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CANOPY TREE RETENTION AND AVIAN DIVERSITY IN THE OREGON CASCADES

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Forested managers are developing and implementing new strategies to sustain ecological productivity, biodiversity, water quality, and other factors (Kessler et al. 1992). This trend has generated considerable debate on the economic, social, and ecological consequences of these new strategies. A centerpiece of "ecological forestry" in the Pacific Northwest (PNW) United States is the retention of variable densities of live trees in harvest units in an attempt to maintain canopy complexity over the full rotation cycle (Franklin 1989; Gillis 1990). This approach contrasts sharply with the traditional practice of clearcutting all live and dead trees to facilitate the establishment and growth of plantations of shade-intolerant species Douglas-fir (*Pseudotsuga menziesii*).

The rationale for canopy tree retention derives from patterns of disturbance and succession in natural PNW forests. The variable disturbance regimes, large tree sizes, and "legacies" of structures surviving disturbances result in natural forests of all ages having high variability in tree size and canopy layering (Spies and Franklin 1991; Hansen et al. 1991). This structural complexity influences several ecological attributes (Franklin et al. 1981). Retaining canopy complexity in managed forests is hypothesized (Swanson and Franklin 1992; Franklin 1992) to: maintain habitat diversity for forest organisms; promote nutrient cycling; maintain beneficial predator/prey relationships among forest invertebrates; provide refugia and inocula for nonvagile mycorrhizae and invertebrates; provide sources of coarse woody debris for both uplands and streams; and enhance dispersal opportunities for species that avoid forest openings.

Critics of canopy tree retention, on the other hand, argue that it increases harvest and regeneration costs, threatens human safety, promotes the spread of forest diseases, and inhibits the growth of regenerating Douglas-firs (Atkinson 1992). Clearly, trade-off analyses are needed on the relative costs and benefits of this silvicultural strategy.

The effects of canopy retention in managed forests on bird communities have yet to be examined in the region. Ecological theory, however, suggests that the relationship between canopy density and avian diversity should be strong. The habitat niche hypothesis maintains that structurally complex forests contain more habitat niches and should thus support more bird species than do more homogeneous forests (MacArthur and MacArthur 1961; Urban and Smith 1989). This hypothesis, which has been found to prevail in natural forests in the region (Ruggiero et al. 1991), suggests that bird diversity is positively correlated with canopy tree retention.

An alternative hypothesis asserts bird diversity is inversely related to canopy density because of food availability (Hansen et al. in press). According to this hypothesis, net primary production (NPP) in closed-canopy conifer stands is mostly fixed as wood and unpalatable conifer leaves. In open-canopy stands, relatively more of the NPP is available to consumers because it is fixed in the form of palatable hardwood and herb leaves, buds, fruits, seeds, and flowers. The higher level of available energy (in plants and invertebrates) and greater number of energy pathways in open canopy forests should support higher bird diversity (Begon et al. 1986). Possibly both habitat niche diversity and energetics influence bird communities, resulting in complex relationships between canopy tree density and bird diversity.

Regardless of the underlying ecological processes, forest managers want to know how canopy tree retention influences biodiversity. Which species and communities respond to canopy tree density and are those responses positive or negative? Do thresholds exist where small changes in tree density result in large changes in biodiversity? What densities and size-class distributions of tree retention best accomplish specific biodiversity and other objectives? Such knowledge can help managers design forests to achieve their management goals better.

In this paper we report on a correlative study of bird response to a gradient of canopy tree retention levels in managed forests at higher elevations in the west Cascades of Oregon. Specific questions were: (1) Do significant relationships exist among canopy tree density and attributes of bird communities?, (2) How strong are these relationships relative to the effects of other habitat measures?, (3) Are the associations between canopy tree density and birds positive or negative, linear or nonlinear?, (4) What size classes of retained trees are most closely associated with variation in the abundance of individual bird species?

METHODS

Study Sites

Habitat structure and breeding birds abundance were measured across 16 managed stands representing a gradient of canopy tree retention levels. The stands were within the McKenzie and Sweet Home Ranger Districts of the Willamette National Forest in western Oregon. Fourteen stands were between Highway 126 to the west and the Mt. Washington

Wilderness to the east. The other two stands were approximately 15 km to the north near the junction of Highway 126 and Highway 20.

This area is on the western edge of the High Cascades Province (Franklin and Dyrness 1973), a high-elevation plateau of volcanic origin (late Pliocene and Pleistocene epochs) that straddles the Cascade crest. Pleistocene glaciers covered the area. Soils are immature, derived from glacial deposits and volcanic ejecta. The climate here is cool and moist, with a mean annual precipitation of 2190 mm, mean January temperature of -1.7° C and a mean July temperature of 14° C (Franklin and Dyrness 1973). A snowpack persists over much of the winter and spring. The study area lies between the *Tsuga heterophylla* and *Abies amabalis* Zones (Franklin and Dyrness 1973). Dominant trees are Douglas-fir, western hemlock (*Tsuga heterophylla*), grand fir (*Abies grandis*), noble fir (*Abies procera*), and silver fir (*Abies amabilis*). Common understory plants are chinquapin (*Castanopsis chrysophylla*), Pacific dogwood (*Cornus nuttallii*), and cascara buckthorn (*Rhanus purshiana*). These stands were generally established 100 to 150 years ago after intense wildfires. Shrub biomass within the study sites appeared to be substantially less than at lower elevations to the west. This might reflect the effects of elevation, snowpack, soils, or wildfire history.

The stands were 9 ha or greater in area, at elevations of 731-1,189 m, and varied in aspect (Table 26.1). Each stand had been subjected to timber harvest. Four sites were

Table 26.1. Attributes of stands sampled in this study.

Location[1]	TRI Number[2]	Area (HA)	Elevation (M)	Aspect[3]/ Slope[4]	Harvest Year	Harvest System[5]	Number of Plots
15-7-8	7109-123	13	914	NE/25	1987	1	6
15-7-31	7110-138	19	914	SE/15	1989	1	6
15-6-25	7110-133	9	762	0	1987	1	6
15-6-25	7110-244	12	884	0	1987	1	6
15-7-27	7110-50	17	1189	W/10	1988	2	6
15-7-28	7110-275	17	1066	W/10	1988	2	8
16-7-8	7112-147	13	1098	SE/12	1988	3	6
15-7-15	7109-137	15	1146	W/15	1985	3	7
14-6-1	3503-95	16	1098	E/15	1987	4	6
14-6-14	3502-64	20	1112	SE/15	1986	4	7
15-7-19	7109-212	13	914	SE/5	1987	4	6
16-7-4	7110-263	13	1113	0	1986	4	6
15-7-15	7109-52	13	1128	W/10	1979	5	6
15-7-19	7109-84	35	914	N/25	1982	5	6
15-6-35	7110-128	19	731	SW/15	1985	5	6
15-6-25	7110-18	82	792	0	1982	5	8

[1] Township (south) - Range (east) - Section

[2] USDA Forest Service Total Resource Inventory Number

[3] Cardinal direction

[4] Percent slope

[5] 1- Clearcut (no retention); 2 - Clearcut (light retention); 3 - Clearcut (moderate retention); 4 - Shelterwood; 5 - Commercial thin.

