

Forecasting Avian Responses to Elwha River Restoration

Carly J. Gelarden and John F. McLaughlin

ABSTRACT

Riparian restoration increasingly employs dam removal, but with limited knowledge about post-removal ecological impacts. Comprehensive ecological study has occurred on few dam removals and rarely on associated terrestrial components. Research supporting the Elwha River restoration program, Washington, USA, helps fill this gap as the largest dam removal project to date. We developed forecasts of avian responses to post-removal forest restoration in Elwha reservoirs. We modeled abundance patterns for 8 species using avian inventory data and habitat variables at local, patch, and landscape scales. We evaluated models using Akaike's Information Criterion and determined the relative importance of each variable and scale using multi-model inference. Local habitat variables best explained abundance patterns for most species. We forecasted avian responses to forest restoration in the drained Lake Mills reservoir with and without conifers. Planting conifers hastened forecasted avian responses. Forecasts suggest birds associated with deciduous forests and edge habitats will colonize restored habitats rapidly, but birds associated with conifers may not respond markedly for more than a century. Birds can provide a measure of early restoration progress, but comprehensive restoration of Elwha avifauna will take longer than the dams have been in place. This conclusion echoes a familiar theme in Pacific Northwest forest restoration: anthropogenic impacts occur rapidly, but full restoration is comparatively slow.

Keywords: dam removal, deciduous specialist, habitat model, restoration targets, revegetation

Dams impact 60 percent of Earth's large rivers (World Commission on Dams 2000) and all large watersheds in the contiguous US (Graf 1999). Dam impacts to riparian hydrology and sediment processes (Andrews 1986, Schmidt and Graf 1990, Topping et al. 2000, Poff et al. 2007) and plant and animal populations (Rood and Mahoney 2000, Gregory et al. 2002) have led researchers and policy makers to evaluate dam removal as a means to achieve restoration objectives (Hart et al. 2002). These efforts have revealed a need for information about ecological responses to dam removal and post-removal restoration, particularly to inform decisions about whether or how large dams should be removed.

A diverse group of researchers is addressing this knowledge gap with

the ongoing removal of two large dams on the Elwha River, Washington USA (Duda et al. 2008). Dam removals on the Elwha River are releasing large volumes of sediment that have accumulated in the reservoirs. Terraces of bare sediment will remain in the drained reservoir beds and new sediment deposits will be created as sediment is transported downriver (Childers et al. 2000, Shafroth et al. 2002, Chenoweth et al. 2011). Plant establishment in sediment deposits is expected to perform important restoration functions, including creating habitats made rare by dam operation (Shafroth et al. 2002) and providing structures required by fish and wildlife. Although much uncertainty remains regarding vegetation responses, even less is known about responses of terrestrial animals (Winter and Crain 2008, Lindenmayer et al. 2010).

For wildlife, the Elwha management goal is to "restore wildlife populations to baseline distribution and abundance" (Woodward et al. 2008).

The project has not identified more specific restoration objectives for wildlife, nor does it include plans for active wildlife management beyond monitoring. Wildlife are expected to occupy restored habitats, but wildlife responses to dam removals and associated restoration have not been forecasted (Chenoweth et al. 2011). Forecasting wildlife responses will support the Elwha project by providing a basis for evaluating the spatial extent and temporal progress of restoration. Because wildlife responses occur one or more trophic levels removed from active restoration interventions, they provide integrative measures of restoration complementary to physical and vegetative monitoring variables (Woodward et al. 2008, Ortega-Alvarez and Lindig-Cisneros 2012).

Our work addresses this need by forecasting avian responses to habitat restoration in the largest restoration site associated with the Elwha project, the larger reservoir bed. Songbirds provide good measures of restoration

progress for several reasons. First, ease in songbird detection and identification make it practical to study many species over large areas (Gibbons et al. 1996). Second, songbirds are impacted by dams, which reduce or displace riparian habitat structures (Stromberg 2001, Shafroth et al. 2002) and avian food resources (Bull and Skovlin 1982, Gray 1993). Third, birds are sensitive to habitat changes (Carignan and Villard 2002, Scott et al. 2003) expected to follow dam removal. Fourth, birds respond to habitat changes throughout the course of restoration programs (Kus 1998, Kus and Beck 2003, Gardali et al. 2006). Finally, public interest in birds can leverage support for further study of ecological responses to riparian restoration.

Effects of restoration on wildlife received limited study before recent interest in avian responses to restoration, reviewed by Ortega-Alvarez and Lindig-Cisneros (2012). Research on avian responses to restoration has considered diverse species, habitat types, restoration needs, and geographic regions, with greatest effort on riparian habitats and in North America (Ortega-Alvarez and Lindig-Cisneros 2012). Many studies address the goal of increasing abundances of all birds or specific conservation targets (Benson et al. 2006, Stralberg et al. 2006). Contrasting needs of different species require trade-offs, which can be informed by modeling for optimal solutions (Stralberg et al. 2006, 2009). At a local scale, avian abundance and nesting success is greatest in restoration sites with diverse plant species and habitat structure (Brand et al. 2010, Maguire and Hadley 2010, Munro et al. 2011). At a landscape scale, birds may respond most to restoration near established or remnant riparian vegetation (Kus 1998, Gardali et al. 2006, Gardali and Holmes 2011). Avian abundances and nest success in restored sites are comparable to remnant riparian habitats in many systems, but species richness often is lower (Jansen 2005, Small et al. 2007,

Smith et al. 2008, Latta et al. 2012). Birds can facilitate habitat restoration, by dispersing seeds into restoration sites (Robinson and Handel 1993, 2000, Ortega-Alvarez and Lindig-Cisneros 2012).

Forecasts presented here show avian density changes during the first century of habitat restoration in the Lake Mills reservoir bed after removal of Glines Canyon Dam. These forecasts can be applied in three ways to inform restoration decisions. First, forecasts can be used to evaluate alternative restoration prescriptions under consideration (Chenoweth et al. 2011) by anticipating effects on terrestrial birds. Second, forecasts can support revegetation efforts by understanding distributions of avian seed dispersers. Third, forecasts can be used as *a priori* scenarios to evaluate restoration results.

