) net primary productivity that is consumable by animals and canopy density; (b) consumable energy and animal community characteristics; and (c) canopy density and animal diversity. Vertical arrows denote the canopy densities for the three stand types studied.

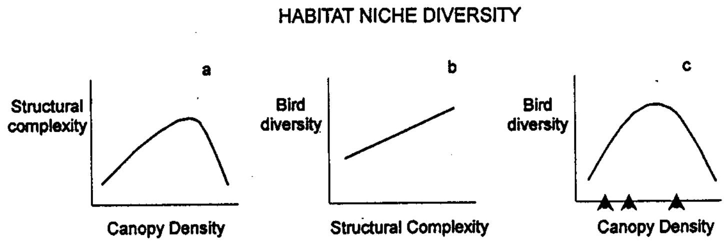

Figure 3. Hypothesized relationships between: (a) canopy density and stand structural complexity; (b) stand structural complexity and animal diversity; and (c) canopy density and animal diversity. Vertical arrows denote the canopy densities for the three stand types studied.

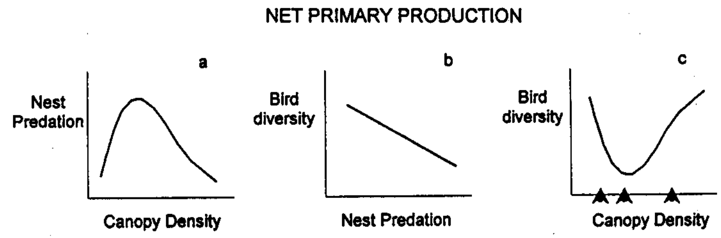

Figure 4. Hypothesized relationships between: (a) canopy density and nest predation rates; (b) nest predation rates and bird reproduction and diversity; and (c) canopy density and bird reproduction and diversity. Vertical arrows denote the canopy densities for the three stand types studied.

METHODS

Experimental Design

Three stand types were studied: structurally-simple, open-canopy stands (clearcuts with no canopy retention) (referred to hereafter as OCSS); structurally-complex, open-canopy stands (harvest units retaining about 4-13 canopy and subcanopy trees per ha) (OCSC); and structurally-complex, closed-canopy stands (natural mature forest) (CCSC). Four replicates of each canopy configuration were established for a total of 12 study sites. The stands were located in western Oregon in the vicinity of the H.J. Andrews Experimental Forest (Figure 5). Attributes of the stands are described in Table 1. Two parallel transects were placed 100 m apart at each site, and 3 plots were spaced at 100-m intervals along each transect. All plots were more than 75 m from the stand edge. Vegetation structure, biomass, nest predation, and bird densities were sampled at each of the six plots in a stand during spring and summer of 1992.

Forest Structure

Habitat attributes measured at each sample plot are listed in Table 2 and the sampling strategy depicted in Figure 6. Forest structural complexity was quantified based on and tree density by 10-cm dbh class and shrub density. Vertical habitat complexity was calculated as tree and shrub size-class diversity (mean Shannon's index among the 24 subplots within a stand). Horizontal habitat heterogeneity was quantified as the standard deviation in tree and shrub size-class diversity within a stand.

Forest Productivity

Vegetation biomass was estimated by life form (tree, shrub, subshrub, forb), plant part (wood, leaf), and palatability, using allometric relationships from the software package BIOPAK (Means, personal communication). Tree biomass was based on dbh, shrub biomass on diameter at the base of the stem, and subshrub biomass was based on percent cover. Herb and forb biomass (hereafter called herb biomass) was measured directly by clipping and measuring dry weights (see Table 2).