See text for explanation.

clearcut, four were clearcut with retention of 2-14 trees per ha, four underwent shelterwood cuts where a mean of 19 trees per ha were retained, and four stands were commercially thinned to a mean of 87 trees per ha. The retention and shelterwood units were harvested between 1985 and 1989, and most were burned and planted with Douglas-fir; the trees retained were 30 cm diameter at breast height (dbh) or larger. The commercial thins were done between 1979 and 1985, and the majority of trees retained were 10-30 cm dbh. In all stands, the trees retained were dispersed, rather than clumped.

Bird and Habitat Sampling

The abundance of breeding birds was sampled using the Variable Circular-Plot method (Reynolds et al. 1980). Plot centers were placed 100 m apart and at least 75 m from stand edges. Six to eight plots were located in each stand, depending on the size of the stand. Censuses began each day at dawn and continued for no more than four hours. Observers walked to a plot center, waited two minutes, and then recorded all birds seen and heard during an eight-minute period. Variables recorded for each bird were: species, distance class to bird at first detection, distance class to bird at nearest detection, distance class of bird from the nearest edge of the stand, and type of stand neighboring that stand edge. Flagging was placed 40 m from each plot center along the four cardinal directions to aid in estimating distance class to a bird. Each plot was censused five times during the period May 15 - June 31, 1991. Observers rotated among plots and stands to minimize bias. The common name, scientific name, and code for each bird species sampled are listed in Table 26.2.

Habitat measurements were centered on the bird census plots. The variables measured involved topography, tree density, understory cover, and canopy cover. Descriptions of the variables and the sampling scheme are presented in Table 26.3 and Figure 26.1. The measurements were made during July and August 1991.

Data Analyses

Only birds registered within 50 m of plot centers were included in the analyses. This prevented overlap in the areas covered from adjacent plots. An analysis by Spencer (1993) in habitats similar to the study area revealed that the songs of all bird species in our area can be detected within 50 m. We calculated relative abundance for each species as the number of individuals registered within the 50-m radius plot at either the first or nearest detection. 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. Total bird abundance was the sum for all species sampled.

Analyses of habitat associations for individual bird species were done only for species with 9 or more registrations. All bird species detected were considered for community-scale bird-habitat analyses. These community variables were: relative abundance of all species combined (ALL), bird species richness (RICHNESS), Shannon's diversity index (SHANNON) and Hill's N2 (HILL'S), a diversity index for the relatively abundant species (Ludwig and Reynolds 1988).

Table 26.2. Bi

Species Code
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GCKI
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Table 26.2. Bird species sampled in this study.

Species Code	Common Name	Latin Name	Registrations[1]
AMRO	American robin	*Turdus migratorius*	12
BRCR	brown creeper	*Certhia americana*	10
CBCH	chestnut-backed chickadee	*Parus rufescens*	6
CHSP	chipping sparrow	*Spizella passerina*	18
DEJU	dark-eyed junco	*Junco hyemalis*	176
DOWO	downy woodpecker	*Picoides pubescens*	6
DUFL	dusky flycatcher	*Empidomax oberholseri*	5
EVGR	evening grosbeak	*Coccothraustes vespertinus*	8
FOSP	fox sparrow	*Passerella iliaca*	2
GCKI	golden-crowned kinglet	*Regulus satrapa*	22
GRJA	gray jay	*Perisoreus canadensis*	3
HAFL	Hammond's flycatcher	*Empidonax hammondii*	14
HAWO	hairy woodpecker	*Picoides villosus*	16
HTWA	hermit/Townsend's warbler[2]	*Dendroica occidentalis* and *D. townsendi*	50
HOWR	house wren	*Troglodytes aedon*	5
MCWA	McGillivray's warbler	*Oporornis tolmiei*	9
OSFL	olive-sided flycatcher	*Contopus borealis*	2
PISI	pine siskin	*Carduelis pinus*	6
PUFI	purple finch	*Carpodacus purpureus*	1
RBNU	red-breasted nuthatch	*Sitta canadensis*	9
RBSA	red-breasted sapsucker	*Sphyrapicus ruber*	2
RUHU	rufous hummingbird	*Selasphorus rufus*	5
SOSP	song sparrow	*Melospiza melodia*	1
STJA	Steller's jay	*Cyanocitta stelleri*	9
TOSO	Townsend's solitaire	*Myadestes townsendi*	1
TRSW	tree swallow	*Tachycineta bicolor*	2
WCSP	white-crowned sparrow	*Zonotrichia leucophrys*	10
WEBL	western bluebird	*Sialia mexicana*	11
WEFL	western flycatcher	*Empidonax difficilis*	6
WETA	western tanager	*Piranga ludoviciana*	20
WIWA	Wilson's warbler	*Wilsonia pusilla*	1
WIWR	winter wren	*Troglodytes troglodytes*	1
YRWA	yellow-rumped warbler	*Dendroica coronata*	5

[1] Number of registrations within 50 m of a plot center during the 5 censuses.

[2] These two species overlap and hybridize in the study area and are very difficult to distinguish by song Consequently they were lumped in this study.

Tree density data were averaged across subplots within each plot. Means and standard deviations were then calculated among plots within each stand and used in the bird habitat analyses. Similarly, understory and canopy cover were averaged among subplots within each plot and the mean calculated among plots within each stand. The four tree

Table 26.3. Habitat attributes used in the analyses of bird habitat relationships. See Figure 26.1 for a depiction of the sampling design.

Attribute	Code[1]	Description
Elevation	ELEV	Elevation above sea level (m) at plot center
Slope	SLOPE	Average slope (%) within 20 m of plot center as measured with a clinometer
Aspect	ASPECT	Average aspect (cardinal direction) within 20 m of plot center as measured with a compass
Tree density	TOT2	Number of trees (per ha) 10-30 cm diameter at breast height (dbh) within 4 5-m radius subplots placed 20 m from plot center
	TOT3	Number of trees (per ha) 30-50 cm dbh as sampled in TOT2
	TOT4	Number of trees (per ha) 50-90 cm dbh as sampled in TOT2
	TOT5	Number of trees (per ha) >90 cm dbh as sampled in TOT2
	TOT2-5	Number of trees (per ha) >10 cm dbh as sampled in TOT2
	TOT45	Number of trees (per ha) >50 cm dbh as sampled in TOT2
	SHADE2	Number of shade-tolerant (grand fir) trees (per ha) 10-30 cm dbh as sampled in TOT2
	SUN2	Number of shade-intolerant (Douglas-fir and noble fir) trees (per ha) 10-30 cm dbh as sampled in TOT2
Canopy cover	CANCOV	Percent cover of all vegetation above 2 m in height measured with the moosehorn technique at 4 points 20 m from plot centers
Understory	UNDCOV	Percent cover of vegetation <2 m in height estimated visually within 4 1-m subplots distributed around each of 4 points 20 m from plot centers

[1] Habitat codes followed by "L" in the text denote a log transformation. Habitat codes followed by "SD" in the text denote standard deviation.

size classes that were >10 cm dbh were aggregated into the variable TOT2-5. We refer to this variable as canopy tree density. Habitat variables were generally not included in the bird habitat analyses if they: had a sample size of 9 or fewer non zero values; had distributions that differed significantly from normal (data transformations were used where helpful); were strongly correlated with other habitat variables; or were judged not have ecological relevance to the bird species. The variables used were: ELEV, ASPECT, UNDCOV, and a log transformation of TOT2-5 (denoted as TOT2-5L). For all analyses, relationships were considered statistically significant at the 0.05 level.