Methods

Study System

The Elwha River is west of Port Angeles, WA. The river flows north over 70 kilometers from Olympic Mountain headwaters to the Strait of Juan de Fuca. Two dams built early in the 20th century, located 7.9 km and 17.7 km above the river mouth, inundated nearly 300 ha of riparian and terrestrial habitat (Figure 1 in McLaughlin 2013, *this issue*). The lower Elwha Dam impounded Lake Aldwell (108 ha) and the upper Glines Canyon Dam impounded Lake Mills (168 ha). Sediment discharges to the Elwha delta decreased 98% relative to pre-dam values (NPS 1995), causing reductions in channel complexity, gravel bars and alluvial terraces, and early successional riparian habitats (Pohl 2004).

Eighty-three percent of the Elwha watershed lies within Olympic National Park. The river flows through alternating bedrock canyons and floodplains (Duda et al. 2008). The river descends steep gradients within the canyons, which confine the

channel between high walls. Gentle gradients and unconstrained channels in valley floodplains support dynamic river meanders and frequent inundation of terrestrial habitats. Vegetation in the watershed is dominated by Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), with a mosaic of other habitats in the riparian corridor, including areas dominated by Western red cedar (*Thuja plicata*), red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*), black cottonwood (*Populus balsamifera trichocarpa*), willow (*Salix* spp.), and mixed conifer-hardwood stands (NPS 1996).

Restoring the reservoir beds is the largest component of Elwha restoration, apart from removal of the dams themselves. Three goals drive the reservoir revegetation plan: (1) minimize invasive, exotic plants; (2) restore ecosystem processes, including sediment stabilization; (3) establish native forests (Chenoweth et al. 2011). All three goals depend on rapidly establishing native plants throughout sediment deposits in the drained reservoirs. Natural forest establishment is expected to be slow in most of the reservoir area, due to few legacy structures, harsh growing conditions, and large distances to source materials (Chenoweth et al. 2011, Michel et al. 2011). Consequently, the reservoir restoration plan emphasizes active revegetation, including aerial seed distribution, live-staking, and planting seedlings of native woody species (Chenoweth et al. 2011). Early revegetation planning focused on deciduous species, but now conifers represent about half the revegetation effort as measured by treatment area and number of plants (Chenoweth et al. 2011). Although deciduous species dominate early seral stages in the Elwha, planting conifers supports the third restoration goal because conifers dominate the Elwha watershed (NPS 1996). Due to uncertainties about which plant species and planting configurations will succeed, the revegetation plan is adaptive. Implementation decisions will

be informed by outcomes of planting experiments conducted during dam removal and reservoir drawdown (Chenoweth et al. 2011). Here we provide complementary analyses to inform restoration decisions by forecasting avian responses to alternative restoration strategies.

Model Development

We defined avian restoration goals and fit avian-habitat models using pre-restoration avian inventory data from the Elwha riparian zone (Gelarden 2008; Appendix Tables A1 and A2). These data define avian “baseline distribution[s] and abundance[s],” for restoration (Woodward et al. 2008). Avian modeling included bird-habitat relationships at three spatial scales: 1) local habitat structure (MacArthur and MacArthur 1961, Willson 1974, Cody 1985); 2) habitat patch properties (Ambuel and Temple 1983, Blake and Karr 1987, Hawrot and Niemi 1996, Bender et al. 1998); and 3) landscape patterns (McGarigal and McComb 1995, Saab 1999, Crozier and Niemi 2003). We modeled abundances of the 8 most common species with *a priori* univariate and bivariate models developed from habitat variables at local, patch, and landscape scales. At each scale, we used 3 habitat variables based on songbird natural histories, avian habitat selection in comparable systems (Saab 1999, Crozier and Niemi 2003), and the range of conditions in the Elwha riparian zone (Appendix Table A3).

We sorted the eight focal species into conifer specialists, deciduous specialists, and habitat generalists, and developed model sets appropriate for each group. Model sets included univariate models (Equation 1) for each of the nine habitat variables (Appendix Table A3) and up to eight bivariate models (Equation 2). We fit models to species count data using Poisson regression (Hastie and Pregibon 2003, Duntelman and Ho 2006, Hardin and Hilbe 2007), because count data are positive, discrete, and typically Poisson distributed (Royle et al. 2004).

