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Bird Assemblages Associated with Vine Maple Gaps in Coastal Western Hemlock Forests of British Columbia

Abstract

Vine maple gaps represent a source of distinct structural and functional heterogeneity within a conifer-dominated forest. We considered whether these gaps provide preferred habitat for some species of birds. We surveyed birds, and measured habitat characteristics, in vine maple gaps and closed canopy plots of two coastal western hemlock forests during two breeding seasons. For one forest, vine maple gaps had more total detections in both years, and more species in one year, than did closed canopy plots. Pacific-slope flycatchers, winter wrens, and American robins were detected significantly more often in vine maple plots for one or more forest-year combinations. Numbers of winter wrens were correlated with high foliage height diversity and cover close to the ground, characteristics common to vine maple gaps of both forests. Pacific-slope flycatchers were associated with abundance of deciduous vegetation and cover at intermediate heights, features that differentiated the plot types from each other at one forest. Our results suggest that vine maple gaps are used more by certain avian species, dependent on forest and year. We recommend studying bird use of vine maple *versus* other gap types, and differences in avian assemblages between forests with and without vine maple gaps, to elucidate the value of maintaining vine maple gaps for bird habitat in these forests.

Introduction

Environmental patchiness enhances opportunities for differential use of space and resources by birds (MacArthur and MacArthur 1961, MacArthur et al. 1962). At the local level, bird diversity has been associated with both complexity of the profile of vertical foliage (e.g., Willson 1974) and horizontal patchiness (e.g., Roth 1976, but see Rotenberry and Wiens 1980). Microhabitat selection by species and distribution of these microhabitats can explain both associations of species with specific sites and resultant bird communities at broader scales (Urban and Smith 1989).

Canopy gaps create vertical and horizontal patchiness within temperate (Runkle 1981) and tropical (Hubbell and Foster 1986, Denslow 1987) forests. These gaps are thought to structure avian communities and promote species diversity and abundance both through the creation of habitat diversity and the minimization of competitive exclusion [e.g., Blake and Hoppes (1986) in the eastern U.S.; Levey (1988) in Costa Rica]. Gap openings may play a significant role in local habitat choice and avian ecology as sites of relatively high insect (or fruit) abundance, greater prey activity, advantageous microclimate, and effective territorial boundaries in comparison to closed canopy areas. Higher light levels in gaps can increase primary productivity and density of insect populations (e.g., Blake and Hoppes 1986). Temperate (Willson et al. 1982, Martin and Karr 1996) and tropical (Levey 1988) avian frugivores also benefit from higher densities of fruit and longer fruiting periods in gaps. Increased foliage biomass and a compact, lower foliage profile may optimize energetics of birds foraging in the understory (Smith and Dallman 1996). The warmer microclimate within gaps may be energetically preferable to birds (for example, on cool but sunny mornings; Wachob 1996) and increase activity levels (and thus visibility) of invertebrate prey. Last, gap openings provide ideal positions for territorial boundaries defended through visible or acoustic display (Smith and Dallman 1996).

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We examined the role of gaps containing vine maple (*Acer circinatum*) as habitat patches used by birds in coastal western hemlock (*Tsuga heterophylla*) forests of southern British Columbia. This work was part of a broader study of vine maple gaps that emphasized their role in maintaining structural, compositional and abiotic patchiness throughout forest succession. Vine maple gaps—termed "priority gaps" because they originate prior to the dominant canopy (McGhee 1996)—are maintained by the presence of vine maple, which resists conifer invasion and inhibits growth of other competitors (del Moral and Cates 1971). These gaps differ in some characteristics (e.g., Schmidt et al. 1998) from developmental gaps, produced by mortality of dominant trees, or edaphic gaps, arising from soil-related or topographic features (Lertzman et al. 1996). Vine maple plots have higher concentrations of some soil nutrients (Ogden and Schmidt 1997, Tasche and Schmidt 2001), which promote adjacent seedling growth, relative to closed canopy plots (Wardman and Schmidt 1998). Foliage and seeds of vine maples provide forage for both birds and mammals (Jensen et al. 1995) and Gomez (1992) noted the role of vine maple as a component of small mammal habitat. In some stands, a significant portion of the herbivory by insects occurs on vine maple, indicating a role of this species in maintaining populations of insects and insectivores (Braun et al. 2002). Thus, these gaps could represent a source of distinct structural, compositional, and functional heterogeneity within a forest.

In this study we examined whether: 1) numbers and species of birds present in vine maple gaps differed from closed canopy plots; 2) specific habitat features (in addition to presence of vine maple) differed between gaps and closed canopy plots; and 3) differences in bird assemblages between the two types of plots were associated with any differences measured in habitat characteristics. We expected that vine maple gaps would provide a distinctive suite and spatial distribution of resources and, thus, would contain more or different species of birds and more individuals than closed canopy habitat. We anticipated more detections and species of foliage gleaners, such as golden-crowned kinglets (*Regulus satrapa*) or pacific-slope flycatchers (*Empidonax difficilus*), and of birds seeking cover close to the ground, such as winter wrens (*Troglodytes troglodytes*) or varied thrushes (*Ixoreus naevius*), within vine maple gaps relative to closed canopy plots.

Methods

Study Locations

Study plots were established in two forests, Haney and Seymour, in a submontane area of the Coastal Western Hemlock zone (CWH; Meidinger and Pojar 1991) of British Columbia (BC). The Malcolm Knapp Research Forest in Haney (hereafter Haney) is approximately 60 km east of Vancouver, BC (49°26' N, 122°58' W). Stands we used at Haney were established after wildfire in 1931. Dominant overstory species included western hemlock, western redcedar (*Thuja plicata*), and minor amounts of Douglas-fir (*Pseudotsuga menziezii*), with a deciduous component of red alder (*Alnus rubra*) and bitter cherry (*Prunus emarginata*). Slopes ranged from 2 - 22° and elevation ranged from 200 - 300 m in our plots, with west to southwest aspects. The Seymour Demonstration Forest (hereafter Seymour) is in the Seymour River Watershed of North Vancouver (49°37' N, 123°5' W). Stands at Seymour were logged about 90 years before we conducted this study. The stands were dominated by Douglas-fir, western hemlock and western redcedar. Red alder and bigleaf maple (*Acer macrophyllum*) were scattered throughout Seymour; however, the overstory had a smaller deciduous component than Haney (Table 1). Slopes at Seymour ranged from 2 - 32° and elevations ranged from 180 - 240 m, with east to southeast aspects.