Stepwise linear regression was used to determine the relative amount of variation in each of the bird variables associated with each habitat variable (ELEV, ASPECT, UNDCOV, AND TOT2-5L). The shapes of the relationship between TOT2-5 and each bird variable were determined by fitting a linear model and two nonlinear models, the natural growth function (y=a+b*(1-exp(-b*x))) and the logistic function (y=a/(1+b*exp(-c*x))). The model with the tightest fit was selected as the best descriptor of the relationship. A log transformation of TOT2-5 was not used in this analysis because we wanted the plots of bird abundance on tree density to be readily interpretable by forest managers. Plots of these curves enable the reader to identify thresholds where small changes in tree density are associated with large changes in bird abundance.

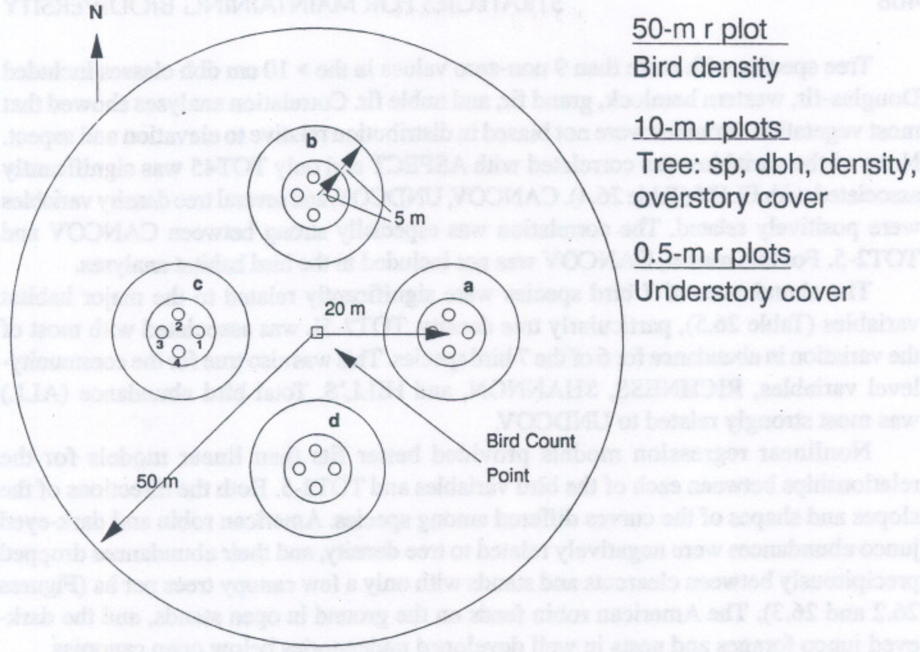

Figure 26.1. Depiction of the vegetation sampling protocol used at each plot within a study stand. See Table 26.3 for a list of the variables sampled.

The final analysis asked which combination of tree density variables (mean and variance of the tree size classes) were most associated with variation in each of the bird variables. Stepwise linear regression (p-value to enter=0.05) was used to select habitat variables that were significantly related to variation in each of the bird variables. The habitat variables included mean and standard deviation of TOT2-5, TOT3, TOT45, and TOT2 differentiated into shade tolerant species (SHADE2) and shade intolerant species (SUN2). This was done to differentiate between habitats with shaded and open understories. The analysis was done separately for untransformed variables and log-transformed variables, and the best models (highest R^2) are reported here.

An assumption of linear regression is that the error term is normally distributed. We tested this assumption for the variable sets selected in the stepwise procedure and found that the residuals for all but one of the species (brown creeper) did not differ significantly from a normal distribution.

RESULTS

A total of 33 species of birds were tallied in the study plots (Table 26.2). Fourteen of these had 9 or more registrations and were subjected to species-level statistical analyses. Species associated with forest canopies and boles were relatively abundant in the sample. Understory associates other than dark-eyed junco were sparse.

Tree species with more than 9 non-zero values in the > 10 cm dbh classes included Douglas-fir, western hemlock, grand fir, and noble fir. Correlation analyses showed that most vegetation variables were not biased in distribution relative to elevation and aspect. None of the variables was correlated with ASPECT and only TOT45 was significantly associated with ELEV (Table 26.4). CANCOV, UNDCOV, and several tree density variables were positively related. The correlation was especially strong between CANCOV and TOT2-5. For this reason, CANCOV was not included in the bird habitat analyses.

The abundances of 7 bird species were significantly related to the major habitat variables (Table 26.5), particularly tree density. TOT2-5L was associated with most of the variation in abundance for 6 of the 7 bird species. This was also true for the community-level variables, RICHNESS, SHANNON, and HILL'S. Total bird abundance (ALL) was most strongly related to UNDCOV.

Nonlinear regression models provided better fits than linear models for the relationships between each of the bird variables and TOT2-5. Both the directions of the slopes and shapes of the curves differed among species. American robin and dark-eyed junco abundances were negatively related to tree density, and their abundances dropped precipitously between clearcuts and stands with only a few canopy trees per ha (Figures 26.2 and 26.3). The American robin feeds on the ground in open stands, and the dark-eyed junco forages and nests in well developed understories below open canopies.

The abundance of the canopy gleaner hermit/Townsend's warbler increased proportionally with tree density (Figure 26.4). This trend began at the origin and continued to the highest tree densities. Golden-crowned kinglet, also a canopy gleaner, exhibited a threshold relationship. It was absent from stands with fewer than 25 trees per ha and increased proportionally with tree density in stands with higher stem densities (Figure

Table 26.4. Pearson correlation coefficients and p-values among habitat variables.

	Elev	Aspect	Cancov	Undcov	Tot2-5	Tot2	Tot3	Tot45	Shade2
Sun2	-0.43	0.27	0.81	0.58	0.93	0.98	0.55	-0.20	0.84
	0.09	0.31	0.00	0.02	0.00	0.00	0.03	0.46	0.00
Shade2	-0.48	0.44	0.95	0.72	0.89	0.91	0.47	-0.09	
	0.06	0.09	0.00	0.00	0.00	0.00	0.07	0.74	
Tot45	0.57	0.00	0.18	0.00	0.12	-0.21	0.15		
	0.02	1.00	0.50	1.00	0.66	0.44	0.59		
Tot3	-0.19	0.32	0.58	0.29	0.66	0.56			
	0.49	0.23	0.02	0.28	0.01	0.02			
Tot2	-0.49	0.31	0.87	0.63	0.95				
	0.05	0.24	0.00	0.01	0.00				
Tot2-5	-0.31	0.33	0.94	0.63					
	0.24	0.22	0.00	0.01					
Undcov	-0.28	0.26	0.74						
	0.30	0.34	0.00						
Cancov	-0.30	-0.39							
	0.26	0.13							
Aspect	0.09								
	0.73								

Table 26.5. Results of stepwise regressions of bird species community attributes against the habitat variables ELEV, ASPECT, UNDCOV, AND TOT2-5L.

