Management and Conservation Article

Forested Buffer Strips and Breeding Bird Communities in Southeast Alaska

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ABSTRACT Forested buffer strips are used to mitigate fragmentation and habitat loss and are a common feature in management of riparian landscapes. Low-elevation, old-growth coastal forests are a rare riparian habitat that can benefit from similar conservation measures. We evaluated the effectiveness of postlogging, forested buffer strips for forest-dwelling birds in the coastal temperate rainforest of southeast Alaska, USA. Our objective was to compare bird composition and density among forested buffer strips of differing widths and controls at the stand and landscape scales. We applied a 2-stage sampling design stratified by forested buffer width and randomly selected 24 managed and 18 control sites to sample over 2 breeding seasons. We estimated abundance of birds using the paired-observer, variable-circular plot method. We modeled combined effects of buffer width and vegetation and landscape characteristics on bird density at 2 spatial scales. Species richness and diversity were greatest in the narrowest buffers, but species composition in the largest buffers (≥400 m) was most similar to that in control blocks. Abundance of 3 of 10 common species differed across forested buffer treatments and controls. Densities of red-breasted sapsucker (*Sphyrapicus ruber*) and Pacific-slope flycatcher (*Empidonax difficilis*) were positively related to buffer width, whereas density of ruby-crowned kinglet (*Regulus calendula*) was negatively associated with buffer width. Parameter estimates for buffer width effects at both spatial scales were similar within species. We found few habitat and landscape variables that clearly affected density of our focal species, and among species no predictor variables affected density in a similar fashion. We recommend retaining forested buffers ≥400 m to support composition and abundance of forest-dwelling birds, particularly those species that rely on interior forest conditions. (JOURNAL OF WILDLIFE MANAGEMENT 72(3):674–681; 2008)

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Habitat fragmentation is the discontinuity in spatial distribution of resources and conditions present in an area at a given scale that affect occupancy, reproduction, or survival in a particular species (Franklin et al. 2002). Habitat fragmentation can strongly influence bird communities and bird distribution and has been identified as a major cause of population declines of breeding migratory songbirds (Robinson et al. 1995, Hagan et al. 1996, Helzer and Jelinski 1999). In forested landscapes, buffers are used to reduce impacts of timber harvesting on forest-dwelling species by not only minimizing effects of fragmentation but also providing suitable habitat. Although forested buffers are prescribed most often along rivers, lakes, and streams (e.g., Darveau et al. 1995, Hagar 1999, Whitaker and Montevecchi 1999), coastal forests represent an increasingly rare riparian ecosystem that would likely benefit from similar prescriptions. Low elevation, high interception of snowfall, and close proximity to marine nutrients contribute to the unique composition, structure, and function of coastal forests, providing high-quality habitat and travel corridors for wildlife (Schoen et al. 1988).

Our purpose was to examine the response of the avian community to differences in width of forested beach buffers in a coastal, temperate rainforest. We define a beach buffer (hereafter, buffer) as a postlogging forested strip that parallels the saltwater edge and extends inland beginning at mean high tide. In southeast Alaska, USA, species such as the bald eagle (*Haliaeetus leucocephalus*), hairy woodpecker (*Picoides villosus*), northwestern crow (*Corvus caurinus*), and brown creeper (*Certhia americana*) are more common in riparian forests adjacent to saltwater than in any other habitat (Kessler and Kogut 1985). We chose to use buffer width as our metric, as opposed to patch area, because buffer width directly relates to forest management policy and it was difficult to delineate boundaries to define area when forested landscape features were interconnected (Kilgo et al. 1998, Hagar 1999, Lambert and Hannon 2000; see Blake and Karr 1987). Our objectives were to 1) measure differences in composition and density of birds in remaining stands of old-growth forest of varying widths (i.e., buffers) and stands of continuous old-growth forest along the beach; and 2) examine further the relationship between bird density, buffer width, and habitat characteristics at 2 spatial scales.