We established eight pairs of plots at Haney and four pairs of plots at Seymour in 1992; three more pairs were added in Seymour in 1993. We expected the increased sample size in 1993 to improve: (1) our ability to detect differences in avian presence between gap and nongap plots overall; and (2) our ability to assess any differences in bird numbers, bird species assemblages, or habitat between plot types within a forest. First, we established the vine maple (VM) plot centers at the centers of gaps dominated by this species. We then paired each VM plot with a closed canopy (CC) plot, placing its center 100 m away from the center of the VM plot in a random compass direction. A CC plot center was adjusted, if necessary, to keep a 100 m minimum distance from other vine maple gaps or edges (e.g., roads, different management areas, or riparian zones), and to maintain a similar elevation to its VM counterpart.

TABLE 1. Mean (stdev) for habitat characteristics of vine maple (VM) and closed canopy (CC) plots in Haney (H) and Seymour (S) forests, and scores from principal component (PC) analysis of these features.

Habitat Variable	Forest-Plot Type							
	H-VM		H-CC		S-VM		S-CC	
Sample Size	8		8		7		7	
Veg Cover, 0 - 0.5 m (%)	46.2	(12.4)	21.1	(14.1)	68.8	(23.0)	41.1	(18.3)
Veg Cover, > 0.5 - 1.0 m (%)	17.9	(14.8)	7.1	(9.2)	28.7	(15.9)	14.4	(17.2)
Veg Cover, > 1.0 - 2.0 m (%)	7.9	(8.8)	3.1	(4.8)	18.9	(8.7)	6.3	(9.6)
Veg Cover, > 2.0 - 5.0 m (%)	21.1	(15.9)	0.8	(2.1)	20.7	(5.7)	7.1	(11.6)
Veg Cover, > 5.0 - 10.0 m (%)	33.8	(14.0)	12.5	(10.1)	22.7	(12.9)	11.7	(12.4)
Veg Cover, > 10.0 - 20.0 m (%)	69.8	(5.9)	80.5	(5.4)	54.6	(12.7)	48.3	(20.0)
Veg Cover, > 20.0 m (%)	61.8	(9.2)	79.8	(11.8)	70.6	(17.7)	83.3	(10.7)
Veg Species, 0 - 0.5 m (No.)	4.1	(1.0)	2.5	(1.5)	6.8	(1.3)	3.4	(1.7)
Veg Species, > 0.5 - 1.0 m (No.)	1.5	(0.9)	0.9	(1.0)	3.4	(1.5)	1.3	(1.1)
Veg Species, > 1.0 - 2.0 m (No.)	0.9	(1.0)	0.4	(0.5)	1.8	(0.7)	0.4	(0.8)
Veg Species, > 2.0 - 5.0 m (No.)	2.4	(0.9)	0.1	(0.4)	1.6	(0.8)	0.6	(0.8)
Veg Species, > 5.0 - 10.0 m (No.)	2.6	(0.7)	1.4	(0.9)	2.0	(0.8)	1.1	(0.7)
Veg Species, > 10.0 - 20.0 m (No.)	4.1	(1.2)	2.8	(1.2)	3.0	(0.8)	2.3	(1.0)
Veg Species, > 20.0 m (No.)	2.9	(0.6)	2.8	(0.7)	2.6	(0.8)	2.7	(1.0)
Vine Maple Stems (No.)[1]	69.4	(50.5)	2.1	(3.1)	33.1	(29.2)	1.4	(2.3)
Vine Maple Basal Area (m²)	0.22	(0.17)	0.01	(0.01)	0.10	(0.08)	0.01	(0.01)
Deciduous Stems (No.)[1]	6.6	(6.3)	2.0	(1.8)	0.4	(0.8)	0.3	(0.8)
Deciduous Basal Area (m²)	0.41	(0.25)	0.20	(0.22)	0.04	(0.08)	0.03	(0.07)
Conifer Stems (No.)[1]	37.2	(7.6)	55.4	(12.7)	31.3	(6.6)	43.1	(10.2)
Coniferous Basal Area (m2)	4.25	(1.05)	5.87	(1.44)	4.92	(1.20)	5.28	(0.61)
Average Open Sky (%)	14.8	(3.8)	11.6	(1.5)	12.1	(4.4)	13.1	(6.4)
Coarse Wood Debris (% Pts)	71.8	(8.1)	72.6	(11.0)	78.6	(8.7)	85.7	(8.6)
Foliage Height Diversity	0.73	(0.07)	0.53	(0.11)	0.76	(0.04)	0.60	(0.09)
Habitat PC1	1.85[a]	(2.21)	-2.61	(1.40)	2.41[a]	(1.59)	-1.54	(1.97)
Habitat PC2	1.99[a]	(1.19)	0.42	(0.66)	-1.58	(0.93)	-1.17	(1.77)
Bird PC1	1.32	(1.10)	1.02	(0.68)	-0.94	(0.85)	-1.73	(1.34)
Bird PC2	0.91[a]	(1.18)	-0.27	(1.14)	-0.21	(1.13)	-0.52	(1.70)

[1] variable not used in PCA of habitat; see Table 4

[a] significant difference for a trait between VM and CC plots in a forest, Wilcoxon signed rank

Bird Counts

We conducted bird surveys from May to July in 1992 and 1993 using 25 m (0.20 ha) fixed-radius point counts (Hutto et al. 1986). We expected the edges of the trees surrounding the gap (i.e., expanded gap portion) to represent one use of gap plots by birds (for perching and hawking into the gap area). We also, however, wanted to ensure detection of all individuals using the census plots, both vine maple gap and closed canopy, with high, and similar, probabilities (e.g., see detection distances reported across habitat types by Schieck 1997, Chambers et al. 1999). Plots size was thus chosen to: (1) incorporate expanded gap area (as per Lertzman and Krebs 1991) and forest area influenced by gap environment; but (2) minimize the effects of varying detectability of species on counts. Plot size also represented a compromise between expanded gap size in Seymour (mean = 215.3 m², stdev = 128.6 m², N = 24) and in Haney, where gaps were two to three times larger (personal observation).