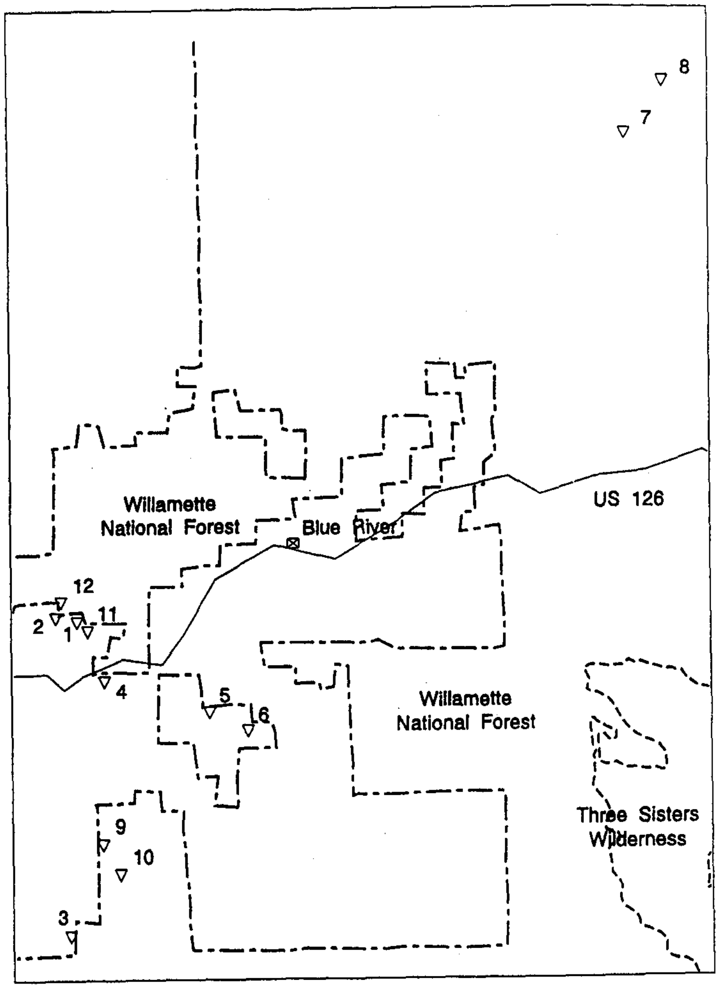

Figure 5. Location of study sites in Western Oregon. From Vega (1993).

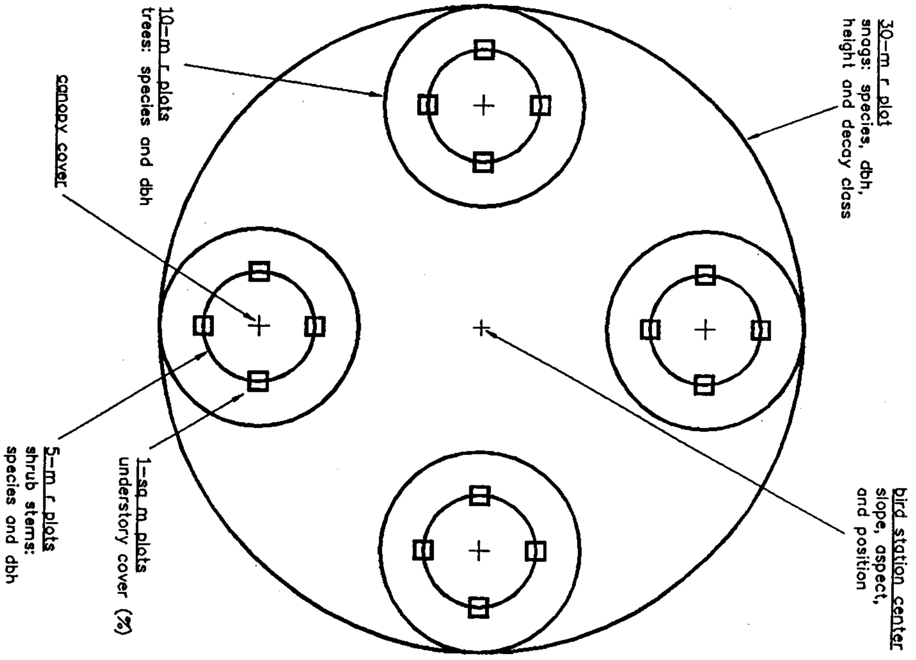

Figure 6. Sampling scheme for habitat attributes. From Vega (1993).

Table 1. Attributes of the 12 stands examined in this study. Modified from Vega (1993).

	CLEARCUT				RETENTION				MATURE FOREST			
STAND[1]	1	2	3	4	5	6	7	8	9	10	11	12
SIZE (ha)	16	17	25	51	28	33	23	19	N/A	N/A	N/A	N/A
ELEVATION (m)	870	940	970	320	590	630	670	780	560	540	620	880
YEAR OF HARVEST	1985	1986	1986-87	1988-89	1989	1989	1990	1990	N/A	N/A	N/A	N/A
SITE PREPARATION[2]	BCB	BCB	N/A	BCB	PTB	BCB	PAB	PTB	N/A	N/A	N/A	N/A
YEAR OF PLANTING	1987	1987-88	1990	1989-90	1991	1990	1991	1991	N/A	N/A	N/A	N/A

[1] Numbers correspond with study site locations shown in Figure 1.

[2] BCB - Broadcast burn, PTB - Partial burn, PAB - Pile and burn.

Table 2. Habitat variables measured in this study.

	Plot-Level Habitat Attributes	
Attribute	Source	Definition and Collection Method
Elevation	Map	Elevation above sea level (m) at plot centre
Slope	Field	Average slope (%) within 20 m of plot centre measured with a clinometer
Aspect	Field	Average aspect (degrees) within 20 m of plot centre measured with a compass
Slope Position	Field	Position within 20 m of plot centre by 4 classes
Tree Density	Field	Density of stems (> =2 cm dbh) (number/ha) by species by 10 cm dbh classes within 4 10-m radius subplots placed 20 m from plot centre. Also, within 30 m radius in retention units. This larger area was sampled because of the highly variable distribution of retention trees.
Shrub Density	Field	Density of shrubs (> =0.5 cm dbh) (number/ha) by species by dbh within 4 5-m radius subplots placed 20 m from plot centre
Snag Density	Field	Density of snags (> =2 cm dbh) (number/ha) by species by 5 size classes within 30 m of plot centre
Snag Height	Field	Height of snags measured by clinometer
Snag Decay Class	Field	Decay class of snags in 5 classes of Cline
Canopy Cover	Field	Percent cover of all vegetation above 2 m in height as determined by the moosehorn technique at 4 points 220 m from plot centres
Understory Cover	Field	Percent cover of understory vegetation in the 0-2m height class within 4 0.5-m subplots distributed around each of 4 points 20 m from plot centres