STUDY AREA

We conducted field trials on the Tongass National Forest (hereafter Tongass) in southeast Alaska, one of the largest tracts of temperate rainforest remaining in the world (Alaback 1991). Southeast Alaska comprised the Alexander Archipelago and a narrow strip of mainland that stretches south from Haines (59°N, 136°W) to Dixon Entrance (54°30′N, 130°W; Harris et al. 1974). The archipelago was roughly 700 km in length, averaged 190 km in width, and was characterized by steep, rugged topography, coastal fjords, and >2,000 islands (Alaback 1982). A cool, wet maritime climate characterized the region with between 75

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cm and 500 cm of precipitation evenly distributed throughout the year, increasing to the south (Harris et al. 1974). The landscape was naturally fragmented by mountainous terrain, wetlands, and various fine-scale disturbances (e.g., wind-throw). Riparian, muskeg, and alpine habitats at elevations >800 m were interspersed with the forests. The forest was characterized by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*), with western redcedar (*Thuja plicata*) and Alaska yellow-cedar (*Chamaecyparis nootkatensis*) more common farther south (Alaback 1982). The forest understory was dominated by blueberry (*Vaccinium* spp.), devil's club (*Oplopanax horridus*), salal (*Gaultheria shallon*), and salmonberry (*Rubus* spp.). Moss, ferns, and lichens covered the forest floor, and downed logs and root wads were scattered throughout the forest understory.

METHODS

Field Sampling

We applied a 2-stage sampling design in which we adapted stratified random sampling (with no replacement) to include a clustering component to minimize travel time between sampling locations (hereafter blocks) and to ensure that we sampled a variety of buffer widths. We randomly selected 12 managed blocks each year, 10 control blocks in 2001, and 8 control blocks in 2002. Managed blocks composed the forested buffer and adjacent clearcut. We chose 3 replicates in each of 4 buffer width classes ($\leq$100 m, 101–250 m, 251–399 m, $\geq$400 m) each year and used the Tongass Geographic Information System (GIS), vegetation classification maps, and aerial photography to measure buffer width and identify sampling blocks that met selection criteria. We selected blocks where the forested component consisted of $\geq$90% old-growth forest, defined as a forest stand where trees averaged $\geq$23 cm diameter at breast height and the stand was $\geq$150 years old (Caouette et al. 2000). No blocks contained anadromous streams, muskegs, or other non-forested conditions, and all clearcuts in managed blocks were 8–35 years in age. We defined control blocks to be those $\geq$5 km linear distance from all harvested stands and consisting of $\geq$90% old-growth forest (as defined above). No sampling blocks exceeded 300 m in elevation.

In each block, we established a rectangular grid of count stations spaced 150 m apart to avoid counting the same bird at multiple stations (Reynolds et al. 1980). We positioned count stations perpendicular to the beach at 25 m, 175 m, 325 m, and 475 m. In managed blocks, count stations extended into the clearcut but were always $\geq$75 m from the respective edge. Number of count stations in managed blocks depended on width of the buffer, but all control blocks contained 12 count stations. See Kissling (2003) for further details on study design.

We collected data during 2 breeding seasons, 29 May–30 June 2001 and 31 May–3 July 2002. We surveyed each block twice during each breeding season. During the second visit, we systematically rotated the order to reduce biases related to variability in bird activity throughout the sampling period (Robbins 1981). All observers participated in a 2-week training period prior to sampling. We began surveys at sunrise (0330–0400 hours) and continued for 5–6 hours, ending by 0930 hours.

We sampled birds at each count station using the paired-observer, variable-circular plot method (POVCP; Kissling and Garton 2006). Each observer recorded species, radial distance to bird, number in group, mode of detection (i.e., song, call note, visual, or a combination), and any movements of the bird on a map. We only recorded birds detected within the same habitat (e.g., forest, clearcut) as the count station. Duration of count was 8 minutes.

We qualitatively described vegetation within a 32-m radius (1 acre) of each count station. We visually estimated percent cover and recorded dominant species in 5 strata: tree, sapling, shrub, herbaceous, and ground layers. We measured percent slope, aspect, elevation, presence of water, and any disturbance factors. We enumerated standing dead trees, downed logs, and stumps. See Kissling (2003) for further details on vegetation sampling.

Data Analysis

We used individual blocks as experimental units for statistical analysis to avoid pseudoreplication (Hurlbert 1984). We eliminated counts conducted under inclement conditions, such as heavy precipitation or loud stream noise. We used an alpha level of 0.05 for all statistical analyses.

Using POVCP methods, we calculated bird density by averaging estimates at each count station over all visits and then averaging over the entire block or area of interest (Kissling and Garton 2006). For control blocks, we averaged density estimates for each species over all count stations. Within managed blocks, we calculated 2 density estimates for each species: average density in the clearcut and average density in the forested buffer.