We recorded all birds seen or heard during a 10 min count, after waiting 2 min before starting each count. We visited plots once per week between dawn and 10 00 hrs, reversing the order of counts each week. During 1992, we surveyed Haney plots five times and Seymour plots six

times. During 1993, birds were surveyed eight times in all plots excepting one pair at Seymour (seven counts).

Habitat Measurements

We divided each of the circular, bird survey plots into eight "pie" wedges and sampled overstory vegetation in four of these (i.e., a total of 0.10 ha): N - NW, W - SW, S - SE, and E - NE. We identified species and measured dbh of all trees ≥ 16 cm dbh. Because vine maple shrubs often have prostrate stems, we measured all vine maple stems ≥ 1 cm diameter at 1.2 m from the base.

To determine foliage height diversity, we sampled understory vegetation and structure within seven different height categories: 0 - 0.5 m, > 0.5 - 1.0 m, > 1.0 - 2.0 m, > 2.0 - 5.0 m, > 5.0 m - 10.0 m, > 10.0 m - 20.0 m, and > 20 m. We recorded presence or absence and species of vegetation for each height at points 6, 16, 20, and 24 m from the center of the plots, on bearings of north, south, east, and west. We also noted presence or absence of and measured any coarse woody debris (cwd) ≥ 10 cm diameter at each point. All sampling of understory vegetation was conducted in 1993.

To determine light environment and canopy cover, we took one black and white, hemispherical photo at 12 m from plot center in each quadrant of a plot (four photos total), using a Nikkor 8 mm fish-eye lens at 1.5 m height. We scanned the photographs, edited them for cloud cover, and analyzed the images for percent open sky using Solarcalc v. 5.12 (Chazdon and Field 1987). The four values from a plot were averaged.

Statistical Analysis

Bird Use of Vine Maple versus Closed Canopy Plots

We calculated mean number of avian species, mean number of individuals of all species combined, and mean number of individuals in a species, for each plot in each year. We tested for influence of plot type (vine maple *versus* closed canopy), forest (Haney *versus* Seymour) and year (1992 *versus* 1993) on these summary bird statistics using non-parametric, repeated measures ANOVAs (Cody and Smith 1991; e.g., see Leupin et al. 2004). Differences between plot types by forest-year combination were examined using Wilcoxon Rank Sum two-tailed tests. For individual species, we tested for differences in mean numbers of birds between plot types for a forest-year combination when $N \geq 10$.

We examined the variation in bird assemblages between plot types and forests using principal component analysis (PCA; Jongman et al. 1995). The mean numbers of individuals for each species in each plot were used in the analysis. Only bird species whose cumulative number of detections were ≥ 10 over the study were included ($N = 12$ species).

Habitat Characteristics of Plots

For each plot, we determined total number of plant species at each height, number and percentage of coniferous, deciduous (excluding vine maple), and vine maple stems, total number of stems, basal area of coniferous, deciduous (excluding vine maple), and vine maple stems, and percentage of sample points with coarse woody debris (cwd) present. We calculated foliage height diversity based on the proportion of total points within a plot for which vegetation was present at each height (Anderson and Ohmart 1986). We examined the variation between plot types and forests in habitat characteristics (i.e., vegetation, cwd, and light) using PCA. Variables with relatively high Pearson correlation coefficients ($R \geq 0.50$) were removed to avoid redundancy, retaining those that were more easily remeasured or more ecologically intuitive. Twenty variables were used in the final PCA of the 30 plots [all univariate variables listed in Table 1, excepting number of stems of vine maple, conifers, and (non vine maple) deciduous trees]. All percentages were arcsine transformed. We used t-tests to examine the differences in habitat Principal Component (PC) scores between vine maple and closed canopy plots for both forests pooled and separately.

Associations between Bird Use and Habitat Features of Plots

To examine whether differences in presence of birds corresponded with habitat differences between plot types, we regressed: (1) bird PC scores; (2) mean number of individuals of all species combined; and (3) mean number of individuals of species that differed between plot types against habitat PC scores that differed between plot types. These bird-habitat associations were

examined using bird data from 1993, the year in which understory vegetation was sampled. The level of significance for all statistical tests in our study was set at $P = 0.05$.

Results

Bird Use of Vine Maple versus Closed Canopy Plots

Mean number of avian species in a plot was significantly influenced by plot type ($F = 12.11$, $P < 0.002$), forest ($F = 20.62$, $P < 0.001$), and year ($F = 15.14$, $P < 0.001$). Mean number of individuals of all avian species combined in a plot was also affected by plot type ($F = 16.33$, $P < 0.001$), forest ($F = 16.33$, $P < 0.001$), and year ($F = 33.14$, $P < 0.001$). There were no significant interactions among these factors. Mean number of individuals and species in a plot were both significantly higher in vine maple than closed canopy plots at Haney in 1992 (Figures 1A and 1B respectively). In 1993, only the mean number of avian species differed between the two plot types at Haney, again higher in the vine maple plots (Figure 1B). Bird abundance measures did not differ between plot types in Seymour (Figure 1).