Table 2 (continued)

Understory Habitat	Field	% cover of understory vegetation in each 1-m height class from 0-5 m, within 4 1-m^2 subplots distributed around each of 4 points 20 m from plot centres.
Shrub Basal	Field	Number of shrubs with basal diameters > =0.5 cm by species within 1 5-m radius subplot 20 m south of plot centre.
Understory Biomass	Field	% cover of vegetation in 1 m^2 subplots located 25m south of plot centres. In following categories: all subshrubs, herbs, forbs; all herbaceous plants; and special plant species.
Herbaceous Biomass	Field/lab	Herbaceous material in 1 m^2 subplots located 25m south of plot centres that did not fall into one of the above categories was clipped at ground level, dried, and weighed.

All deciduous tree and shrub leaves, subshrubs, and herbs were considered highly palatable to consumers. All coniferous leaves were considered moderately palatable to consumers.

A first approximation of average annual NPP of wood was made by dividing tree wood biomass by approximate time since last disturbance (100 years). Shrub wood biomass was divided by 5, based on the estimated average age of shrubs across the sites. Leaf NPP for conifers was calculated by dividing foliar biomass by 5, the average life span (in years) of conifer needles. The annual NPP of deciduous tree leaves, subshrubs, and herbs was assumed to be equal to the biomass estimates.

Nest Predation

Relative rates of nest predation among stand types were estimated by an artificial nest experiment (Vega 1993). In June 1993, 12 artificial cup nests constructed from grass were placed at shrub height in each study site. One nest was placed in each of two directions from each bird census point. Nests were located approximately 25 meters from each point along bearings that were roughly perpendicular to one another. The nests were wired onto a sturdy shrub stem approximately 0.5-1.0 m from the ground. Two Japanese quail eggs were placed in each nest. In order to minimize the extent to which human scent influenced the activity of predators, rubber gloves and boots were worn while placing nests and eggs in the study sites. After six days, observers checked the nests and recorded whether or not they were depredated. Signs of depredation included at least one broken or missing egg, or a missing nest.

Bird Censusing

The Variable Centred Plot method (Reynolds et al. 1980) was used to sample birds during the breeding season. Observers walked to a sample point, waited two minutes, then recorded all birds seen or heard for an eight minute period. The bird species, means of detection, distance class from census point, distance from stand edge and type of stand edge were recorded. Flagging was placed 40 m from each census point along the four cardinal directions. These markers helped to determine distance of an observed bird from the census point. The observers, order of censusing stands, and order of visiting census points were systematically altered to minimize sampling biases. Censusing was done each day during the four hours following dawn. Four or five censuses were conduced at each site during May 15-June 20 1993.

Only birds registered within 50 m of plot centres were included in the analyses. This prevented overlap in the areas covered from adjacent plots. Plots of bird detection distance indicated that the songs of all bird species in the study area can be detected within 50 m (Vega 1993); thus we calculated the relative abundance of each species as the number of individual registered within the 50-m radius plot surrounding the plot centre. The results for each species were averaged over plots within a stand and across censuses and are reported as mean number of registrations/ha/census. Only species registered more than 12 times were included in the analyses.

Analyses were done on individual bird species, the understorey bird community (25 species that nest and/or forage primarily on the ground or in the shrub layer), the overstorey bird community (23 species that nest and forage primarily in the

overstorey, and the entire bird community. Variables examined included relative bird abundance, bird species richness, and bird diversity (Shannon's index).

Data Analyses

The data were analyzed both to determine the extent to which the faunal communities differed among the three stand types and to test the three hypotheses on the processes underlying these responses. Differences in bird communities among stand types were evaluated using Analysis of Variance. The hypotheses were examined by plotting data as depicted in Figs. 2-4 and analyzing with linear regression.

RESULTS

Bird Community Attributes

Fifty species of birds were registered across the 12 stands. Most of these were uncommon; only 20 species had more than 12 registrations (Table 3). Eleven of these birds differed significantly in abundance among the stand types (Table 4). Lazuli bunting and Willow flycatcher were more abundant in OCSS than in the other stand types (Figure 7). Dark-eyed junco was more abundant in OCSS than CCSC. Steller's jay, a nest predator, reached highest abundance in OCSC. MacGillivray's warbler and Song sparrow were more abundant in both open-canopy stand types than in closed forest. Species significantly associated with closed-canopy stands were Brown creeper, Golden-crowned kinglet, Hammond's flycatcher, Hermit/Townsend's warbler, and Winter wren. Chestnut-backed chickadee was significantly more abundant in CCSC than in OCSS.

Total bird abundance and species richness were slightly higher in OCSS and OCSC than in OCSS, but these differences were not significant (Table 5). Shannon's diversity index was significantly higher in OCSC than in OCSS, and intermediate in CCSC. Understorey bird abundance, richness, and diversity differed significantly among treatments, being higher in the open-canopy stand types. The overstorey bird community was significantly associated with closed-canopy stands.

Table 3. Bird species with greater than 12 registrations in this study.