Species[1] Code	Variables Included	Partial R^2	Overall F-Value	Overall Prob > F
AMRO	TOT2-5L	.47	12.4	.003
DEJU	TOT2-5L	.34	7.1	.018
GCKI	TOT2-5L	.50	14.3	.002
HAFL	TOT2-5L	.55	23.7	.0001
	ELEV	.23		
HTWA	TOT2-5L	.67	27.4	.0001
	ELEV	.12		
MCWA	UNDCOV	.26	5.0	.043
RBNU	TOT2-5L	.39	8.8	.010
ALL	UNDCOV	.45	11.7	.004
RICHNESS	TOT2-5L	.59	19.1	.0001
	UNDCOV	.12		
	ELEV	.12		
SHANNON	TOT2-5L	.76	29.8	.0001
	ELEV	.06		
HILL'S	TOT2-5L	.68	30.4	.0001

[1] Bird and habitat codes are defined in Tables 26.2 and 26.3 and in the text. The significance level for allowing a habitat variable to stay in the model was 0.05. Only statistically significant models are shown. Insignificant models resulted for chipping sparrow, hairy woodpecker, house wren, Steller's jay, white-crowned sparrow, western bluebird, and western tanager.

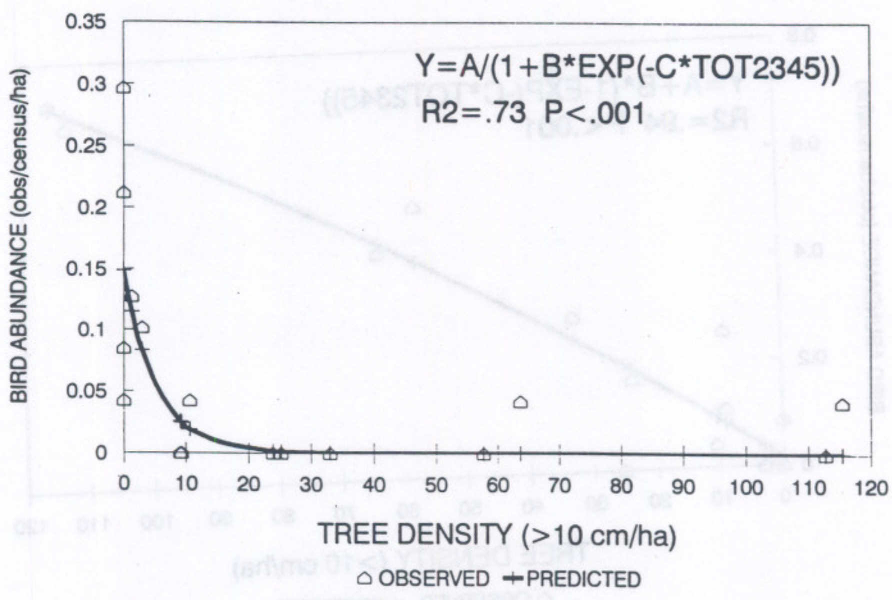

Figure 26.2. Data points and nonlinear regression line describing the relationship between canopy tree density and the American robin.

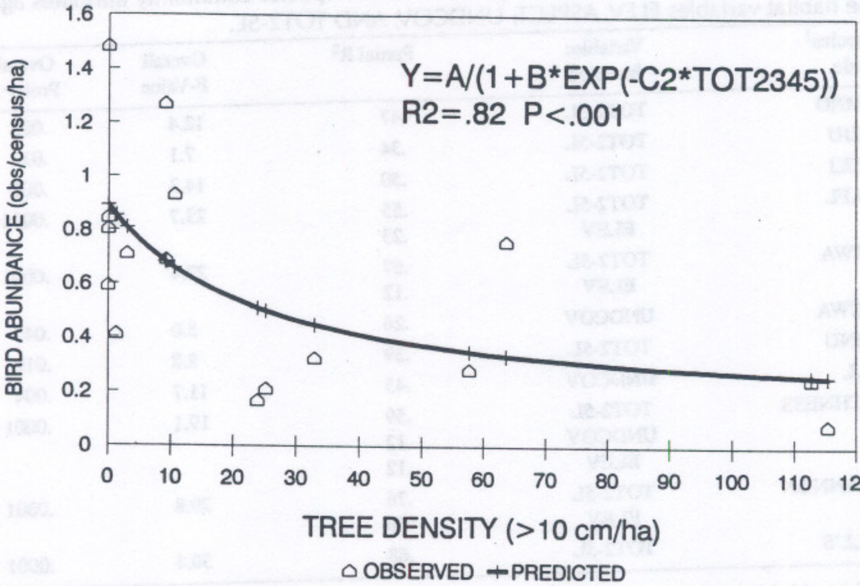

Figure 26.3. Data points and nonlinear regression line describing the relationship between canopy tree density and the dark-eyed junco.

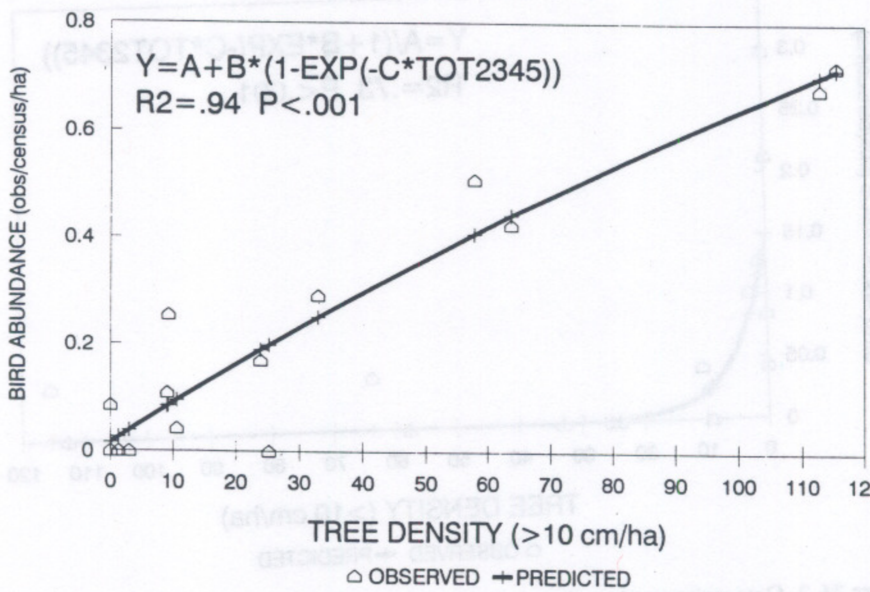

Figure 26.4. Data points and nonlinear regression line describing the relationship between canopy tree density and the hermit/Townsend's warbler.