Of 12 species with ≥10 detections for a forest-year combination, three were detected significantly more often in vine maple plots for at least one forest-year combination and showed a consistent trend in the other forest or year: pacific-slope flycatcher, winter wren, and American robin (*Turdus migratorius*) (Table 2). Relative use of vine maple *versus* closed canopy plots varied with year or forest for golden-crowned kinglets, chestnut-backed chickadees (*Parus rufescens*) and Townsend's warblers (*Dendroica townsendi*). Numbers of flycatchers, wrens, and kinglets in plots were significantly influenced by year. Flycatchers and wrens also had significant forest and plot effects (Table 2).

Two principal components gave insight into the variation in bird assemblages between plot types and forests. Bird PC1 explained 21.9% of the variation in bird associations. High values indicated relatively large numbers of pacific-slope flycatchers, Townsend's warblers, and Swainson's thrushes (*Catharus ustulatus*), whereas low values indicated many brown creepers (*Certhia Americana*; Table 3). This axis separated both closed canopy and vine maple plots in Haney
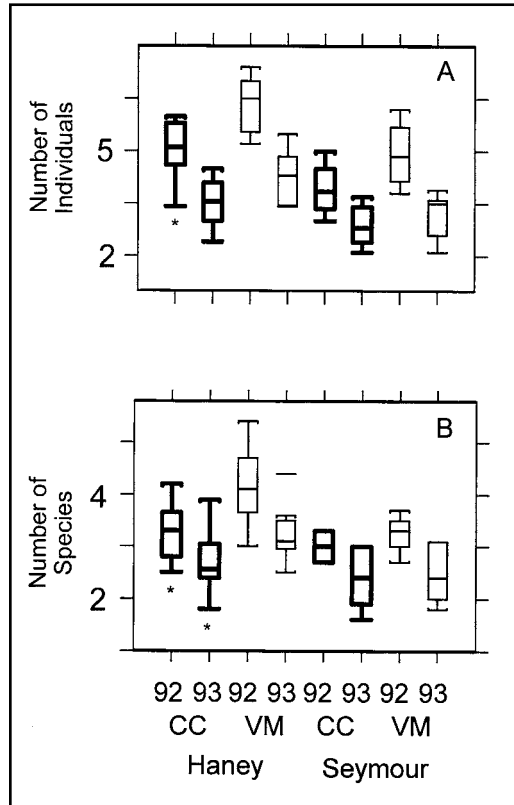

Figure 1. Boxplots for A) numbers of individuals; and, B) numbers of avian species in point counts within vine maple (VM) and closed canopy (CC; thicker lines) plots. Summaries are for two forests, Haney (H) and Seymour (S), and two years, 1992 (92) and 1993 (93). Boxes indicate the median (solid line inside box) and the distance between the upper and lower quartiles (IQD, upper and lower ends of the box). Whiskers indicate a distance of 1.5·IQD and outliers are shown by horizontal lines. * indicates a (mean) summary statistic that differs significantly between closed canopy and vine maple plots for that forest-year combination.

from their counterparts in Seymour, implicating an effect of forest rather than plot type on bird assemblages ($P < 0.001$; Figure 2A; Table 2). Bird PC2, explaining 15.3% of the variation in bird associations, indicated plots with many winter wrens and golden-crowned kinglets *versus* those with many Steller's jays (*Cyanocitta stelleri*; Table 3). Scores along bird PC2 significantly distinguished closed canopy from vine maple plots in Haney (Figure 2A).

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TABLE 2. Mean (±1 SE) number of detections of species in vine maple (VM) and closed canopy (CC) survey plots at Haney and Seymour forests in 1992 and 1993. Data are given for forest-year combinations where $N \geq 10$ detections for a species.

| | | 1992 | | | | 1993 | | | |
| | | Haney | | Seymour | | Haney | | Seymour | |
Species	Scientific Name	VM (8)[1]	CC (8)	VM (4)	CC (4)	VM (8)	CC (8)	VM (7)	CC (7)
Pacific-slope flycatcher[2]	Empidonax difficilis	1.94[a] (0.15)	1.41 (0.18)	1.17 (0.29)	0.88 (0.18)	1.41 (0.11)	1.19 (0.11)	0.61 (0.08)	0.39 (0.08)
Steller's jay	Cyanocitta stelleri							0.09 (0.07)	0.11 (0.07)
Chestnut-backed chickadee	Parus rufescens	0.78 (0.18)	0.86 (0.19)	0.71 (0.17)	0.46 (0.20)	0.77 (0.10)	0.88 (0.10)	0.90 (0.17)	0.98 (0.06)
Brown creeper	Certhia americana							0.13 (0.05)	0.22 (0.14)
Winter wren[3]	Troglodytes troglodytes	0.76[a] (0.14)	0.38 (0.09)	1.62 (0.12)	1.33 (0.12)	0.62[a] (0.08)	0.36 (0.07)	0.53 (0.05)	0.50 (0.16)
Golden-crowned kinglet[4]	Regulus satrapa	1.06 (0.16)	1.09 (0.11)	0.75 (0.05)	0.67 (0.10)	0.48 (0.15)	0.33 (0.07)	0.52 (0.16)	0.48 (0.12)
Swainson's thrush	Catharus ustulatus					0.11 (0.04)	0.06 (0.03)		
American robin	Turdus migratorius					0.20[a] (0.06)	0.02 (0.02)	0.16[a] (0.08)	0.02 (0.02)
Varied thrush	Ixoreus naevius							0.05 (0.04)	0.13 (0.05)
Black-throated gray warbler	Denroica nigrescens	0.38 (0.10)	0.22 (0.12)						
Townsend's warbler	Dendroica townsendi	0.33 (0.11)	0.41 (0.08)			0.47 (0.08)	0.45 (0.10)		
Pine siskin	Carduelis pinus	0.57 (0.09)	0.41 (0.17)						

[a] significant effect of plot type for a forest-year combination, Wilcoxon rank-sum
[1] number of plots
[2] significant year, forest, and plot effects, nonparametric repeated measures ANOVA
[3] significant year, forest, plot, and year*forest effects, nonparametric repeated measures ANOVA
[4] significant year effect, repeated measures ANOVA

TABLE 3. Component loadings from principal component (PC) analysis of bird assemblages in vine maple and closed canopy plots at Seymour and Haney forests. See Table 2 for scientific names and mean numbers of detections of each species by plot type and forest.