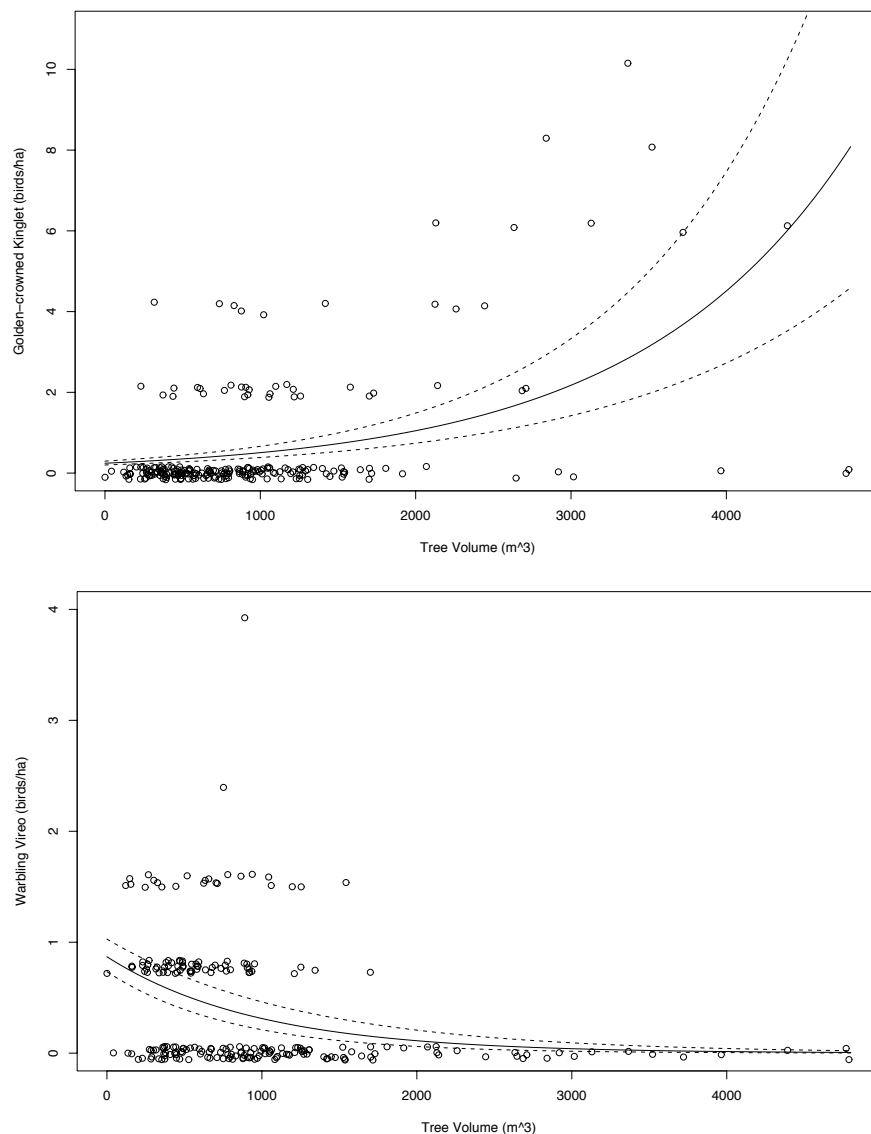


Figure 1. Avian abundance-habitat models for two species. Models (Equation 1) were fit to data on species density and tree volume (m^3), the habitat variable in the Kullback-Leibler best model for most species. Avian density data are plotted as open circles (o), models are plotted as solid lines (-), with $\pm$ standard errors as dashed lines (- -). Point locations include a small amount of random jitter to distinguish overlapping points. Top: Golden-crowned kinglet (*Regulus satrapa*), a conifer forest specialist. Bottom: Warbling vireo (*Vireo gilvus*), a deciduous forest specialist.

$$y_{ij} = \exp(\alpha + \beta x_i + \varepsilon_{ij}) \quad (1)$$

$$y_{ijk} = \exp(\alpha + \beta_1 x_i + \beta_2 z_j + \varepsilon_{ijk}) \quad (2)$$

In Equations 1 and 2, y represents point-specific bird counts; x and z are drawn from the nine predictor variables (Appendix Table A3); α , β_1 , β_2 are fitted parameters; and ε is residual deviance. Results of a Chi-squared goodness of fit test on a global model containing all nine variables (Hosmer and Lemeshow 2000, Burnham and Anderson 2002) confirmed the habitat

variables accounted for species abundance patterns in all eight focal species (P -values ranged from 0.02 to $<10^{-16}$). Poisson regression models assume abundance-habitat relationships are monotonic, which was consistent with data for each species (see Figure 1).

Model Selection and Multimodel Inference

We evaluated empirical support for each model relative to the candidate set for a given species using information-theoretic methods (Burnham

and Anderson 2002). We conducted Poisson regressions and model selection in S-Plus (version 3.4 for UNIX), using independently validated custom functions. Prior to model selection, we checked for overdispersion, which is common in avian count data (Anderson and Burnham 2002). Overdispersion was not an issue in Elwha data: residual deviance was smaller than residual degrees of freedom for six of eight species, and the largest dispersion parameter (1.30, for chestnut-backed chickadee [*Poecile rufescens*]) was lower than values from 88% of data sets analyzed in Franklin et al. (2002). We determined the model confidence set using the likelihood ratio method (Burnham and Anderson 2002), with a threshold value of $C = 1/4$. We used multi-model inference to evaluate relative importance of local, patch, and landscape scales in species abundance patterns. We summed Akaike weights (w_i) for univariate models containing each of the three habitat variables for a given scale, in which w_i were re-scaled to the set of univariate models.

Forecasting Avian Responses

We forecasted avian responses to two restoration scenarios in the Lake Mills reservoir during the first century following dam removal. We focused on the upper reservoir because habitat restoration effort will be greatest there (Chenoweth et al. 2011), and forecasts for reaches below the dams are precluded currently by uncertainty in sediment and vegetation distributions. We limited forecasts to one century due to large uncertainty in habitat structure beyond that time horizon. The first restoration scenario contains deciduous trees and shrubs only. The second scenario includes planted conifers and succession toward conifer-dominated forest. Uncertainties in post-dam sediment and habitat distributions render forecasting difficult at patch and landscape scales (Doyle et al. 2003, Bromley 2008, Chenoweth et al. 2011). Hence, our forecasts

address avian responses to local scale forest growth.

We translated restoration scenarios into trajectories of forest growth and succession using forest chronosequence data from unconstrained reaches in the lower Queets River, Olympic National Park (Van Pelt et al. 2006). Although the Queets riparian zone differs from the Elwha somewhat, it provides a reasonable surrogate because it contains the same deciduous species and similar conifer growth rates (McArdle and Meyer 1930). We fit Queets data (Van Pelt et al. 2006) on stand volume and composition to stand age using nonlinear least squares regression. We fit a saturating function, Equation 3, to data on tree volume (m^3/ha), and a declining sigmoid function, Equation 4, to data on the deciduous proportion (%) of forest volume.

$$V = \frac{at}{b + t} \quad (3)$$

$$D = 100 \left[1 - \frac{(t/a)^2}{b + (t/a)^2} \right] \quad (4)$$

In the equations above, V represents volume (m^3/ha), D is percent deciduous, t is time (years), and a and b are fitted constants.

We forecasted density changes in eight focal species during the two restoration scenarios by combining forest growth and succession trajectories (Equations 3 and 4) with species-habitat models (Equations 1 and 2). We developed three forecasts for each species, using two univariate models in V and D and a bivariate model (V, D). We developed model-averaged forecasts (Clark et al. 2001) for each species and restoration scenario by summing the forecasts, weighted by Akaike weights (w_i) (Burnham and Anderson 2002).