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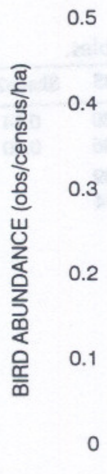

Figure 26.5.
canopy tree

26.5). Hammond's flycatcher, a sallying insectivore, showed a similar relationship (Figure 26.6). The curve for brown creeper, which forages on the bark on tree boles and branches, was sigmoidal, with the lower asymptote at about 10 trees per ha and the upper asymptote at about 30 trees per ha (Figure 26.7). Red-breasted nuthatch, also a bark forager, had a logistic relationship with tree density (Figure 26.8). Overall, these habitat associations were quite strong: tree density accounted for more than 70% of the variation in abundance for 6 of the 7 bird species with significant models (Figures 26.2-26.8).

The bird community measures were also tightly related to tree density. Total bird abundance increased proportionally with TOT2-5 (Figure 26.9). The three measures of diversity, RICHNESS, SHANNON, and HILL'S, each had logistic curves, reaching asymptotes at about 15-30 trees per ha (Figures 26.10-26.12). Tree density was associated with 96% to 99% of bird diversity. Forest structural complexity is a possible factor underlying the relationships between bird diversity and tree density. We found that an index of structural complexity (mean number of tree size classes per stand) was also related to TOT2-5 (Figure 26.13). This index was significantly correlated with bird diversity (SHANNON) (n=16, R=0.70, p<0.003).

Bird species differed in their associations with the various tree size classes. TOT2-5 was the first variable selected in the stepwise regressions for American robin, dark-eyed junco, golden-crowned kinglet, and hermit/Townsend's warbler (Table 26.6). Red-breasted nuthatch was associated with variation in tree density (TOT2-5SD). Brown creeper, hairy woodpecker, and Steller's jay were significantly related to the mean and variance of large trees. Shade-tolerant trees 10-20 cm dbh and large trees was associated with most of the variation in Hammond's flycatcher density.

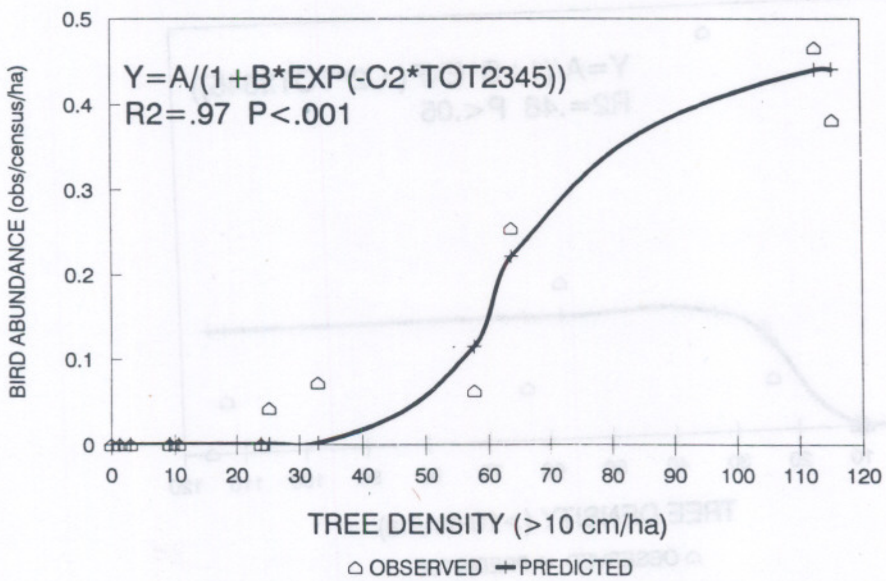

Figure 26.5. Data points and nonlinear regression line describing the relationship between canopy tree density and the golden-crowned kinglet.

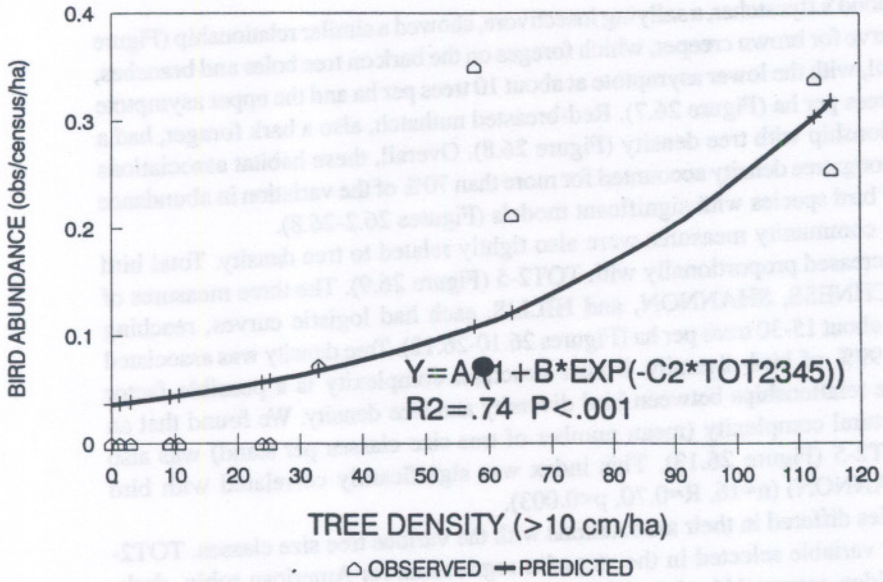

Figure 26.6. Data points and nonlinear regression line describing the relationship between canopy tree density and the Hammond's flycatcher.

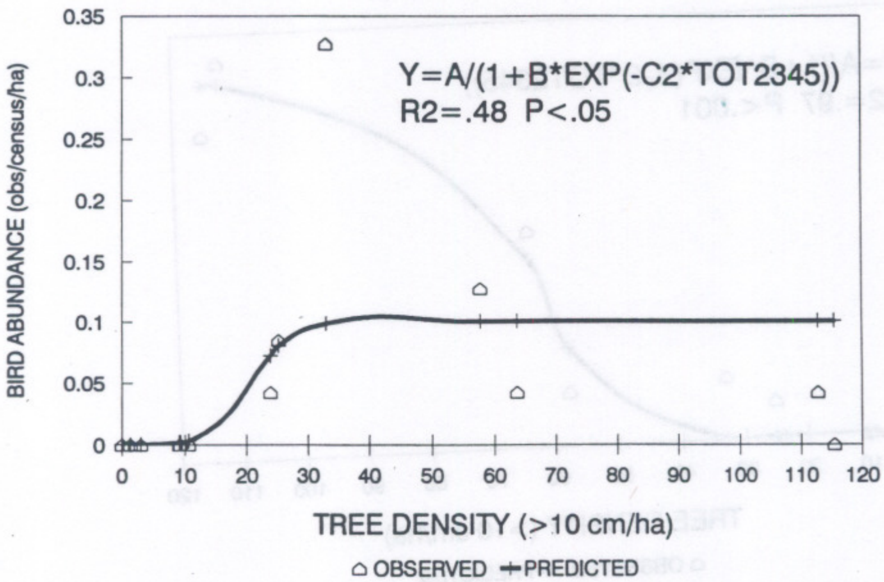

Figure 26.7. Data points and nonlinear regression line describing the relationship between canopy tree density and the brown creeper.