Bird Species	Bird PC1	Bird PC2
American robin	0.16	0.23
Brown creeper	-0.41	0.23
Black-throated gray warbler	0.04	0.30
Chestnut-backed chickadee	-0.16	0.20
Golden-crowned kinglet	-0.35	0.39
Pine siskin	0.12	-0.23
Pacific-slope flycatcher	0.48	0.27
Steller's jay	0.01	-0.42
Swainson's thrush	0.30	0.24
Townsend's warbler	0.49	0.14
Varied thrush	-0.23	-0.14
Winter wren	-0.10	0.45
Percent Variance Explained	21.9	15.3

TABLE 4. Component loadings from principal component (PC) analysis of habitat features measured in vine maple and closed canopy plots at the Seymour and Haney forests. Sample sizes as in Table 1.

| Habitat Variable	Habitat PC1	Habitat PC2
Vegetation Cover, 0 - 0.5 m (%)	0.27	-0.21
Vegetation Cover, > 0.5 -1.0 m (%)	0.28	-0.22
Vegetation Cover, > 1.0 - 2.0 m (%)	0.28	-0.22
Vegetation Cover, > 2.0 - 5.0 m (%)	0.30	0.06
Vegetation Cover, > 5.0 - 10.0 m (%)	0.23	0.26
Vegetation Cover, > 10.0 - 20.0 m (%)	-0.06	0.36
Vegetation Cover, > 20.0 m (%)	-0.20	-0.25
Vegetation Species, 0 - 0.5 m (No.)	0.24	-0.16
Vegetation Species, > 0.5 - 1.0 m (No.)	0.27	-0.27
Vegetation Species, > 1.0 - 2.0 m (No.)	0.28	-0.20
Vegetation of Species, > 2.0 - 5.0 m (No.)	0.30	0.09
Vegetation Species, > 5.0 - 10.0 m (No.)	0.21	0.27
Vegetation Species, > 10.0 - 20.0 m (No.)	0.12	0.34
Vegetation Species, > 20.0 m (No.)	-0.04	0.12
Vine Maple Basal Area (m²)	0.25	0.28
Deciduous Basal Area (m²)	0.11	0.33
Coniferous Basal Area (m²)	-0.16	-0.10
Average Open Sky (%)	0.09	0.05
Coarse Wood Debris (% Pts)	0.00	-0.23
Foliage Height Diversity	0.34	-0.04
Percent Variance Explained	38.9	17.4
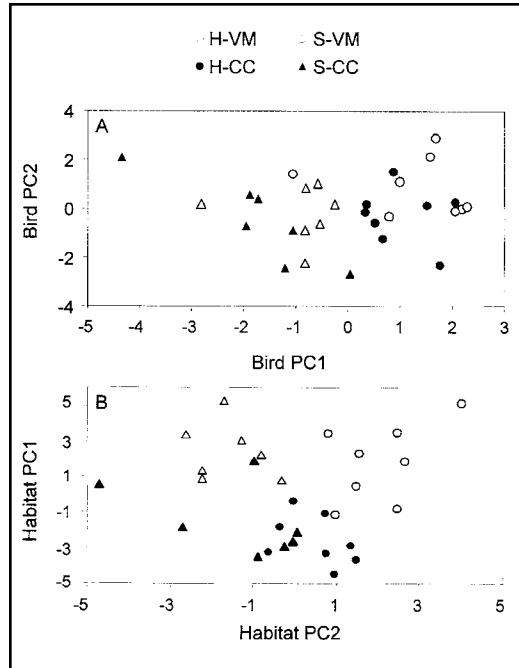
Figure 2. Scores on Principal component (PC) 1 *versus* Principal Component 2 from analysis of variation in: A) bird assemblages; and, B) habitat characteristics within vine maple (VM) and closed canopy (CC) plots at Seymour (S) and Haney (H) forests. For birds, only those species ($N = 12$) for which cumulative detections were ≥ 10 individuals over the course of the study were included in the analysis.

Habitat Characteristics of Vine Maple versus Closed Canopy Plots

The first two principal components explained 38.9% and 17.4% respectively of the variance in vegetation characteristics of the plots. Habitat PC 1 represented a gradient from plots with high foliage height diversity and relatively more species and coverage between 0.5 and 5.0 m height *versus* plots with more canopy coverage (>20.0 m) and more coniferous basal area (Table 4). Scores differed significantly between vine maple and closed canopy plots along Habitat PC 1 for Haney ($P = 0.001$) and Seymour ($P = 0.01$; Figure 2B; Table 1); differences were greater at Haney (Table 1). Habitat PC 2 arranged plots with relatively more species and coverage at intermediate heights (>5 - 20 m) and higher amounts of vine maple and other deciduous basal area *versus* plots with cover at lower (0.0 - 2.0 m) and greater heights (>20 m). Scores along Habitat PC 2 also differed between plot types in Haney ($P = 0.008$) but not Seymour

(Figure 2B). Thus, the Haney plot types separated along two multivariate habitat axes; Seymour plots differed along one multivariate habitat axis. Further, vine maple plots in Haney had more cover and species at intermediate heights, more vine maple, and more deciduous trees relative to VM plots at Seymour (differences along Habitat PC 2, $P < 0.001$; Figure 2B; also Table 1).