We calculated several response variables to evaluate community parameters among treatments: number of individual species (estimated), evenness, and diversity. For these analyses, we used the cumulative number of detections by one observer. For species richness, we used rarefaction curves to calculate the estimated number of species per 100 detections because we sampled treatments with different intensity (Krebs 1999). We calculated Simpson's measure of evenness to quantify unequal representation in the community; low evenness values suggest presence of rare species (Krebs 1999). We measured species diversity using the exponential form (N_1) of the Shannon–Wiener function, which is sensitive to changes in rare species of a community (Krebs 1999).

We tested for differences among means of common species (i.e., species detected at $\geq$30 count stations each yr) across treatment levels using univariate analysis of variance (ANOVA; PROC GLM; SAS Institute, Cary, NC). If data deviated from the normal distribution or homogeneity of variances, we used square-root transformation to improve distributions (Zar 1999). Initially, we included treatment $\times$ year in the ANOVAs but eliminated the interaction term because it was not statistically significant ($P > 0.05$) for any species. Therefore, we combined densities across years to conduct multiple comparison tests. We used the Tukey–Kramer test, appropriate for unequal sample sizes, to identify differences between treatment means for species with a significant ANOVA.

For individual species with a significant treatment effect, we modeled combined effects of buffer width and vegetation variables on bird density at the stand and landscape scales (PROC REG; SAS Institute). We conducted these analyses to verify that the effect of buffer width was genuine and that observed changes in density were not a result of differences in habitat characteristics or inappropriate scale. Because it was difficult and subjective to delineate boundaries for control blocks, we used data collected in managed stands only.

At the stand scale, we estimated vegetation characteristics at each block by averaging variables over all stations in the forested buffer. To reduce multicollinearity, we eliminated habitat variables having variable inflation factors $\geq$10 (Der and Everitt 2002). Initially we considered both linear and quadratic terms of uncorrelated vegetation variables, but examining scatter plots determined that density was more strongly correlated to linear terms and therefore we eliminated quadratic terms from further consideration. We considered these independent variables: percent slope, number of standing dead trees per hectare, percent canopy cover, year, and buffer width (m). Again, if density deviated from normal distribution or homogeneity of variances, we used the square-root transformation to improve distributions (Zar 1999). Based on life-history characteristics, published literature, and personal field observations, we developed a set of candidate models for each species. We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to rank models from most to least supported given the data (Burnham and Anderson 2002). Because no single model received overwhelming support (Akaike wt > 0.90), we calculated model-averaged estimates of regression coefficients and their unconditional standard errors from all models that had a ΔAIC_c value $<$4 (Burnham and Anderson 2002).

We characterized the landscape of each block by delineating a 300-ha area centered on the block and calculating landscape metrics using the Tongass GIS (McGarigal and McComb 1995). Landscape metrics included hectares of old-growth, hectares of young-growth (trees with an average dbh $<$23 cm and $<$150 yr old), kilometers of roads, and edge density (m/ha). We also considered buffer width (m) and year in the candidate models. We eliminated variables with a variable inflation factor $\geq$10 to reduce multicollinearity (Der and Everitt 2002). We developed 11 candidate models a posteriori and ran all models for each species. We used the same model selection statistics described above and report similar results.

RESULTS

We established 347 stations ($n = 778$ visits) in 42 sampling blocks that met all criteria. Control blocks ($n = 18$) included 149 stations and managed blocks ($n = 24$) contained 148 stations in forested buffers. We detected 7,369 birds of 43 species over the 2-year period. We recorded 17 species at $\geq$5 count stations each year (Fig. 1), but 10 of these species accounted for 88% of the detections ($n = 5{,}806$). Pacific-slope flycatcher (*Empidonax difficilis*; 18% of detections) and winter wren (*Troglodytes troglodytes*; 18%) were most common, followed by Townsend's warbler (*Dendroica townsendii*; 11%), varied thrush (*Ixoreus naevius*; 10%), and hermit thrush (*Catharus guttatus*; 10%).