Results

Model Selection

Local habitat structure was more important than patch or landscape variables for six of eight species (Appendix Table A6). Landscape structure was second in importance for those six species and most important for the other two species. Habitat patch characteristics were least important for all eight species. Model selection results for model confidence sets for the eight focal species are in Appendix Table A4. Fitted parameter estimates for those models are in Appendix Table A5.

Results of model selection and fitting were consistent among species with the same *a priori* habitat associations. Conifer specialists, golden-crowned kinglet (*Regulus satrapa*) and winter wren (*Troglodytes troglodytes*), were more abundant in conifer forests with large volume (Figure 1A) and less abundant in areas with high habitat interspersation (Appendix Table A5). Deciduous specialists, song sparrow (*Melospiza melodia*), Swainson's thrush (*Catharus ustulatus*), and warbling vireo (*Vireo gilvus*), were more abundant in younger deciduous forests with high habitat interspersation (Figure 1B, Appendix Table A5). Habitat generalist patterns were intermediate quantitatively and qualitatively (Appendix Table A5). Habitat relationships were clearer for habitat specialists than generalists, similar to Seoane et al. (2005).

Forest Restoration Models

The saturating model for forest volume growth fit data from Van Pelt et al. (2006) well: stand age accounted for most variation in stand volume for both deciduous and mixed deciduous-coniferous stands (Table 1, Figure 2A). The sigmoid model of succession from deciduous to conifer-dominated forests also fit data in Van Pelt et al. (2006) reasonably well (Table 1, Figure 2B), although data from stands of intermediate age were variable. In restoration

scenario 2, conifers occupy roughly half the canopy after 100 years.

Avian Forecasts

Forecasted avian responses to the two habitat restoration scenarios were mostly similar (Figure 3), but changes were greater and more rapid with conifer planting (Figure 3B). In both scenarios, mean total forecasted avian density remained between 6 and 8 birds per hectare throughout the 100-year forecast period. Forecasted density changes were nearly compensatory among species.

Forecasts for five of the eight focal species reached management goals within 10 years in both restoration scenarios (Figure 3, Appendix Table A2). These species include all of the deciduous specialists and two of the habitat generalists: American robin (*Turdus migratorius*) and dark-eyed junco (*Junco hyemalis*). Mean forecasts for the two conifer specialists and chestnut-backed chickadees remained below restoration management goals throughout the 100 year forecast period.

Forecasted trajectories for individual species were consistent with habitat associations of those species and forecasted habitat changes. Habitat generalists (chestnut-backed chickadee, American robin, dark-eyed junco) dominated the avifauna in both restoration scenarios (Figure 3). In restoration scenario 1, deciduous habitat specialists maintained intermediate densities, while conifer specialist densities remained near zero (Figure 3A). In scenario 2, forecasts of deciduous specialists and conifer specialists followed opposing trajectories, reflecting changes in their respective habitats. In scenario 2, conifer specialist densities grew to equal or exceed deciduous specialists within the 100-year forecast window, but remained small relative to their densities in existing large volume conifer forests (Figure 3B). For both restoration scenarios, compounded uncertainty was large relative to forecasted changes in avian densities (Figure 3).

Table 1. Parameter estimates for forest growth and succession models fit to data in Van Pelt et al. (2006). Restoration scenario 1 constrains forest composition to 100% deciduous because that scenario does not include conifers in the first century. Parameters *a* and *b* are defined in Equation 3 for volume and Equation 4 for % deciduous.

Model	<i>a</i>	SE	<i>b</i>	SE	<i>R</i> ²
Volume, scenario 1	2106.6	1731.1	160.3	176.5	0.756
Volume, scenario 2	3648.9	652.7	221.0	67.8	0.918
% Deciduous, scenario 2	100.0	13.9	0.915	0.254	0.734