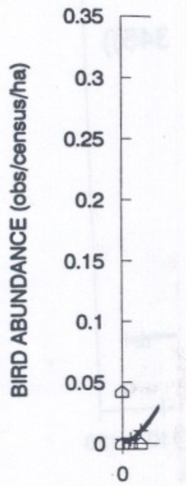

Figure 26.8. Data
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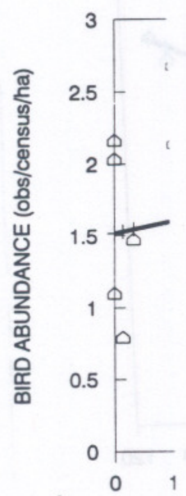

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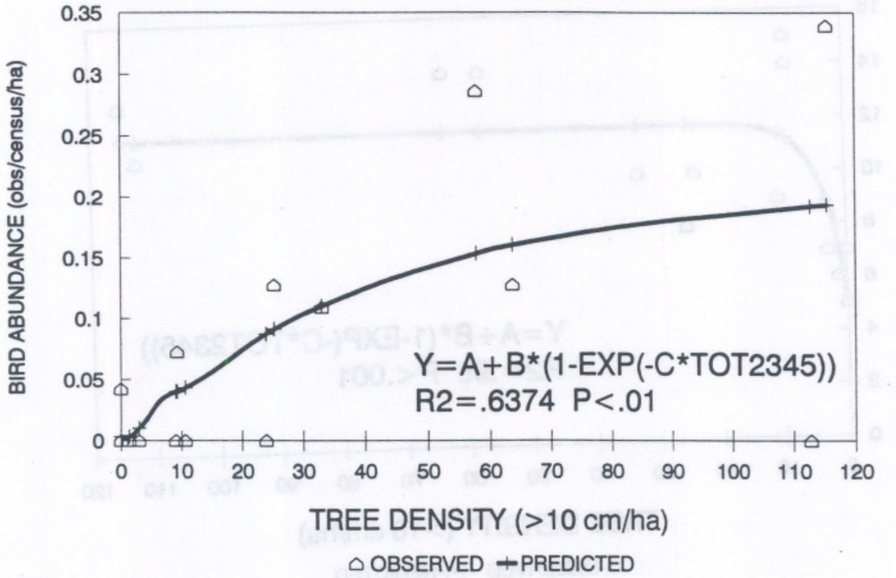

Figure 26.8. Data points and nonlinear regression line describing the relationship between canopy tree density and the red-breasted nuthatch.

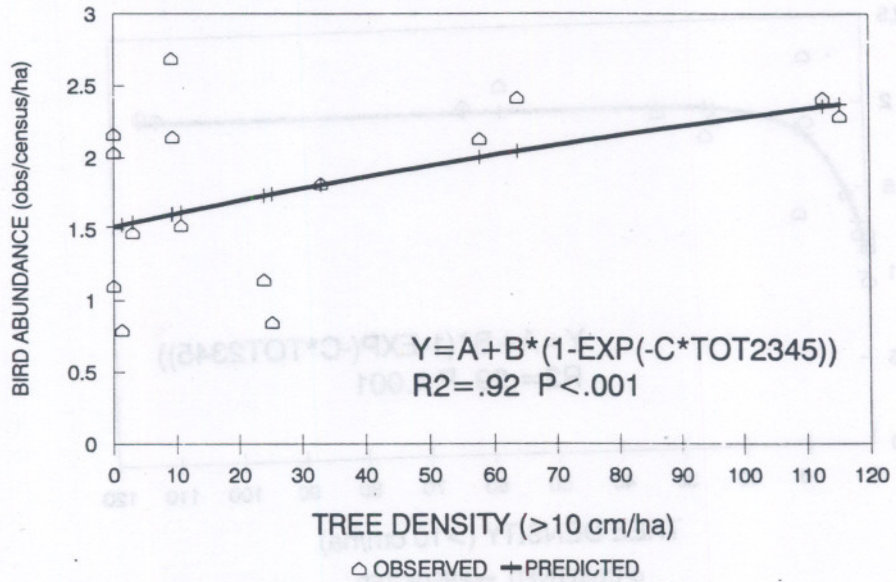

Figure 26.9. Data points and nonlinear regression line describing the relationship between canopy tree density and total bird abundance.

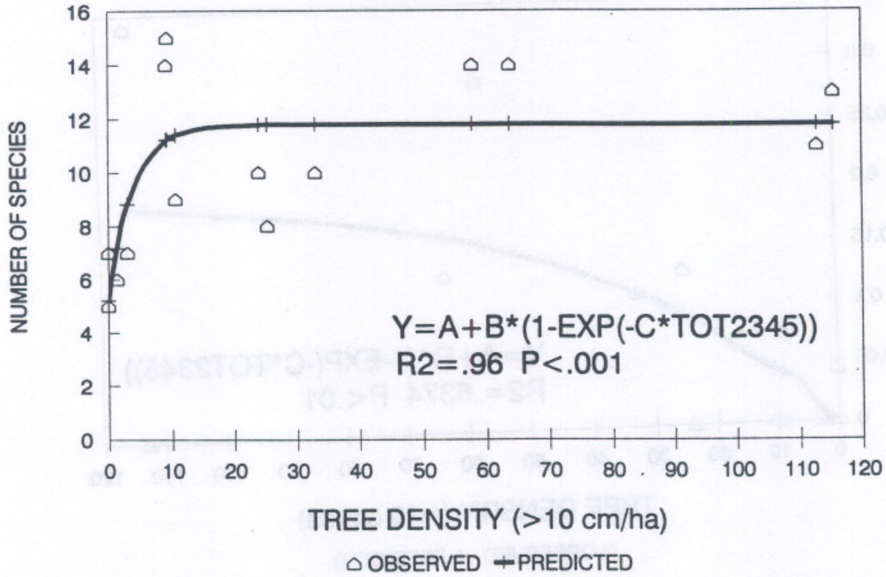

Figure 26.10. Data points and nonlinear regression line describing the relationship between canopy tree density and bird species richness.