Species richness and diversity were greatest in the narrowest buffers, but evenness values were lowest in the widest buffer and control blocks, suggesting presence of rare species. Buffers between 250 m and 399 m in width tallied the fewest individual species ($n = 13$, range = 13–16) and lowest diversity ($N_1 = 8.73$, range = 8.73–11.76; Table 1). Similarly, this treatment level (buffer width = 250–399 m) had a high evenness value of 0.43 (range = 0.25–0.52). Species composition in the largest buffers ($\geq$400 m) was most similar to that in control blocks (Table 1).

Density of only 3 species (red-breasted sapsucker [*Sphyrapicus ruber*], $F = 2.98$, df = 41, $P = 0.03$; Pacific-slope flycatcher, $F = 2.53$, df = 41, $P = 0.05$; and ruby-crowned kinglet [*Regulus calendula*], $F = 2.64$, df = 41, $P = 0.05$) differed among treatments (Fig. 1). Densities of other forest-associated species, such as golden-crowned kinglet ([*R. satrapa*], $F = 0.33$, df = 41, $P = 0.86$), varied thrush ($F = 0.30$, df = 41, $P = 0.87$), and Townsend's warbler ($F = 0.33$, df = 41, $P = 0.86$), varied surprisingly little across treatments. Similarly, densities of many ground- and shrub-nesting species (e.g., winter wren, $F = 1.67$, df = 41, $P = 0.18$; Swainson's thrush [*C. ustulatus*], $F = 1.07$, df = 41, $P = 0.39$; and hermit thrush, $F = 1.89$, df = 41, $P = 0.13$) were comparable across all treatments. Chestnut-backed chickadees (*Poecile rufescens*; $F = 0.62$, df = 41, $P = 0.65$) and ruby-crowned kinglets exhibited similar patterns but densities of chestnut-backed chickadees were slightly more variable and therefore not statistically different among treatments. Several species and species assemblages exhibited notable patterns, but too few detections prevented statistical analyses or conclusive results. We detected hairy woodpeckers and Steller's jays (*Cyanocitta stelleri*) exclusively in large buffers ($\geq$250 m) and controls (Fig. 1). Similarly, we recorded most brown creeper (83%; $n = 45$) and raptor (79%; $n = 24$) detections in the largest buffers ($\geq$400 m) and controls.

When considering habitat and landscape characteristics for the 3 species with an overall treatment effect, width remained a useful predictor variable at both spatial scales. At the stand scale, additional habitat variables were not consistently included in the top-ranked models (Table 2), which is not surprising because we selected managed blocks to have similar forest structure. However, at the landscape scale, amount of young-growth (ha) and edge density (m/ha) were included in several of the top-ranked models along with width (Table 3).