COMMON NAME	LATIN NAME	CODE	REGISTRATIONS[1]
Brown creeper	*Certhia americana*	BRCR	22
Chestnut-backed chickadee	*Parus rufescens*	CBCH	86
Dark-eyed junco	*Junco hyemalis*	DEJU	129
Evening grosbeak	*Coccothraustes vespertinus*	EVGR	13
Golden-crowned kinglet	*Regulus satrapa*	GCKI	24
Hammond's flycatcher	*Empidonax hammondii*	HAFL	60
Hairy woodpecker	*Picoides villosus*	HAWO	17
Hermit/Townsend's warbler[2]	*Dendroica occidentalis and D. townsendi*	HTWA	63
House wren	*Troglodytes aedon*	HOWR	18
Lazuli bunting	*Passerina amoena*	LABU	14
MacGillivray's warbler	*Oporornis tolmiei*	MGWA	106
Pine siskin	*Carduelis pinus*	PISI	25
Rufus-sided towhee	*Pipilo erythrophthalmus*	RSTO	57
Rufous hummingbird	*Selasphorus rufus*	RUHU	25
Song sparrow	*Melospiza melodia*	SOSP	25
Steller's jay	*Cyanocitta stelleri*	STJA	19
Swainson's thrush	*Catharus ustulatus*	SWTH	15
White-crowned sparrow	*Zonotrichia leucophrys*	WCSP	60
Willow flycatcher	*Empidonax traillii*	WIFL	39
Winter wren	*Troglodytes troglodytes*	WIWR	53

[1] Number of registrations within 50 m of a plot centre across all stands and censuses.
[2] These two species hybridize in the study area and are difficult to distinguish by song. Consequently, they were lumped in this study.

Table 4. Results of ANOVA and Multiple Range Tests for bird species across the three stand types. Stand types are: OCSS - open-canopy, structurally-simple; OCSC - open-canopy, structurally-complex; CCSC - closed-canopy, structurally-complex. Density is mean registrations/census/ha across the 12 stands. Data values with similar superscripts (e.g., ^{a}) differ significantly ($P < =0.05$). Codes for bird species are defined in Table 3.

	BIRD ABUNDANCE					
CODE	OCSS	OCSC	CCSC	R^2	F	P-VALUE
BRCR	0.0^{a}	0.0^{b}	0.25^{ab}	.71	10.9	.0040
CBCH	0.0^{a}	0.32	0.62^{a}	.45	3.7	.0700
DEJU	0.88^{a}	0.46	0.03^{a}	.54	5.2	.0300
EVGR	0.0	0.0	0.03	.27	1.7	.2400
GCKI	0.0^{a}	0.04^{b}	0.22^{ab}	.80	17.7	.0008
HAFL	0.0^{a}	0.01^{b}	0.64^{ab}	.68	9.4	.0063
HAWO	0.03	0.14	0.01	.28	1.8	.2225
HTWA	0.0^{a}	0.0^{b}	0.74^{ab}	.78	15.9	.0011
HOWR	0.04	0.15	0.0	.25	1.5	.2780
LABU	0.15^{ab}	0.0^{a}	0^{b}	.53	5.1	.0335
MGWA	0.54^{a}	0.58^{b}	0^{ab}	.48	4.2	.0528
PISI	0.0	0.26	0.0	.29	1.8	.2204
RSTO	0.25	0.34	0.01	.32	2.1	.1759
RUHU	0.16	0.11	0.0	.30	1.9	.1997
SOSP	0.14^{a}	0.13^{b}	0.0^{ab}	.46	3.8	.0626
STJA	0.0^{a}	0.20^{ab}	0.0^{b}	.68	9.4	.0062
SWTH	0.05	0.0	0.11	.19	1.1	.3903
WCSP	0.54	0.10	0.0	.20	1.1	.3698
WIFL	0.38^{ab}	0.03^{a}	0.0^{b}	.57	6.0	.0218
WIWR	0.0^{a}	0.0^{b}	0.51^{ab}	.55	5.6	.0265

Table 5. Results of ANOVA and Multiple Range Tests across the three stand types for measures of taxonomic diversity and abundance of the total bird community, understorey birds, and overstorey birds. Stand types are: OCSS - open-canopy, structurally-simple; OCSC - open-canopy, structurally-complex; CCSC - closed-canopy, structurally-complex. Abundance is mean registrations/census/ha across the 12 stands. Data values with similar superscripts (e.g., ^{a}) differ significantly ($P < =0.05$).

BIRD COMMUNITY	TREATMENT					
	OCSS	OCSC	CCSC	R^2	F	P-VALUE
TOTAL						
ABUNDANCE	4.15	3.69	3.80	.02	0.1	.8938
RICHNESS	12.5	17.3	15.5	.32	2.1	.1780
SHANNON'S INDEX	1.88^{a}	2.40^{a}	2.20	.51	4.6	.0412
UNDERSTOREY						
ABUNDANCE	3.83^{ab}	2.14^{a}	0.80^{b}	.69	10.1	.0050
RICHNESS	10.25^{a}	9.00^{b}	4.50^{ab}	.73	11.9	.0030
SHANNON'S INDEX	1.70^{a}	1.76^{b}	1.07^{ab}	.58	6.2	.0201
OVERSTOREY						
ABUNDANCE	$.15^{a}$	1.38^{b}	2.9^{c}	.80	18.0	.0007
RICHNESS	1.25^{a}	7.0^{b}	10.0^{c}	.89	38.0	.0001
SHANNON'S INDEX	$.07^{a}$	1.6^{b}	1.85^{b}	.92	50.1	.0001