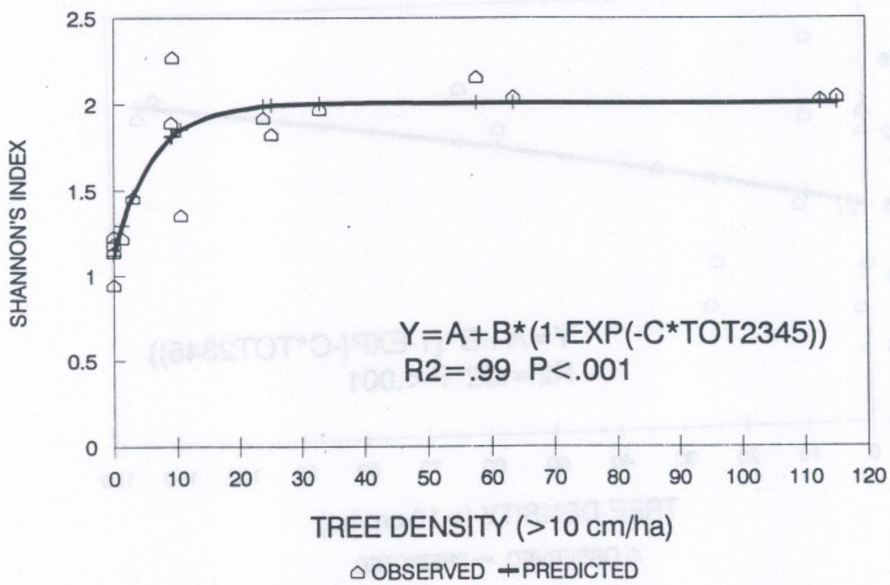

Figure 26.11. Data points and nonlinear regression line describing the relationship between canopy tree density and bird diversity (Shannon's index).

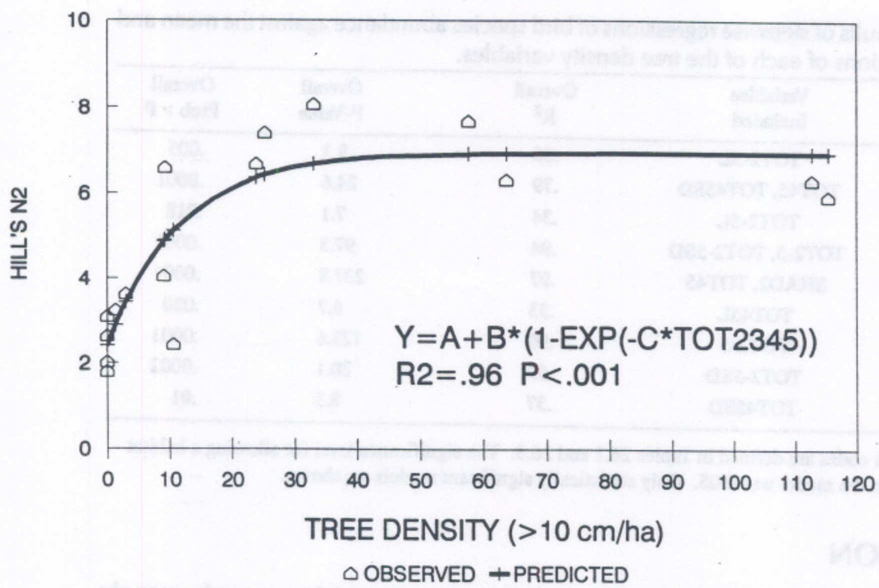

Figure 26.12. Data points and nonlinear regression line describing the relationship between canopy tree density and bird diversity (Hill's N2).

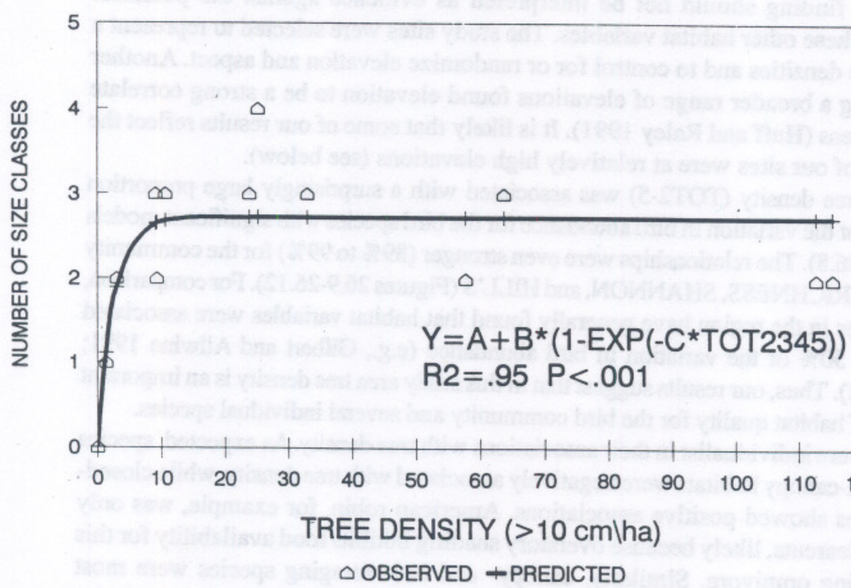

Figure 26.13. Data points and nonlinear regression line describing the relationship between canopy tree density and the number of canopy tree size classes present.

Table 26.6. Results of stepwise regressions of bird species abundance against the mean and standard deviations of each of the tree density variables.

Species[1] Code	Variables Included	Overall R^2	Overall F-Value	Overall Prob > F
AMRO	TOT2-5L	.56	8.3	.005
BRCR	TOT45, TOT45SD	.79	24.6	.0001
DEJU	TOT2-5L	.34	7.1	.018
GCKI	TOT2-5, TOT2-5SD	.94	97.3	.0001
HAFL	SHAD2, TOT45	.97	237.8	.0001
HAWO	TOT45L	.33	6.7	.020
HTWA	TOT2-5	.90	123.6	.0001
RBNU	TOT2-5SD	.59	20.1	.0002
STJA	TOT45SD	.37	8.3	.01

[1] Bird and habitat codes are defined in Tables 26.2 and 26.3. The significance level for allowing a habitat variable to stay in the model was 0.05. Only statistically significant models are shown.

DISCUSSION

The results suggest that the density of canopy trees in managed forest stands strongly influences breeding bird abundance and diversity. Significant relationships were found between tree density variables and 13 of the 18 bird species and community variables with sufficient sample sizes for analysis. Moreover, the density of trees greater than 10 cm dbh (TOT2-5) was associated with more of the variation in the bird variables than were the other major habitat variables (elevation, aspect, and understory cover).

The latter finding should not be interpreted as evidence against the potential importance of these other habitat variables. The study sites were selected to represent a gradient of tree densities and to control for or randomize elevation and aspect. Another study surveying a broader range of elevations found elevation to be a strong correlate with bird richness (Huff and Raley 1991). It is likely that some of our results reflect the fact that most of our sites were at relatively high elevations (see below).

Canopy tree density (TOT2-5) was associated with a surprisingly large proportion (48% to 97%) of the variation in bird abundance for the bird species with significant models (Figures 26.2-26.8). The relationships were even stronger (89% to 99%) for the community variables ALL, RICHNESS, SHANNON, and HILL'S (Figures 26.9-26.12). For comparison, previous studies in the region have generally found that habitat variables were associated with less than 50% of the variation in bird abundance (e.g., Gilbert and Allwine 1991; Manuwal 1991). Thus, our results suggest that in this study area tree density is an important determinant of habitat quality for the bird community and several individual species.