Associations between Bird Presence and Habitat Features of Plots

No summary bird variables separating vine maple from closed canopy plots (multivariate measures, mean or maximum number of individuals or species) were associated with multivariate habitat characteristics ($R^2 < 0.10$ in all cases). Rather, relationships with habitat features were primarily specific to avian species. For example, the number of winter wrens was predicted by habitat PC1 ($R^2 = 0.34$, $F = 16.02$, $P < 0.001$, Figure 3A), suggesting high foliage height diversity and cover close to the ground were important to this species. In general, those plots with higher foliage height diversity (and numbers of winter wrens) were vine
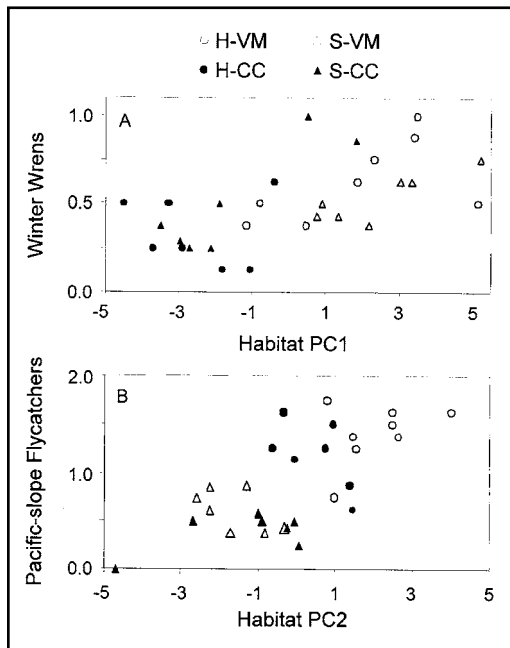

Figure 3. Associations of (A) winter wrens with habitat principal component (PC) 1 and (B) pacific-slope flycatchers with habitat PC 2 for vine maple (VM) and closed canopy (CC) plots at Haney (H) and Seymour (S) forests.

maple plots, regardless of the forest (Figures 2B and 3A). Numbers of pacific-slope flycatchers were predicted by habitat PC2 ($R^2 = 0.44$, $F = 23.81$, $P < 0.001$; Figure 3B), suggesting the flycatchers used plots with a relatively high deciduous component and cover at intermediate heights. This relationship was driven more by the difference in habitat between Haney and Seymour than by the difference in closed canopy *versus* vine maple plots (Figure 2B). We found weak associations between numbers of American robins and habitat PC1 ($R^2 = 0.14$, $F = 5.84$, $P = 0.02$) and between golden-crowned kinglet detections and habitat PC2 ($R^2 = 0.12$, $F = 5.16$, $P = 0.03$).

Discussion

Variability in Bird-Habitat Associations with Forest and Year

Vine maple gaps appeared to provide either more or different resources than closed canopy plots, for specific forest-year combinations. Small sample sizes limited our ability to examine consistency of use of vine maple gaps *versus* closed canopy across forests and years. However, we were able to demonstrate greater presence in the gaps of some species for specific forest-year combinations, and to associate those preferences with differences in habitat between the plot types. For example, American robins, showed an affinity for vine maple gaps in both forests (in 1993) and their numbers were associated with habitat features, such as high foliage height diversity and cover close to the ground, that differentiated vine maple plots from closed canopy plots in both forests. Winter wrens were relatively strongly and positively associated with this same suite of habitat features and were seen more often in vine maple plots at both forests in both years. However, vine maple plots appear to be preferred for different habitat characteristics by other species. Pacific-slope flycatchers were also more common at vine maple plots, but detections correlated with habitat features that differentiated plot types only in Haney, and which differed from habitat features associated with winter wrens. Though one multivariate measure of bird assemblages differed between plot types at Haney, indicating relatively more winter wrens and golden-crowned kinglets in vine maple plots, the measure did not correlate with habitat features that differentiated the plot types in that forest. Instead, the numbers of wrens and kinglets separately related

to different suites of habitat features, both of which distinguished vine maple from closed canopy plots in Haney. Thus, our ability to relate differences in bird detections to differences in habitat was forest- and species-dependent.

Levey (1988) suggested that stronger contrast between gap and understory sites in a forest should increase the number of species preferring one microhabitat to another (contrasting results with Schemske and Brokaw 1981). If contrast among habitats influences resource partitioning in temperate forests, our results indicate that the perceived degree of contrast between plot types is not determined by uniform variables across all bird species or forests. Alternatively, birds may be responding to features that we did not measure as differentiating forests or gaps from closed canopy plots. For example, winter wrens tend to prefer smaller gaps (Fuller 2000), a factor we did not include in habitat analysis.

We observed annual variation in numbers of birds in plots, and in the level of preferential use of vine maple gaps. This may be due to annual shifts in habitat or in prey differences between plot types within and between forests (but see Martin and Karr 1986). Springs with relatively poor growth of shrubs and herbs should emphasize differences between closed canopy and vine maple plots, and strengthen preferences for vine maple plots at these times. At both Haney and Seymour, the spring and summer of 1993 were wetter and cooler than those in 1992 (Environment Canada 2004); we would expect greater contrast between plot types and greater preference for vine maple gaps in 1993. However, both winter wrens and pacific-slope flycatchers were relatively more common in gaps in 1992, and detected more times in total during 1993, contrary to these expectations. For other species, such as Townsend's warbler and chestnut-backed chickadee, the preferred plot type tended to differ between years. Again, these gaps may provide different resources for different species, and these resources may vary differently between forests across years (e.g., with yearly climate differences). Significant, interactive effects of year, location, and vegetation type (coniferous versus deciduous) have been shown to influence the density and abundance of invertebrates at the stand level (Willson and Comet 1996). Thus, at least for insectivores, these effects could obscure differences in use between plot types measured over only two seasons.