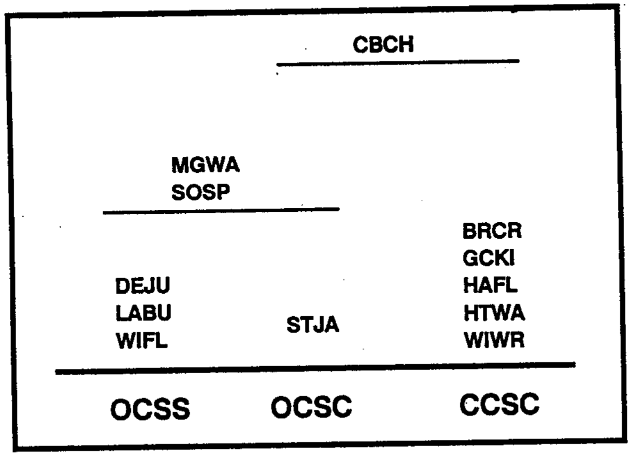

Figure 7. Significant associations among bird species and stand types. Stand types are: OCSS - open-canopy, structurally-simple; OCSC - open-canopy, structurally-complex; CCSC - closed-canopy, structurally-complex. Codes for bird species are defined in Table 3.

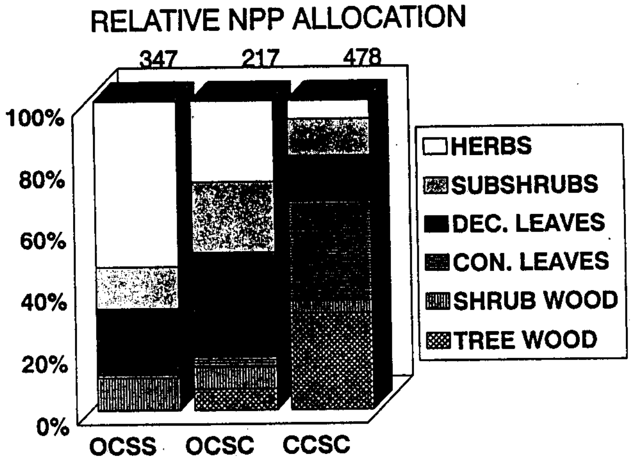

Figure 8. Relative proportion of annual NPP allocated among plant types and parts. Numbers above each bar indicate total NPP in $g/m^2/year$. Stand types are: OCSS - open-canopy, structurally-simple; OCSC - open-canopy, structurally-complex; CCSC - closed-canopy, structurally-complex.

294 not wood 173 286

Table 6. Results of linear regressions relating total, understorey, and overstorey birds to total leaf biomass. "NS" indicates that the relationships in not significant.

BIRD COMMUNITY	R^2	SIGN OF RELATION-SHIP	P-VALUE
TOTAL			
ABUNDANCE	.02	NS	.63
RICHNESS	.00	NS	.84
SHANNON'S INDEX	.00	NS	.97
UNDERSTOREY			
ABUNDANCE	.50	-	.01
RICHNESS	.77	-	.0002
SHANNON'S INDEX	.63	-	.002
OVERSTOREY			
ABUNDANCE	.51	+	.008
RICHNESS	.39	+	.02
SHANNON'S INDEX	.27	+	.08

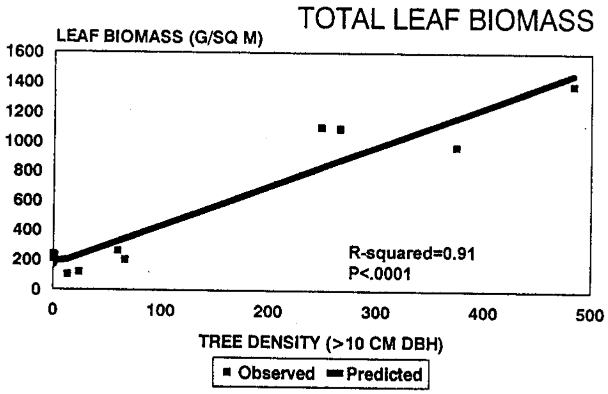

Figure 9. Relationship between annual NPP of all leaves and canopy tree density.

Energy Hypothesis

Relatively more NPP was allocated to consumable plant parts and less to wood in the open-canopy stands (Figure 8). But total NPP was greatest in closed-canopy stands, and consequently, total leaf NPP increased with canopy tree density (Figure 9). NPP of palatable leaves and herbs decreased with increasing canopy density, but these differences were not statistically significant (n=12, r^2=.12 , P<.27; n=12, r^2=.27, P<.08, respectively).

Under this hypothesis, we would expect birds to respond to total biomass of consumable biomass, rather than annual NPP. However, none of the variables for the overall bird community was significantly associated with total leaf biomass (Table 6). Understorey bird abundance, richness, and diversity were negatively associated with total leaf biomass. Understorey bird abundance was positively correlated with herb biomass (Figure 10). Overstorey bird abundance, richness, and diversity increased with total leaf biomass (Table 6) and conifer leaf biomass (e.g., Figure 11).