At the stand scale, red-breasted sapsucker density was

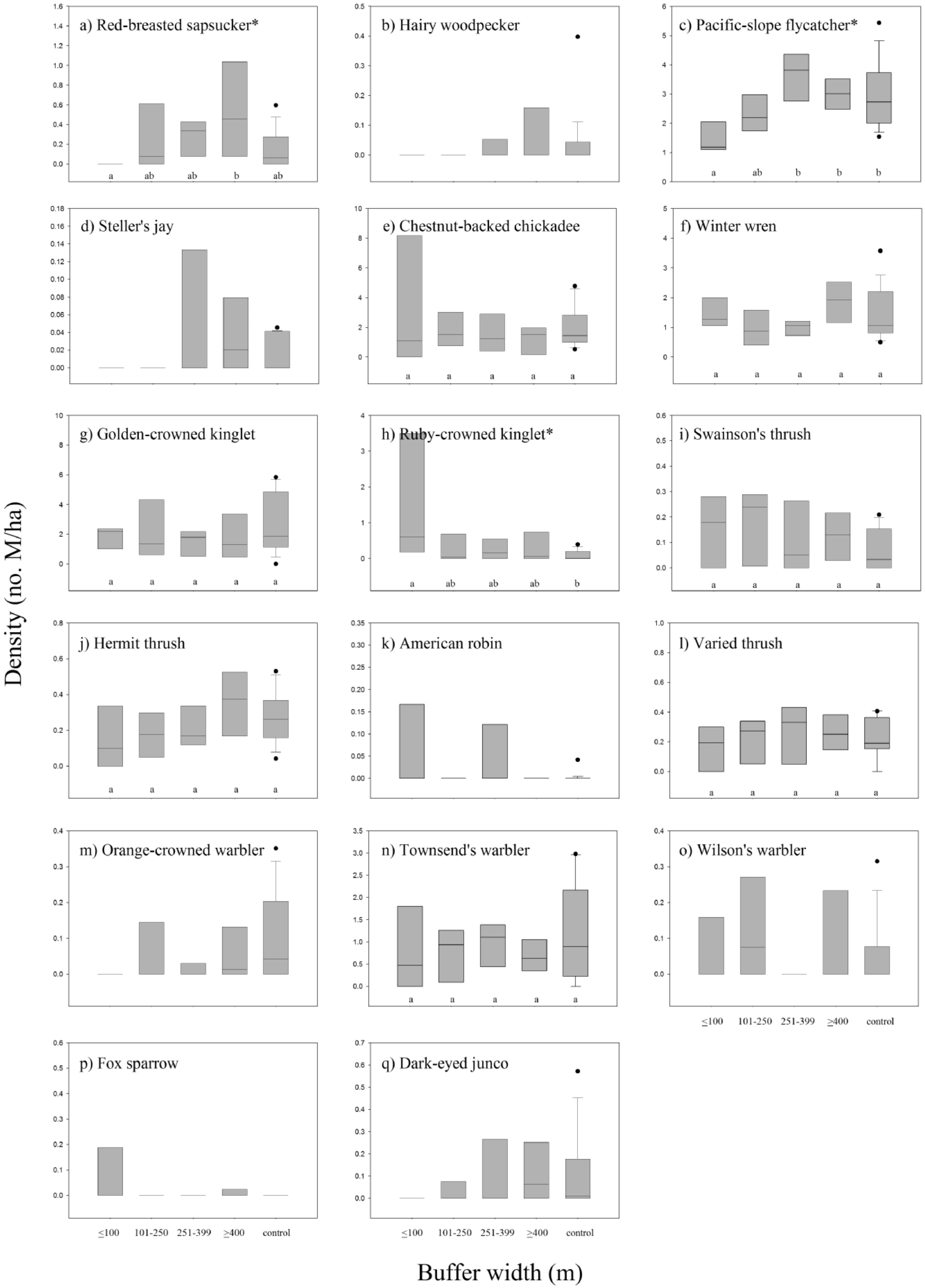

Figure 1. Densities (median and range) of 17 avian species in varying buffer width classes and in controls, southeast Alaska, USA, 2001 and 2002. Means with the same letter are not statistically different ($P > 0.05$). Asterisks indicate an overall significant treatment effect. Means with no letter signifies that sample size was inadequate for statistical test.

Table 1. Diversity measures of breeding bird communities in varying widths of buffers and controls, southeast Alaska, USA, 2001 and 2002.

Measure	Buffer width (m)				
	<100	101–250	250–399	>400	Control
Estimated no. of species/ 100 detections	17	16	13	14	15
Simpson's measure of evenness	0.52	0.38	0.43	0.32	0.25
Shannon–Wiener	11.22	11.76	8.73	10.86	10.97

described by 4 models with ΔAIC_c <4 that incorporated buffer width, number of standing dead trees per hectare, percent slope, and year (Table 2). Buffer width was included in all 4 models, all of which explained about one-third of the variation in density (range of $R^2 = 0.31$–0.33; Table 2). Red-breasted sapsucker density was positively related to buffer width at the stand scale, peaking in buffers ≥400 m (Fig. 1), but the magnitude of the width effect was extremely small ($\beta_{width} = 0.001$; Table 4). The effect of the other predictors was not clearly estimated (CIs included zero; Table 4). At the landscape scale, red-breasted sapsucker density was best predicted by one model only that included width and young-growth (Table 3). As buffer width and hectares of young-growth increased on the landscape, densities of red-breasted sapsuckers also increased (Table 5). The coefficient of determination for this model was 0.60 (Table 3).

Similarly, Pacific-slope flycatcher density at the stand scale was described by 4 models, and width was included in all 4 models, whereas year, percent slope, and percent canopy contributed to ≥1 model (Table 2). Densities increased as buffer width increased (Table 4) and peaked in buffers ≥250 m in width (Fig. 1). In addition, density increased with decreasing percent slope and increasing percent canopy cover, although confidence intervals for this predictor contained zero (Table 4). Results were similar at the landscape scale, with width included in 3 of 4 top models (Table 3). There was also a year effect, with greater densities observed in 2002 versus 2001. Other important landscape characteristics included hectares of young-growth, edge density, and kilometers of road. Again, as young-growth and edge density increased on the landscape, density of Pacific-slope flycatchers in the buffers also increased (Table 5). Roads were negatively associated with density, but confidence intervals for this predicator variable contained zero. Top-ranked landscape models (R^2 = 0.22–0.37; Table 3) explained less variation than those at the stand scale (R^2 = 0.22–0.49; Table 2).