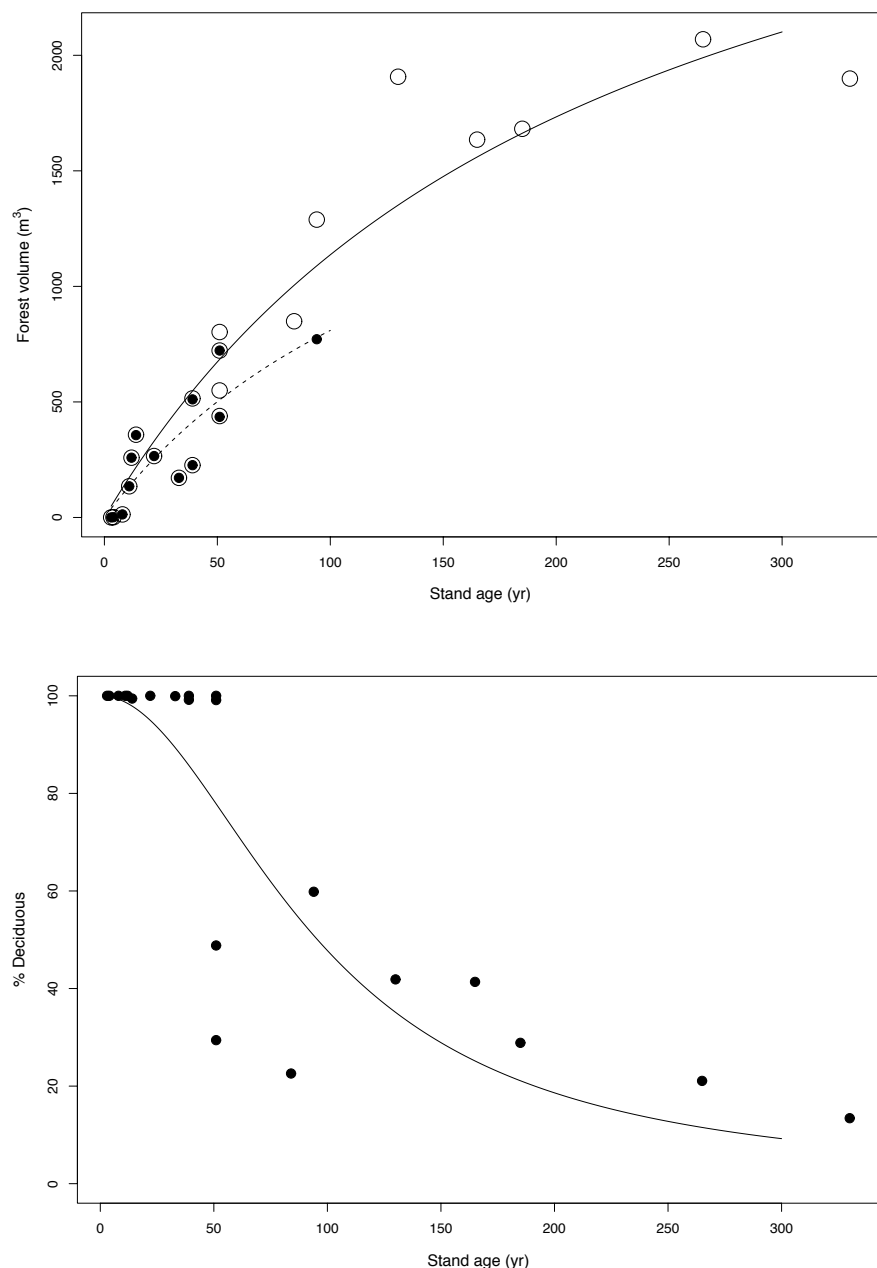


Figure 2. Forest growth models for restoration scenarios. Data are from Van Pelt et al. (2006); models are plotted as lines. Top: Saturating model (Equation 3) for growth in forest volume. Restoration scenario 1, deciduous stands: data are plotted as solid circles (●) and the growth model is plotted with a dashed line (- -). Restoration scenario 2, mixed deciduous and coniferous planting: data are plotted as open circles (○) and the growth model is plotted with a solid line (-). Bottom: Restoration scenario 2: sigmoid model (Equation 4) of succession from dominance by deciduous species to conifers.

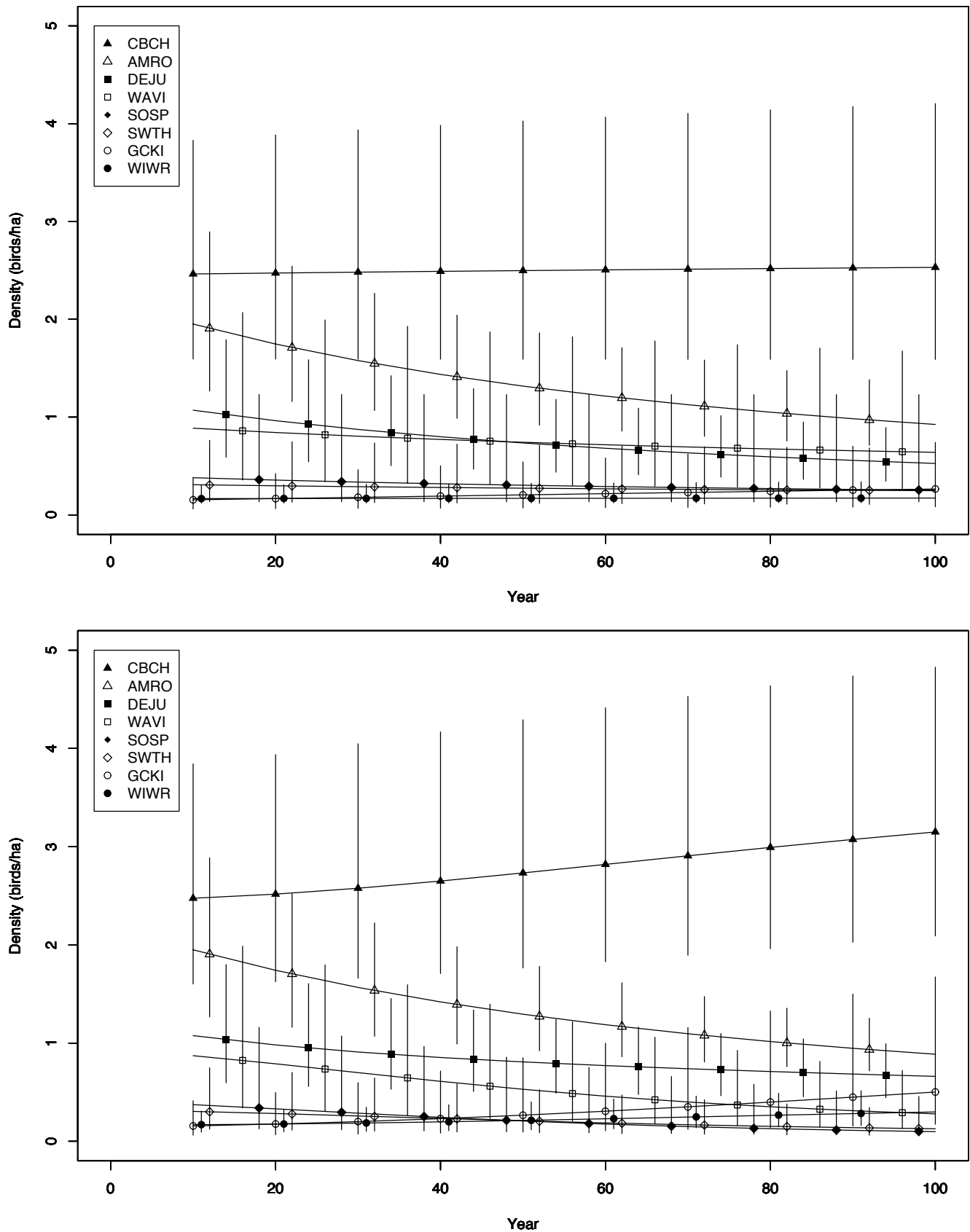


Figure 3. Forecasted avian densities, model-averaged forecasts. (Top) Restoration scenario 1, deciduous plants only. (Bottom) Restoration scenario 2, mixed deciduous and conifer planting. Species-specific trajectories are model-averaged forecasts (Equations 1 and 2) generated from models of growth in forest volume (Equation 3) and changes in percent deciduous (Equation 4). Species codes: Chestnut-backed Chickadee (CBCH), American Robin (AMRO), Dark-eyed Junco (DEJU), Warbling Vireo (WAVI), Song Sparrow (SOSP), Swainson's Thrush (SWTH), Golden-crowned Kinglet (GCKI), Winter Wren (WIWR).