Species-specific Differences in Avian Use of Plot Types

The most consistent differences in birds between gaps and closed canopy sites were differences in numbers of detections of certain species. Hansen et al. (1994) also found that neither bird abundance nor overall richness was associated with habitat complexity, but that individual species responded to habitat features. These results are similar to those for treefall gaps *versus* closed canopy plots in tropical forests (Wunderle 1987, Levey 1988) but contrast with results from a temperate, old-growth, European forest, where numbers of individuals and species were greater in gap plots, and overall bird assemblages differed, but few individual species differed in their use of plot types (Fuller 2000). In our study, pacific-slope flycatchers and winter wrens were most consistently more abundant in vine maple gaps. The pacific-slope flycatcher primarily forages by hovering and gleaning insects from foliage (Ehrlich et al. 1988). Other species that hawk and glean, such as the black-throated green warbler (*Dendroica virens*), prefer gap habitat *versus* contiguous forest sites (Smith and Dallman 1996), perhaps due to increased activity (visibility) of insects, an advantageous thermo-regulatory environment for the birds, or the use of gaps as edges of territories for good visibility and song projection. Flycatchers were generally detected above the majority of the vine maple canopy, lending support to the hypothesis of a preference for increased light. Flycatchers (and total richness and individuals) are strongly correlated with greater insect abundance in treefall gaps of eastern deciduous forests (Blake and Hoppes 1986). Vine maples support a generalist insect community and have a high rate of folivory relative to associated, overstory conifer species (Braun et al. 2002) or other understory species. This supports a hypothesis of higher use of gaps over closed canopy plots by flycatchers due to greater insect availability, and would be consistent with our finding of an increase in numbers of insectivores (i.e., the flycatchers, kinglets, and wrens) at these plots, rather than a noticeable shift in the suite of bird species between plot types.

Winter wrens, in contrast to the pacific-slope flycatchers, were likely more prevalent due to the nesting and foraging safety provided by the abundance of cover at lower levels in the gaps. This species prefers to nest in dense cover close to the ground in British Columbia (0.8 - 1.8 m in

height; Campbell et al. 1997). The wrens may also respond to the greater abundance of insect species associated with increased deciduous foliage in the gaps (Martin and Karr 1986). In western temperate ecosystems, deciduous forests with dense vegetation within 3 m above ground (similar to our gap plots) have higher abundances of both litter and foliage invertebrates than do understories of conifer forests (Willson and Comet 1996). Willson (1974) also determined that a high percentage of groundcover increased the number of species and individuals of insectivorous-low foliage gleaners, e.g., winter wrens.

Stand- and Forest-level Role of Vine Maple Gaps

Vine maple gaps may structure the avian community at a stand (complex of gap and non gap sites) or forest (complex of multiple stands) rather than plot level. Stand-level differences in available energy and habitat complexity influence the abundances of individual species (Hansen et al. 1994) and proximate habitat selection (e.g., plot type; Freemark and Merriam 1986, Lehmkuhl et al. 1991, Hansen et al. 1994). Observations of Fuller (2000) and Smith and Dallman (1996) also implicate the importance, at a stand level, of treefall gaps. Numbers of Pacific-slope flycatchers were associated with habitat PC 2, indicating the flycatchers used plots with a relatively high deciduous component and cover at intermediate heights. This factor distinguished Haney from Seymour, suggesting the use of vine maple gaps may also be dependent on their context at the stand or forest level. Future studies could profitably compare stands with varying abundances and spatial arrangements of gap and non gap habitats.

Vine Maple Gaps as Distinct Habitats

Vine maple gaps appeared to provide a preferred microhabitat for some avian species within the forests we studied. We found differences in numbers of total individuals, species, and individuals within certain species between vine maple gaps and closed canopy plots, even though sample sizes were small. We are confident differences in detection rates did not overly influence our results; studies examining differences in detection rates for forest species indicate high levels of detection even at 50 m (compared to our 25 m; e.g., Schieck 1997). We expect the increased presence of pacific-slope flycatchers and winter wrens we detected in vine maple gaps relative to closed canopy plots would be emphasized with leveling of any bias in detection probabilities (based on Schieck 1997).

Influences of forest and year on differences in species presence in vine maple gaps and on bird-habitat relationships emphasized the importance of examining the function of vine maple gaps across broader time scales and in the context of forest attributes at both the plot and stand levels. We did not examine other gap types in our study, and thus can not address differences in bird assemblages or habitat associations among gap types. However, vine maple gaps provide, by definition, a different composition of tree species, a factor shown to account for variation in bird species composition, beyond that explained by choice of (non vine maple) gap over non gap plots, in European temperate forests (Fuller 2000). Vine maple gaps are distinct habitats within the conifer matrix of these coastal western hemlock forests in terms of site productivity, soil characteristics, and microclimate; additionally, vine maple is a preferred forage species for insects. Our results provide preliminary evidence that vine maple gaps also provide a distinctive set of resources, relative to developmental or edaphic gaps, for forest birds.

Literature Cited

Anderson, B. W., and R. D Ohmart. 1986. Vegetation. Pages 639-660 *In* A. Y. Cooperrider, R. J. Boyd, and H. R. Stuart (editors), Inventory and Monitoring of Wildlife Habitat. USDI. Bureau of Land Management, Denver, Colorado.

Blake, J. G., and W. G. Hoppes. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. Auk 103:328-340.

Braun, D. M., B. Runcheng, D. C. Shaw, and M. VanScoy. 2002. Folivory of vine maple in an old-growth Douglas-fir-western hemlock forest. Northwest Science 96:315-321.

Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, M. C. E. McNall, and G. E. J. Smith. 1997. The Birds of British Columbia, vol. 3. University of British Columbia Press, Vancouver, British Columbia.

Chambers, C. L., W. C. McComb, and J. C. Tappeiner II. 1999. Breeding bird responses to three silvicultural treatments in the Oregon Coast Range. Ecological Applications 9:171-185.

Chazdon, R. L., and C. B. Field. 1987. Photographic estimation of photosynthetically active radiation: evaluation of a computerized technique. Oecologia 73:525-532.

Cody, R. P., and J. K. Smith. 1991. Applied Statistics and the SAS Programming Language. Prentice Hall, New Jersey.

Del Moral, R., and R. G. Cates. 1971. Allelopathic potential of the dominant vegetation of western Washington. Ecology 52:1030-1037.

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. Annual Review of Ecology and Systematics 18:431-451.

Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The Birder's Handbook. Simon and Schuster, New York.

Environment Canada. 2004. Monthly data report for 1992 and 1993 for N Van Seymour Hatchery, B.C. and Haney (University of British Columbia Research Forest Administration). Available online at http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html.

Freemark, K. E., and H. G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biological Conservation 36:115-141.

Fuller, R. J. 2000. Influence of treefall gaps on distributions of breeding birds within interior old-growth stands in Białowie a Forest, Poland. Condor 102:267-274.

Gomez, D. M. 1992. Small mammal and herpetofauna abundance in riparian and upslope areas of five forest conditions. M.S. Thesis, Oregon State University, Corvallis, Oregon.

Hansen, A. J., R. M. Vega, A. W. McKee, and A. Moldenke. 1994. Ecological processes linking forest structure and avian diversity in Western Oregon. Pages 217-245 *In* T. J. B. Boyle and C. E. B. Boyle (editors), Biodiversity, Temperate Ecosystems, and Global Change. Springer-Verlag, Berlin.

Hubbell, S. P., and R. B. Foster. 1986. Canopy gaps and the dynamics of a neotropical forest. Pages 77-96 *In* M. J. Crawley (editor), Plant Ecology. Blackwell Scientific Publications, Oxford.

Hutto, R. L., S. M. Pletschet, and P. Hendricks. 1986. A fixed-radius point count method for nonbreeding and breeding season use. Auk 103:593-602.

Jensen, E. C., D. J. Anderson, J. C. Tappeiner II, and J. C. Zasada. 1995. The reproductive ecology of broadleaved trees and shrubs: vine maple, *Acer circinatum* Pursh. Research Contribution 9b. Forest Research Laboratory, Oregon State University, Corvallis, Oregon.

Jongman, R. H. G., C. J. F. Ter Braak, and O. F. R. van Tongeren (editors). 1995. Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge.

Lehmkuhl, J. F., L. F. Ruggeiro, and P. A. Hall. 1991. Landscape-scale patterns of forest fragmentation and wildlife richness and abundance in the southern Washington Cascade Range. Pages 425-442 *In* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff (editors), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USDA Forest Service General Technical Report PNW-GTR-285. Pacific Northwest Research Station, Portland, Oregon.

Lertzman, K. P, and C. J. Krebs. 1991. Gap-phase structure of a subalpine old-growth forest. Canadian Journal of Forest Research 21:1730-1741.

Lertzman, K. P., G. D. Sutherland, A. Inselberg, and S. C. Saunders. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. Ecology 77:1254-1270.

Leupin, E. E., T. E. Dickinson, and K. Martin. 2004. Resistance of forest songbirds to habitat perforation in a high-elevation conifer forest. Canadian Journal of Forest Research 34:1919-1928.

Levey, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. Ecology 69:1076-1089.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

MacArthur, R. H., J. W. MacArthur, and J. Preer. 1962. On bird species diversity-prediction of bird censuses from habitat measurements. American Naturalist 96:167-174.

Martin, T. E., and J. R. Karr. 1996. Patch utilization by migrating birds: resource oriented? Ornis Scandinavica 17:165-174.

McGhee, R. A. 1996. Ecology and management of hardwoods in coniferous forests: a case study of vine maple persistence. M.R.M. Research Project, Simon Fraser University, Burnaby, British Columbia.

Meidinger, D., and J. Pojar.1991. Ecosystems of British Columbia. British Columbia Ministry of Forests, Victoria, British Columbia.

Ogden, A., and M. G Schmidt. 1997. Litterfall and soil characteristics in canopy gaps occupied by vine maple in a coastal western hemlock forest. Canadian Journal of Soil Science 77:703-711.

Rotenberry, J. T., and J. A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61:1228-1250.

Roth, R. R. 1976. Spatial heterogeneity and bird species diversity. Ecology 57:773-782.

Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology 62:1041-1051.

Schemske, D. W., and N. V. L. Brokaw. 1981. Treefalls and the distribution of understory birds in a tropical forest. Ecology 62:938-945.

Schieck, J. 1997. Biased detection of bird vocalizations affects comparisons of bird abundance among forested habitats. Condor 99: 179-190.

Schmidt, M. G., A. E. Ogden, and K. P. Lertzman. 1998. Seasonal comparison of soil temperature and moisture in pits and mounds under vine maple gaps and conifer canopy in a coastal western hemlock forest. Canadian Journal of Soil Science 78:291-300.

Smith, R., and M. Dallman. 1996. Forest gap use by Black-throated Green Warblers. Wilson Bulletin 108:588-591.

Tasche, N. C., and M. G. Schmidt. 2001. The impact of vine maple on site fertility of coastal temperate forests. Forest Ecology and Management 147:263-279.

Urban, D. L., and T. M. Smith. 1989. Microhabitat pattern and the structure of forest bird communities. American Naturalist 133:811-829.

Wachob, D. G. 1996. The effect of thermal microclimate on foraging site selection by wintering mountain chickadees. Condor 98:114-122.

Wardman, C. W., and M. G. Schmidt. 1998. Growth and form of Douglas-fir adjacent to persistent vine maple gaps in southwestern British Columbia. Forest Ecology and Management 106:223-233.

Willson, M.F. 1974. Avian community organization and habitat structure. Ecology 55:1017-1029.

Willson, M. F., and T. A. Comet. 1996. Bird communities of northern forests: ecological correlates of diversity and abundance in the understory. Condor 98:350-362.

Willson, M. F. and D. J. Moriarty. 1976. Bird species diversity in forest understory. Oecolgia 25:373-379.

Willson, M. F., E. A. Porter, and R. S. Condit. 1982. Avian frugivore activity in relation to forest light gaps. Caribbean Journal of Science 18:1-4.

Wunderle, J. M. Jr., Diaz, A. Velazquez, I., and Scharrón, R. 1987. Forest openings and the distribution of understory birds in a Puerto Rican rainforest. Wilson Bulletin 99:22-37.