Abundance of ruby-crowned kinglets was less predictable at the stand scale, with 6 models with ΔAIC_c values <4 (Table 2). Important predictors included width, year, percent canopy, and percent slope, but coefficients of determination were low (0.02–0.21; Table 2). Density was negatively associated with all predictor variables (Table 4). Ruby-crowned kinglet density tended to be greatest in stands with little canopy cover and relatively flat topography. At the landscape scale, density of ruby-crowned kinglets was

Table 2. Model selection statistics for models explaining the combined effect of forested buffer width and vegetation on bird densities at the stand scale in old-growth forests of southeast Alaska, USA, 2001 and 2002. Models are in order of increasing change in Akaike's Information Criterion adjusted for small sample size (Δ_i AIC_c) with corresponding model weights (w_i).

Species	Model (g_i)[a]	Δ_i AIC_c	w_i	R^2
Red-breasted sapsucker[b]	Width	0	0.505	0.31
	Dead + width	1.93	0.192	0.33
	Width + yr	2.29	0.160	0.32
	Slope + width	2.63	0.135	0.32
	Dead + slope	9.88	0.004	0.02
	Dead + yr	9.88	0.004	0.02
	Slope + yr	9.99	0.003	0.01
	Canopy + dead + slope + width + yr	11.84	0.001	0.34
	Dead + slope + yr	13.11	0.001	0.02
Pacific-slope flycatcher	Width + yr	0	0.434	0.39
	Width + yr + slope	0.23	0.388	0.48
	Width	3.02	0.096	0.22
	Width + yr + slope + canopy	3.45	0.078	0.49
	Yr + slope	9.91	0.003	0.09
	Slope + canopy	11.83	0.001	0.00
Ruby-crowned kinglet[b]	Width	0	0.321	0.14
	Width + yr	0.08	0.309	0.21
	Width + canopy	2.28	0.103	0.16
	Slope	2.32	0.101	0.02
	Width + slope	2.89	0.076	0.14
	Canopy + yr	3.81	0.048	0.04
	Slope + canopy	4.75	0.030	0.03
	Width + slope + canopy + yr	6.28	0.014	0.22
	Slope + canopy + yr	7.03	0.009	0.05

[a] Variables included in models (identifiers in parentheses): % slope (slope), no. of standing dead trees/ha (dead), % canopy cover (canopy), yr, and buffer width (width).

[b] We square-root transformed densities.

described by 3 models with ΔAIC_c <4 that included the global model (Table 3). All predictor variables at the landscape scale were negatively associated with density except for roads (Table 5). Generally, model selection statistics and explanatory power of models were not in accordance with one another. Models that contained kilometers of roads had high explanatory value ($R^2 \geq 0.28$) but did not rank very high using ΔAIC_c (Table 3).

DISCUSSION

We designed this study to test effects of varying buffer width on bird community composition and density. We found that community composition changed with buffer width. Species richness and diversity were maximized in the narrowest buffers, most likely the result of an increased edge-to-interior ratio. Other studies have reported similar results (e.g., Darveau et al. 1995, Hagar 1999, Pearson and Manuwal 2001). However, our results also demonstrate that although diversity and richness were greatest in narrow buffers, the community contained few rare or uncommon species. Even relatively common forest species, such as Steller's jay and hairy woodpecker, were absent from narrow buffers (Fig. 1). We observed the least diversity and richness

Table 3. Model selection statistics for models explaining the combined effect of forested buffer width, fragmentation metrics, and vegetation on bird densities at the landscape scale in old-growth forests of southeast Alaska, USA, 2001 and 2002. Models are in order of increasing change in Akaike's Information Criterion adjusted for small sample size (Δ_i AIC$_c$) with corresponding model weights (w_i).