Habitat Niche Hypothesis

Vertical habitat diversity increased with canopy tree density (Figure 12) while horizontal habitat heterogeneity was not related to tree density (R^2=.007, P=.79). None of the overall bird community variables were related to vertical habitat diversity (Table 7). Understorey birds where inversely related to vertical habitat complexity, while overstorey birds were positively related to vertical habitat complexity (Figures 13-14). No bird variables were significantly associated with horizontal habitat heterogeneity (statistical results not shown).

Distinguishing the relative strengths of bird responses to energy availability and habitat niche diversity was difficult because of strong correlations among these variables. Total leaf, conifer leaf, and deciduous leaf biomass were positively associated with vertical habitat complexity, while palatable leaf and herb biomass were negatively correlated with habitat complexity (Table 8).

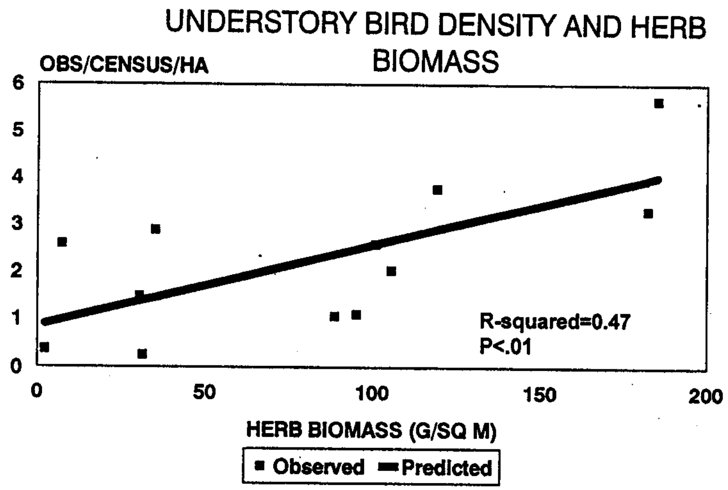

Figure 10. Relationship between the abundance of the understorey bird community and biomass of herbs.

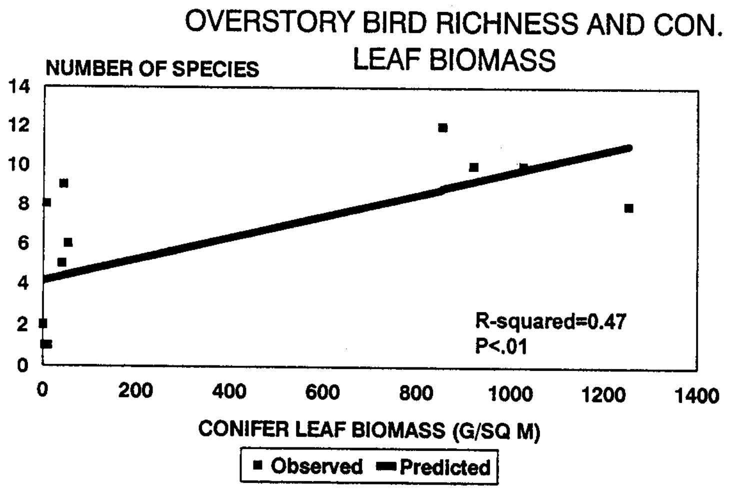

Figure 11. Relationship between overstorey bird diversity and biomass of coniferous leaves.

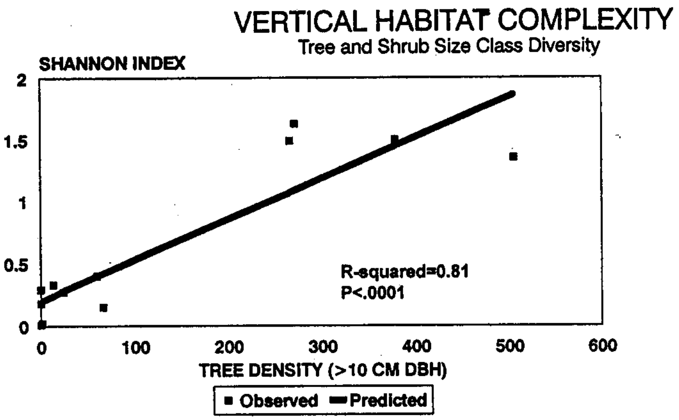

Figure 12. Relationship between vertical habitat complexity and density of canopy trees.

Table 7. Results of linear regressions relating total, understorey, and overstorey birds to vertical habitat complexity. "NS" indicates that the relationships in not significant.