Species were individualist in their associations with tree density. As expected, species requiring open-canopy habitats were negatively associated with tree density, while closed-canopy species showed positive associations. American robin, for example, was only abundant in clearcuts, likely because overstory shading inhibits food availability for this ground-foraging omnivore. Similarly, canopy- and bole-foraging species were most abundant in dense stands probably because the high canopy volumes and dense boles conferred foraging and nesting opportunities.

All of these relationships between birds and tree density were best described by nonlinear models. These curves revealed interesting thresholds where small changes in tree density were associated with large differences in bird abundance. The abundances of golden-crowned kinglet and Hammond's flycatcher, for example, were positively associated with tree density only above a threshold of about 25 trees per ha. The relationship between bird abundance and tree density for brown creeper became positive at about 10 trees per ha and plateaued above about 30 trees per ha. It is difficult to speculate on the ecological factors that may explain these thresholds. For example, golden-crowned kinglet and hermit/Townsend's warbler have similar foraging habits, yet hermit/Townsend's warbler showed very different responses to stands with few canopy trees (cf. Figures 26.4 and 26.5).

The bird community variables were all positively associated with tree density. Total bird abundance varied at lower tree densities but was consistently high above about 30 trees per ha. The high abundance of hermit/Townsend's warbler, golden-crowned kinglet, and Hammond's flycatcher in the densest stands accounts for this trend. Bird richness and diversity increased with tree density up to a threshold and then leveled off. The low bird abundance and diversity values in stands with few trees were due to the relative paucity in the study area of species specializing in open-canopy habitats.

Bird species differed in their response to the size classes of the retained trees. The abundances of the open-canopy specialists American robin and dark-eyed junco were inversely related to tree density in general, regardless of size-class distribution. Similarly, canopy-gleaning species (golden-crowned kinglet and hermit/Townsend's warbler) probably benefit from increased canopy volume and thus were positively associated with canopy tree density regardless of the size-class distribution. On the other hand, birds that forage and nest in larger trees with furrowed bark (brown creeper, hairy woodpecker) were associated with the density of trees > 50 cm dbh. Interestingly, Hammond's flycatcher was associated both with shade-tolerant trees 10-30 cm dbh and with large trees, suggesting it requires habitats with complex, multi-layered canopy configurations. Knowledge of these habitat associations can allow managers to design stands to favor particular groups of species (see below).

Ecological Mechanisms

What ecological processes underlie these positive associations between tree density and bird diversity and abundance? The results provide partial support for the hypothesis that habitat niche diversity is a fundamental determinant of bird diversity (MacArthur and MacArthur 1961). An index of habitat diversity (tree size-class richness) increased logistically with tree density and was positively correlated with bird diversity (SHANNON). This correlation was not significant, however, when the four sites with no canopy trees were omitted from the analysis. Thus, the analysis simply revealed that stands with 1 or more of the tree size classes had higher bird diversity than stands with 0 tree size classes. A larger sample over a greater range of structural configurations is needed to better understand the relationships among canopy tree retention, habitat niche diversity, and bird diversity.

The data did not support the hypothesis (Hansen et al. in press) that bird diversity is highest in open-canopy stands because of increased available energy. In fact, understory vegetation and understory birds were poorly represented across all the study stands. These findings conflict with other studies from lower elevations, where Turner and Long (1975) found that productivity of conifer leaves and understory plants was higher in young open-canopy stands than in closed-canopy forests. Also, Hansen et al. (unpubl. data) found in the Oregon Coast Range that bird richness and abundance did not differ significantly between 5- to 10-year-old clearcuts and 90- to 130-year-old natural forest. The patterns of bird diversity and abundance reported here may be unique to the High Cascades Province. The high elevation, heavy snow packs, soils, or fire history appear to have suppressed the shrub communities and caused the understory bird community to be depauperate.

This conclusion suggests that vegetation and bird response to silvicultural treatments vary among topographic and geomorphic settings. The relative influences on bird communities of niche habitat diversity and stand energetics likely vary across the region. Studies across a range of environmental settings are needed to better understand these ecological relationships and to allow managers to tailor silvicultural strategies to local conditions.

Limitations of the Study

The study has various limitations that necessitate additional research on the topic. Our sample of stands was relatively small in number and included a very limited range of structural configurations within each tree-density class. For example, all units with light to moderate retention contained only trees >30 cm dbh, but those with the heaviest retention contained trees 10-50 cm dbh. The study involved only stands 2-11 years past harvest and it reveals little about older stands. Our study area was high in elevation and on soils that are somewhat unique in the region. Only birds were studied; they might or might not reflect biodiversity patterns for other taxonomic groups. Finally, birds were sampled for only one breeding season, and we do not know how much variability can be expected among years. We also do not know how birds may use these stands during other times of the year. Future studies should endeavor to sample a greater range of structural configurations, forest age classes, topographic and geomorphic settings, and taxonomic groups.

The study only hinted at the sorts of ecological processes linking forest structure and biodiversity. Studies are needed to test the habitat niche hypothesis, the stand energetics hypothesis, and other possible hypotheses relevant to the question.

A final limitation is that the study dealt only with the stand level. Landscape-scale factors such as stand diversity, grain size, juxtapositioning, and connectivity are known to influence vertebrate habitat quality and population viability. Difficult as these studies are to design and execute, landscape-scale research is needed to determine how canopy tree retention should be distributed across stands and landscapes to maintain viable populations of vertebrate species.

CONCLUSIONS

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CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT

This study is one of the first in the PNW to quantify the responses of birds to the increasingly common forestry practice of canopy tree retention. The study has several implications for management. Most importantly, the results provide evidence that canopy tree retention strongly influences bird species and community attributes. The statistical associations we found between the bird attributes and canopy tree density may be the strongest animal habitat relationships yet documented in the region. This suggests that canopy structure is a fundamental driver of various ecological properties, including species diversity. Clearly, canopy tree retention is an important silvicultural tool for achieving a more ecological forestry.

Furthermore, the study revealed specific canopy tree densities that appear to be thresholds for influencing bird populations and communities. Such data should enable managers to design stands for specific biodiversity goals. For example, bird diversity reached a plateau in stands with about 20-25 trees per ha (Figs. 11, 12). Retaining fewer trees than this would probably reduce bird diversity, but retaining more trees would not necessarily increase bird diversity. Similar data for wood production, harvest costs, sedimentation rates, and other responses could be used to select tree retention levels that best satisfy diverse management goals.

The individualistic responses of bird species to canopy retention levels emphasize the importance of setting specific management objectives. Managing for "biodiversity" is a hollow goal. Any management action will benefit some species and hinder others. Managers should carefully evaluate which species or community attributes they are most concerned with and design silvicultural strategies accordingly (Hansen et al. 1993).

Where the goal is to maintain habitats for all native bird species, our results indicate that a range of canopy tree densities and size-class distributions should be maintained across the landscape. This would accommodate open-canopy specialists as well as species requiring structurally-complex stands. However, determining the distribution of tree densities and size classes that best promote various biodiversity goals will require further work.

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