Discussion

Forecasted Restoration Responses

Avian forecasts suggest deciduous specialists and generalists will occupy restored habitats rapidly, but conifer specialists will respond slowly. Forecasts show compensatory temporal changes in species densities, although changes in some species are obscured by forecast uncertainty (Figure 3). In the scenario without conifers, most species change little during the first century. Planting conifers hastens restoration progress, but after 100 years neither forest structure nor forecasted densities of conifer specialists approach management goals (Appendix Table A2) or densities in older conifer forests of the Elwha basin (compare Figure 1A and Figure 3B). Tree volumes in the oldest Elwha riparian forests exceed 100-year restoration forecasts by a factor of four, and total avian density in old forests exceeds 100-year avian forecasts by 60%.

Forecast results suggest that birds can provide measures of restoration success on two time scales. Responses of some species should be rapid, with mean densities significantly greater than zero (Figure 3). Concern about restoration effectiveness should be raised if chestnut-backed chickadees, American robins, and dark-eyed juncos do not consistently occupy restored habitats within 10–20 years. Conifer specialists can be used to evaluate long-term restoration success, but their responses may not be detectable for more than a century.

Scale of Avian Responses

We found greatest empirical support for local habitat characteristics as determinants of Elwha bird distributions and abundances. This may be due to Elwha landscape structure or relatively low dispersion rates of most of our focal species. Implications of this result are encouraging, because forest restoration is most easily conducted at a local scale and because

uncertainty in geomorphic processes precludes habitat forecasts at patch and landscape scales. The importance of tree volume and type to seven of eight species suggests birds respond strongly to forest age or successional stage. These results are consistent with reports from some systems, where avian abundances increased with stand maturity (Hobson and Bayne 2000, Vernier and Pearce 2005). Patch and landscape scales were more important in systems with greater natural and anthropogenic fragmentation (Mazerolle and Villard 1999, Saab 1999, Crozier and Niemi 2003). The relatively undeveloped landscape in Olympic National Park improves prospects for achieving avian restoration goals in the Elwha (Lindenmayer et al. 2010, Ortega-Alvarez and Lindig-Cisneros 2012).

Avian forecasts at the local habitat scale can be applied to anticipate responses at coarser scales. Slow succession to large volume conifer-dominated forests is expected on slopes above the Elwha floodplain, while younger deciduous forests will occupy frequently disturbed floodplain sites (Kloehn et al. 2008, Chenoweth et al. 2011). Precise locations of these areas will not be known until distributions of sediment terraces and deposits become established following dam removal and subsequent flood events (Bromley 2008, Chenoweth et al. 2011). Nevertheless, this bimodal distribution of forest age and structure will generate a mosaic of habitat patches and associated birds that should maximize avian diversity at a landscape scale.

Forecast Limitations and Uncertainty

Forecasting avian responses to restoration conducted on a watershed scale is difficult for reasons evident here. Biotic responses follow a sequence of processes whose individual uncertainties compound (Clark et al. 2001). Uncertainties in post-dam sediment and habitat distributions render

forecasting difficult (Doyle et al. 2003, Bromley 2008, Chenoweth et al. 2011). Spatially-explicit revegetation plans will not be available until the post-removal sediment distribution is known (Chenoweth et al. 2011). Sediment distribution will be determined by volume and timing of water entering the reservoir bed (Bromley 2008). River and stream flows will be determined by storm behavior and snowmelt in the years following dam removal (Grant et al. 2007), which cannot be forecasted precisely. Uncertainty in these geomorphic driving processes precludes spatially explicit biotic forecasts. For similar reasons, studies to anticipate sediment movement during dam removal employed physical models (Bromley 2008), and the reservoir revegetation plan is contingent on post-removal sediment distribution (Chenoweth et al. 2011). Due to these uncertainties, we restricted avian forecasts to a local habitat scale. This limitation was not unduly confining, because local variables were markedly more important than patch or landscape variables for most species (Appendix Table A6). Figure 2 may underestimate rates of forest growth in reservoir substrates due to harsh growing conditions (Chenoweth et al. 2011, Michel et al. 2011). Forecasted responses reported here may not apply to rare birds or other species of conservation concern, because we restricted modeling to common species due to sample size considerations.

Local forecasts confront four kinds of errors (Peters et al. 2004). First, our data may contain measurement errors in bird detections and distance estimates (Alldredge et al. 2007). Second, bird-habitat models may err by failing to consider relevant habitat variables or functional forms. This kind of error could be reduced by increasing the number or complexity of candidate models, but at the risk of greater error due to spurious relationships (Anderson and Burnham 2002, Peters et al. 2004). Third, errors in estimating model parameters occur with every

statistical method, measured here by standard errors plotted in Figure 1. For many bird species, such errors are unlikely to be resolved with different statistical methods or increased sampling effort (Seoane et al. 2005). Fourth, process error results from variability in avian abundances due to daily activity and inter-annual population dynamics. These errors combine in our forecasts to generate wide error bars in Figure 3.