BIRD COMMUNITY	R^2	SIGN OF RELATIONSHIP	P-VALUE
TOTAL			
ABUNDANCE	.07	NS	.80
RICHNESS	.03	NS	.61
SHANNON'S INDEX	.02	NS	.63
UNDERSTOREY			
ABUNDANCE	.57	-	.005
RICHNESS	.66	-	.001
SHANNON'S INDEX	.50	-	.009
OVERSTOREY			
ABUNDANCE	.71	+	.0006
RICHNESS	.60	+	.003
SHANNON'S INDEX	.40	+	.03

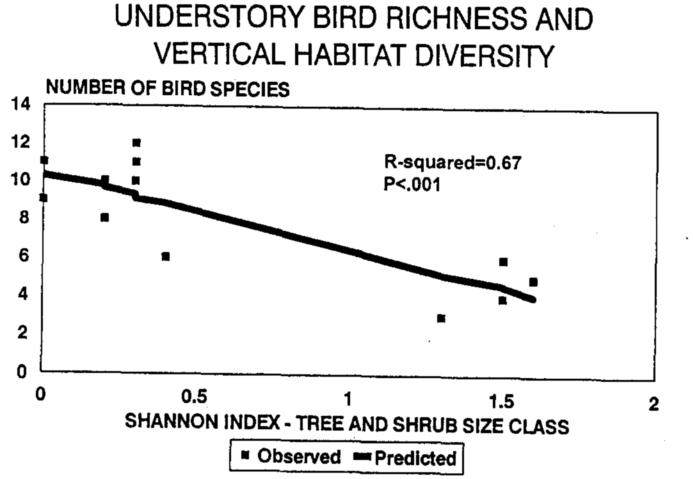

Figure 13. Relationship between understory bird richness and vertical habitat complexity.

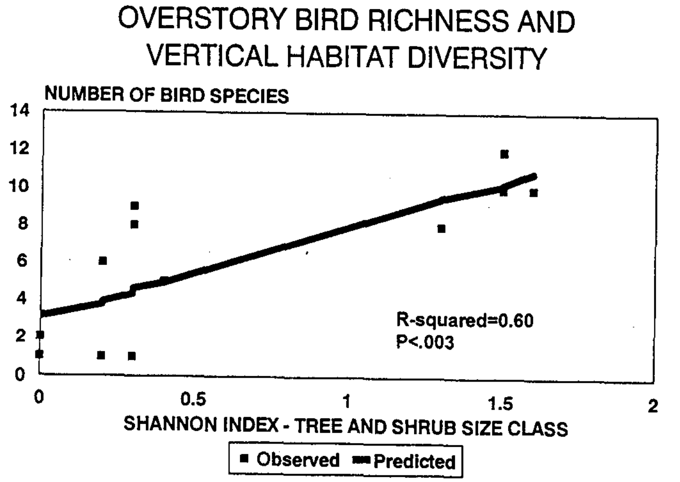

Figure 14. Relationship between overstory bird richness and vertical habitat complexity.

Table 8. Correlation coefficients and (p-values) among habitat complexity variables and plant biomass variables. Habitat complexity variables involve the diversity of tree and shrub size classes. Biomass variables are total biomass of different plant types and plant parts.

BIOMASS VARIABLES	HABITAT COMPLEXITY VARIABLES		
	RICHNESS	SHANNON DIVERSITY	SHANNON DIVERSITY SD[1]
ALL LEAVES	+0.93 .0001	+.94 .0001	-.17 .6000
CONIFEROUS LEAVES	+.94 .0001	+.96 .0001	-.14 .6500
DECIDUOUS LEAVES	+.52 .0800	+.55 .0600	+.60 .0400
PALATABLE LEAVES	-.39 .2000	-.37 .2400	-.17 .5700
HERBS	-.61 .0300	-.61 .0400	-.47 .1200

[1] SD - Standard deviation.

Nest Predation Hypothesis

Mean predation rates were 47% in OCSC stands, 24% in OCSS stands, and 6% in CCSC stands. The differences between OCSC and each of the other two treatments were significant ($P < .05$).

DISCUSSION

Bird Response to Stand Type

We found that several bird species differed in abundance among the three stand types. Those species associated with closed-canopy forest included a bark forager (Brown creeper), conifer foliage gleaners (e.g., Golden-crowned kinglet), a flycatcher (Hammond's flycatcher), and a forest understorey feeders (Winter wren). Three of the open-canopy associates avoided stands with low densities of emergent trees (Dark-eyed junco, Lazuli bunting, and Willow flycatcher). Only Steller's jay, a common nest predator, was uniquely associated with structurally-complex, open-canopy stands. These results are consistent with a study across a broader range of stand types (Hansen et al. in prep.) that found guilds of species uniquely associated with each of four stand types: OCSS, OCSC, CCSC, and closed-canopy, structurally-simple stands.

The overall bird community showed weak patterns across the stand types. Neither total bird density nor richness differed among treatments, but bird diversity was significantly higher in OCSC than in OCSS. Vega (1993) analyzing the same data set with nonparametric statistical tests, did not find significant differences in bird diversity among stand types. Our findings do not strongly support any of the three hypotheses, which predicted that diversity will be either intermediate or low at intermediate canopy densities (see Figure 2c, 3c, 4c). Stronger patterns emerged when the community was divided into understorey and overstorey species. The understorey community was significantly associated with the two open canopy stand types, while the overstorey community was associated with the closed canopy stand type. Bird diversity was relatively high in OCSC for both understorey and overstorey bird communities, and this accounts for the total community reaching highest diversity in this stand type.