Species	Model (g_i)[a]	Δ_i AIC$_c$	w_i	R^2
Red-breasted sapsucker[b]	Width + young-growth	0	0.924	0.60
	Young-growth	6.20	0.042	0.41
	Width + young-growth + roads + old-growth + edge + yr	7.17	0.026	0.72
	Width	11.88	0.002	0.26
	Young-growth + edge + yr	12.15	0.002	0.42
	Young-growth + roads + edge	12.17	0.002	0.42
	Width + old-growth	13.55	0.001	0.29
	Width + yr	14.17	0.001	0.27
	Old-growth	18.95	0.000	0.00
	Old-growth + roads + edge	23.06	0.000	0.08
	Old-growth + edge + yr	25.04	0.000	0.00
Pacific-slope flycatcher	Width + yr	0	0.580	0.29
	Width	3.02	0.128	0.22
	Width + young-growth	3.35	0.109	0.30
	Young-growth + roads + edge	3.91	0.082	0.37
	Width + old-growth	5.45	0.038	0.24
	Young-growth	6.09	0.028	0.11
	Young-growth + edge + yr	7.21	0.016	0.28
	Old-growth	8.98	0.007	0.00
	Old-growth + roads + edge	9.28	0.006	0.22
	Old-growth + edge + yr	9.87	0.004	0.20
	Width + young-growth + roads + old-growth + edge + yr	10.69	0.003	0.50
Ruby-crowned kinglet[b]	Old-growth + edge + yr	0	0.303	0.06
	Young-growth + edge + yr	0.20	0.274	0.07
	Width + young-growth + roads + old-growth + edge + yr	0.23	0.270	0.44
	Width + young-growth	4.33	0.035	0.10
	Width + old-growth	4.53	0.031	0.11
	Old-growth	4.72	0.029	0.00
	Young-growth	5.03	0.025	0.01
	Old-growth + roads + edge	6.34	0.013	0.28
	Width + yr	7.00	0.009	0.19
	Width	7.08	0.009	0.09
	Young-growth + roads + edge	9.20	0.003	0.36

[a] Variables included in models (identifiers in parentheses): ha of old-growth (old-growth), ha of young-growth (young-growth), km of roads (roads), edge density (edge), yr, and buffer width (width).
[b] We square-root transformed densities.

Table 4. Model-averaged results with lower (LCI) and upper (UCI) 95% confidence intervals of models on the effect of stand-scale variables on density of 3 species in forests of southeast Alaska, USA, 2001 and 2002. We averaged regression parameters from all models that had a change in Akaike's Information Criterion adjusted for small sample size (ΔAIC$_c$) <4. The year variable considered 2001 versus 2002.

Species	Parameter[a]	Estimate	LCI	UCI
Red-breasted sapsucker[b]	Intercept	0.068	−0.304	0.439
	Width	0.001	0.000	0.002
	Yr	0.062	−0.234	0.358
	Slope	−0.002	−0.030	0.026
	Dead	−0.025	−0.098	0.049
Pacific-slope flycatcher	Intercept	0.262	−1.585	2.110
	Width	0.004	0.002	0.007
	Yr	1.148	0.253	2.042
	Slope	−0.072	−0.012	−0.025
	Canopy	0.012	−0.032	0.054
Ruby-crowned kinglet[b]	Intercept	0.981	0.180	1.782
	Width	−0.001	−0.002	0.000
	Yr	−0.257	−0.686	0.173
	Slope	−0.009	−0.032	0.013
	Canopy	−0.006	−0.028	0.015

[a] Variables included in models (identifiers in parentheses): % slope (slope), no. of standing dead trees/ha (dead), % canopy cover (canopy), yr, and buffer width (width).
[b] We square-root transformed densities.

in midsize buffers, which lack both high edge-to-interior ratio and large tracts of continuous forest.

Generally, species associated with trees and snags were most affected by changes in buffer width compared to species associated with ground and shrub layers. Manuwal and Manuwal (2002) reported similar results when evaluating amount of canopy cover and bird density. In our study, densities of red-breasted sapsucker (cavity nester) and Pacific-slope flycatcher (tree nester) were positively related to buffer width, whereas ruby-crowned kinglet (tree nester) density was negatively correlated with buffer width. Other studies in the Pacific Northwest have associated Pacific-slope flycatcher abundance with area of mature forest, but none have reported a similar relationship for red-breasted sapsuckers (Aubry et al. 1997, Hagar 1999, George and Brand 2002). Other forest-associated species (e.g., golden-crowned kinglet, varied thrush, Townsend's warbler) regularly occurred in narrow buffers in our study. In contrast, absence of hairy woodpecker, Steller's jay, and brown creeper from narrow buffers ($\leq$250 m) may indicate these species avoid edge habitats or the forested area was small relative to their territory size. These species and the