This work can be applied or extended in several directions. First, avian forecasts can be made spatially-explicit after dam removal, when restored habitat distributions become known. Second, the hierarchical Bayesian approach of Russell et al. (2009) could be employed to model habitat occupancy of more species, including rare birds. Third, the role of birds as restoration agents can be measured, particularly their role in creating new habitats via seed dispersal (Robinson and Handel 1993, 2000, Wang and Smith 2002, Kohri et al. 2011, Uriarte et al. 2011). Birds can disperse seeds into exposed Elwha reservoir beds, thereby hastening establishment of native vegetation and reducing spread of invasive plants (McLaughlin, unpublished). Fourth, avian monitoring data can be compared with forecasts to evaluate restoration progress.

Conclusions

Avian forecasts reported here suggest both promising and sobering implications for Elwha restoration and other large dam removals. First, birds associated with deciduous forests and edge habitats are expected to colonize restored habitats rapidly, reaching management goals within a decade. This represents a positive restoration feedback, because these species include important zoochorous seed dispersers (McLaughlin, unpublished). Second, forecast uncertainty is large, due to both variability in avian habitat use and compounding

uncertainties in processes shaping restoration substrates. Third, planting conifers will hasten avian responses, but conifer specialists are not likely to reach pre-dam densities for centuries, until restored forests achieve large volumes. These conclusions echo familiar themes in Pacific Northwest restoration: anthropogenic impacts occur rapidly, some riparian components can be restored rapidly also, but complete forest restoration is comparatively slow.

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Carly J. Gelarden, Cardno ENTRIX, Inc., 200 1st Ave West, #500, Seattle, WA 98119

John F. McLaughlin (corresponding author), Department of Environmental Sciences, Huxley College of the Environment, Western Washington University, Bellingham, WA 98225-9181, wildlife.wvu@gmail.com

Table A1. Species detected during an avian inventory of the Elwha riparian zone (Gelarden 2008).

Common Name	Zoological Name
American Dipper	<i>Cinclus mexicanus</i>
American Robin	<i>Turdus migratorius</i>
Belted Kingfisher	<i>Ceryle alcyon</i>
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>
Black-throated Warbler	<i>Dendroica nigrescens</i>
Blue Grouse	<i>Dendragapus obscurus</i>
Brown Creeper	<i>Certhia americana</i>
Brown-headed Cowbird	<i>Molothrus ater</i>
Chestnut-backed Chickadee	<i>Poecile rufescens</i>
Common Raven	<i>Corvus corax</i>
Common Yellowthroat	<i>Geothlypis trichas</i>
Dark-eyed Junco	<i>Junco hyemalis</i>
Golden-crowned Kinglet	<i>Regulus satrapa</i>
Hairy Woodpecker	<i>Picoides villosus</i>
Hammond's Flycatcher	<i>Empidonax hammondi</i>
Harlequin Duck	<i>Histrionicus histrionicus</i>
MacGillivray's Warbler	<i>Oporornis tolmiei</i>
Northern Flicker	<i>Colaptes auratus</i>
Olive-sided Flycatcher	<i>Contopus cooperi</i>
Orange-crowned Warbler	<i>Vermivora celata</i>
Pacific-slope Flycatcher	<i>Empidonax difficilis</i>
Pileated Woodpecker	<i>Dryocopus pileatus</i>
Purple Finch	<i>Carpodacus purpureus</i>
Red Crossbill	<i>Loxia curvirostra</i>
Red-breasted nuthatch	<i>Sitta canadensis</i>
Rufous Hummingbird	<i>Selasphorus rufus</i>
Song Sparrow	<i>Melospiza melodia</i>
Spotted Sandpiper	<i>Actitis macularia</i>
Spotted Towhee	<i>Pipilo maculatus</i>
Steller's Jay	<i>Cyanocitta stelleri</i>
Swainson's Thrush	<i>Catharus ustulatus</i>
Townsend's Warbler	<i>Dendroica townsendi</i>
Varied Thrush	<i>Ixoreus naevius</i>
Violet-green Swallow	<i>Tachycineta thalassina</i>
Warbling Vireo	<i>Vireo gilvus</i>
Western Tanager	<i>Piranga ludoviciana</i>
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>
Willow Flycatcher	<i>Empidonax traillii</i>
Wilson's Warbler	<i>Wilsonia pusilla</i>
Winter Wren	<i>Troglodytes troglodytes</i>
Yellow Warbler	<i>Dendroica petechia</i>
Yellow-rumped Warbler	<i>Dendroica coronata</i>

Table A2. Habitat-specific density estimates for bird species with >10 detections. Numbers following habitat types are number of plots sampled. Numbers in body of table are avian density estimates (standard deviation): number of birds/ha. Density estimates were calculated using DISTANCE 5.0 Release 2 (Thomas et al. 2006).