Evaluation of Hypotheses

a) Energy and Habitat Niche Hypotheses

As predicted by the Energy Hypothesis, relatively more of annual NPP was fixed in forms available to consumers in the stands with fewer canopy trees. Closed-canopy stands, however, had substantially higher total NPP. Hence, contrary to prediction, annual NPP of available energy was greatest in these stands. These findings differ from a previous attempt to quantify NPP in the region. Turner and Long (1975) found that annual production of available energy was substantially higher in stands just prior to canopy closure than in other stands that had recently undergone canopy closure. It is likely that our open-canopy stands, all of which were created 2-5 years prior to the study, had not yet generated sufficient biomass to utilize available solar energy fully.

Vertical habitat complexity did increase with canopy tree density, as predicted by the Habitat Niche Hypothesis. This finding is consistent with many other studies in finding that habitat complexity increases during the course of succession (see review in Brown 1991).

Contrary to both the Energy and Habitat Niche hypotheses, neither bird community abundance, nor richness, nor diversity were correlated with either available NPP or vertical habitat complexity. The explanation for these findings may lie in the responses of the understorey and overstorey bird communities to these factors. Overstorey birds were strongly associated with both total leaf biomass and with vertical habitat complexity. Understorey birds were negatively associated with these variables. Moreover, understorey bird abundance was positively correlated with herb biomass. Thus, the abundances of individual bird species are closely related to either available energy or to habitat complexity, as predicted by the hypotheses. But the relationships are positive for some species and negative for other species. Consequently, no significant relationship was found when all species are combined for the community-level analysis.

Does the available energy or habitat complexity account for more of the variation in bird abundance? This question cannot be answered fully by our results because these factors were strongly correlated in our study sites. Total leaf, conifer leaf, and deciduous leaf biomass were positively associated with vertical habitat complexity, while palatable leaf and herb biomass were negatively correlated with habitat complexity. Overstorey bird abundance, richness, and diversity were somewhat more strongly associated (R^2 was .14-.28 greater) with vertical habitat complexity than with the energy variables, suggesting that this group might respond more strongly to habitat structure than to available food. The opposite may be the case for understorey birds, given that they were negatively associated with vertical habitat complexity but positively associated with herb weight.

These correlations among available energy and habitat complexity, however, suggest that birds select habitat based on both factors, in order to meet their food, cover, nesting, and other requirements. Bird species differ in food and habitat requirements, partially based on their life history attributes (Urban et al. 1992). Local patters of diversity likely reflect both the distributions of foods and habitats as well as the collective life history attributes of the species comprising the community. Both resource distributions and bird life histories may vary from place to place (Hansen and Urban 1992, Hansen et al. 1992). The important implication is that simple hypotheses about factors controlling species diversity cannot be generalized to all locations.

Whereas MacArthur and MacArthur (1961) found foliage height diversity (a measure of vertical habitat complexity) to correlate strongly with bird diversity in New England forests, we have not found this to be the case in our study sites in western Oregon. Approximately half of the birds in our area are understorey associates with food and/or habitat requirements that are best met at sites that have only a few vegetation layers, with those being near the ground. Knowledge of both resource distributions and the life history attributes of the local animal community are necessary for predicting local patterns of animal diversity (Hansen and Urban 1992).

b) Nest Predation Hypothesis

The results suggested that shrub nesting birds encounter higher nest predation rates in open-canopy stands with emergent canopy trees than in either open stands without emergent trees or in closed forests. Both the abundance of the Steller's Jay, a likely nest predator, and predation rates on artificial nests were significantly higher in the OCSC stands than in the other two stand types. Previous studies have found that predation rates on artificial nests are related to forest patch size, distance from forest edge, and edge type (Wilcove 1985, Small and Hunter 1988, Yahner and Wright 1985). Our study is the first, to our knowledge, to examine nest predation rates as a function of canopy tree density. The results suggest that emergent trees in open-canopy stands provide perches for avian nest predators and facilitate surveillance of nests of prey species, allowing the predators to achieve higher rates of nest location and predation. This effect is apparently reduced in closed forests, because trees are sufficiently dense to impair visibility for the predators.

Implications for Management

Retention of canopy trees in harvest units is an important strategy in the "ecological" forestry practices that have recently emerged in the Pacific Northwest (Swanson and Franklin 1992, Franklin 1992). The rationale for this practice is that it approximates the structural configurations that result from natural disturbances like wildfire, and that various organisms and processes are dependent on this structural pattern. Consequently, retention cuts are being widely implemented on Federal Lands in the PNW, and are advocated nationally under current USDA Forest Service policy.

Our results indicated that canopy tree density strongly influenced pathways and abundance of NPP, habitat complexity, and rates of avian nest predation. These ecological processes, in turn, were associated with patterns of density, richness, and diversity in understorey and overstorey bird communities in our study area. Total bird diversity was greatest in the open-canopy stands with some emergent trees, which might be seen as offering support for the practice of canopy tree retention in harvest units. Nest predation rates were especially high in this stand type, however. Moreover, bird species clearly responded individually to canopy tree density, with some being most strongly associated with each of the three stand types that were studied. It appears that managers can best maintain native bird species in the study area by creating an array of stand structures and ages across the landscape. The relative proportions of the stand types that will best maintain native bird species will likely vary from one geographic location to another, as a function of local resource distributions and animal life history attributes. Conserving species diversity nationally will likely require research and management strategies that are tailored to local ecosystems and animal communities.

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