Table 5. Model-averaged results with lower (LCI) and upper (UCI) 95% confidence intervals of models on the effect of landscape scale variables on density of 3 species in forests of southeast Alaska, USA, 2001 and 2002. We averaged regression parameters from all models that had a change in Akaike's Information Criterion adjusted for small sample size (ΔAIC_c) <4. The year variable considered 2001 versus 2002.

Species	Parameter[a]	Estimate	LCI	UCI
Red-breasted sapsucker[b]	Intercept	−0.270	−0.548	0.009
	Width	0.001	0.000	0.002
	Young-growth	0.007	0.003	0.010
Pacific-slope flycatcher	Intercept	−1,287.828	−2,388.410	−187.246
	Width	0.004	0.001	0.007
	Young-growth	0.013	0.001	0.027
	Yr	0.998	0.147	1.85
	Roads	−0.410	−0.904	0.084
	Edge	0.492	0.128	0.857
Ruby-crowned kinglet[b]	Intercept	470.295	−643.656	1,584.245
	Width	0.000	−0.002	0.001
	Young-growth	−0.004	−0.012	0.004
	Yr	−0.235	−0.791	0.322
	Roads	0.337	0.079	0.594
	Edge	−0.056	−0.275	0.163
	Old-growth	0.000	−0.008	0.009

[a] Variables included in models (identifiers in parentheses): ha of old-growth (old-growth), ha of young-growth (young-growth), km of roads (roads), edge density (edge), yr, and buffer width (width).
[b] We square-root transformed densities.

Pacific-slope flycatcher have been associated with old-growth forests along shoreline and were more abundant in large buffers (≥250 m), so these species may be of special concern to managers (Kessler and Kogut 1985).

We found few habitat and landscape variables that clearly affected density of our focal species (e.g., many CIs included zero), which was not surprising, especially at the stand scale, because our criteria for selecting study blocks controlled for major differences in forest composition and structure. Each species, however, responded to varying buffer width differently and at different scales but consistent with the species biology. At both scales, our models performed well when explaining variation in densities of species that are relatively specialized in their habitat use, such as red-breasted sapsucker and Pacific-slope flycatcher. However, densities of species with comparatively small territories (e.g., Pacific-slope flycatcher) were best predicted at the stand scale, as opposed to those with larger territories (e.g., red-breasted sapsucker) that were best explained at the landscape scale. Consequently, densities of habitat generalists with small territories, such as ruby-crowned kinglets, were less predictable and difficult to interpret in relation to buffer width regardless of spatial scale.

One of the more interesting results from our study was the relationship between bird density in the buffer and young-growth on the landscape. Although red-breasted sapsuckers and Pacific-slope flycatchers clearly benefited from the characteristics of forested buffers and were positively related to buffer width at both spatial scales, both species appeared to reach a fragmentation threshold where density began to stabilize or decline and wide forested buffers became increasingly important on the landscape. The relationship between landscape structure and abundance of breeding birds has been well documented in recent years, but not in the context of specific management prescriptions (e.g., McGarigal and McComb 1995, Fletcher and Koford 2002).

MANAGEMENT IMPLICATIONS

Results of our study support the retention of forested beach buffers to mitigate loss of habitat for most forest-dwelling landbirds. We conclude that forested beach buffers ≥250 m in width can support densities of forest-associated birds similar to that of large continuous old-growth stands. However, rare or uncommon species (e.g., brown creeper, hairy woodpecker, Steller's jay), which tend to be of interest to managers, will benefit most from buffers ≥400 m in width. Undoubtedly, all forest-dwelling species will benefit from the retention of large forested buffers, but species sensitive to area of mature forest, such as Pacific-slope flycatcher and red-breasted sapsucker, will benefit most. Neither of these species responded positively to silvicultural modifications, including thinning and gapping (Dellasala et al. 1996), and therefore viable populations of Pacific-slope flycatchers and red-breasted sapsuckers should be supported by the existing old-growth reserve system including retention of beach buffers.

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