Common Name	Zoological Name	Red Alder (47)	Big leaf Maple (45)	Shrub (16)	Douglas Fir (83)	Western Hemlock (33)
American Robin	<i>Turdus migratorius</i>	1.44 (1.65)	1.67 (1.66)	0.90 (0.85)	0.76 (1.47)	0.83 (1.33)
Black-headed Grosbeak*	<i>Pheucticus melanocephalus</i>	0.09 (0.14)	0.05 (0.12)	0.06 (0.15)	0.01 (0.05)	0.00 (0.00)
Brown Creeper*	<i>Certhia americana</i>	0.01 (0.03)	0.01 (0.04)	0.04 (0.11)	0.02 (0.06)	0.02 (0.06)
Black-throated Gray Warbler*	<i>Dendroica nigrescens</i>	0.01 (0.03)	0.01 (0.03)	0.00 (0.00)	0.01 (0.04)	0.01 (0.03)
Chestnut-backed Chickadee	<i>Poecile rufescens</i>	2.68 (3.55)	2.17 (3.16)	3.10 (5.29)	3.71 (4.44)	3.87 (4.09)
Dark-eyed Junco	<i>Junco hyemalis</i>	0.81 (1.07)	0.54 (0.86)	1.43 (1.59)	0.80 (1.16)	0.86 (0.93)
Golden-crowned Kinglet	<i>Regulus satrapa</i>	0.31 (1.03)	0.41 (1.01)	0.00 (0.00)	1.21 (2.15)	0.76 (1.65)
Hammond's Flycatcher	<i>Empidonax hammondi</i>	0.44 (0.66)	0.47 (0.66)	0.48 (0.75)	0.37 (0.56)	0.44 (0.52)
McGillivray's Warbler*	<i>Oporornis tolmiei</i>	0.01 (0.03)	0.01 (0.02)	0.00 (0.00)	<0.01 (0.01)	0.00 (0.00)
Pacific-slope Flycatcher	<i>Empidonax difficilis</i>	0.42 (0.62)	0.45 (0.66)	0.25 (0.31)	0.47 (0.73)	0.40 (0.76)
Song Sparrow	<i>Melospiza melodia</i>	0.27 (0.39)	0.23 (0.40)	0.14 (0.26)	0.06 (0.19)	0.03 (0.18)
Spotted Sandpiper*	<i>Actitis macularia</i>	0.01 (0.03)	0.00 (0.00)	0.03 (0.08)	0.01 (0.03)	0.01 (0.31)
Steller's Jay*	<i>Cyanocitta stelleri</i>	<0.01 (0.02)	0.00 (0.00)	0.01 (0.04)	0.01 (0.05)	0.02 (0.04)
Swainson's Thrush	<i>Catharus ustulatus</i>	0.22 (0.31)	0.26 (0.27)	0.10 (0.21)	0.07 (0.18)	0.08 (0.18)
Townsend's Warbler*	<i>Dendroica townsendi</i>	<0.01 (0.01)	<0.01 (0.01)	0.00 (0.00)	0.01 (0.02)	<0.01 (0.01)
Varied Thrush*	<i>Ixoreus naevius</i>	<0.01 (0.01)	<0.01 (0.01)	0.00 (0.00)	<0.01 (0.01)	<0.01 (0.01)
Warbling Vireo	<i>Vireo gilvus</i>	0.62 (0.72)	0.47 (0.54)	0.67 (0.65)	0.17 (0.42)	0.09 (0.25)
White-crowned Sparrow*	<i>Zonotrichia leucophrys</i>	0.06 (0.15)	0.04 (0.13)	0.15 (0.26)	0.04 (0.13)	0.03 (0.08)
Western Tanager*	<i>Piranga ludoviciana</i>	0.01 (0.03)	<0.01 (0.02)	0.00 (0.00)	0.01 (0.03)	0.01 (0.04)
Wilson's Warbler*	<i>Wilsonia pusilla</i>	0.15 (0.26)	0.16 (0.29)	0.14 (0.18)	0.05 (0.16)	0.02 (0.10)
Winter Wren	<i>Troglodytes troglodytes</i>	0.20 (0.35)	0.24 (0.38)	0.12 (0.21)	0.38 (0.50)	0.52 (0.49)
Yellow Warbler*	<i>Dendroica petechia</i>	0.02 (0.05)	<0.01 (0.02)	0.06 (0.10)	<0.01 (0.01)	0.01 (0.04)
TOTAL		7.78	7.19	7.68	8.17	8.01

*Density estimates for these species were generated using detection probabilities from the Olympic National Park avian inventory (Siegel et al. 2004).

Table A3. Habitat variables used to model avian abundances in the Elwha riparian zone. Local habitat variables were measured during avian inventory sampling (Gelarden 2008). We calculated patch and landscape metrics for each sample point by applying FRAGSTATS (McGarigal et al. 2002) to the OLYM habitat data layer (Pacific Meridian Resources 1996). We computed landscape metrics using a moving 1 km² window. Details are in Gelarden (2008) and McGarigal and McComb (1995).

Variable	Description
Local habitat structure	
CC (%)	Mean percent forest canopy cover within the plot.
DECID (%)	Percent by volume of deciduous trees within the measured plot.
VOL (m ³)	Total tree volume (height x diameter) within the measured plot.
Patch variable	
PA (ha)	Area of the sampled patch.
PARA	Ratio of patch perimeter (m) to area (m ²); shape complexity.
EDGE (%)	Patch edge contrast index
Landscape variable	
PROP	Proportion of landscape consisting of a given habitat type.
PR	Patch richness, number of habitat patches within landscape.
IJI (%)	Interspersion/juxtaposition index; landscape heterogeneity.

Table A4. Results of avian-habitat model selection, using Akaike's information criterion. Model selection results are listed for each model in the confidence set for a given species. Model variables are defined in Table A3. $n = 224$. K : number of parameters; ΔAIC : rescaled AIC score, $\Delta AIC_i = AIC_i - \min(AIC)$; w : Akaike weight.

Species	Model	K	AIC	ΔAIC	w	R^2
<i>Coniferous Species</i>						
Golden-crowned Kinglet	VOL+IJI	3	180.4	0	0.992	0.337
Winter Wren	DECID+ IJI	3	219.4	0	0.667	0.100
<i>Deciduous Species</i>						
Song Sparrow	VOL+IJI	3	166.4	0	0.530	0.225
	DECID+PA	3	167.8	1.49	0.251	0.219
Swainson's Thrush	VOL+DECID	3	170.3	0	0.214	0.122
	VOL+IJI	3	170.6	0.25	0.189	0.121
	DECID	2	170.7	0.39	0.176	0.109
	DECID+PA	3	193.6	0	0.337	0.209
Warbling Vireo	DECID+EDGE	3	194.4	0.84	0.221	0.206
	VOL+DECID	3	194.7	1.13	0.192	0.205
	DECID+PROP	3	195.0	1.44	0.164	0.204
<i>Generalist Species</i>						
American Robin	VOL+IJI	3	250.7	0	0.680	0.124
Chestnut-backed Chickadee	PROP	2	308.7	0	0.256	0.023
	DECID	2	310.0	1.30	0.133	0.019
	DECID+IJI	3	310.6	1.97	0.096	0.024
	IJI	2	311.2	2.56	0.071	0.015
	DECID+EDGE	3	311.3	2.65	0.068	0.021
Dark-eyed Junco	VOL+DECID	3	226.0	0	0.516	0.084
	VOL+IJI	3	227.6	1.61	0.232	0.077
	VOL	2	228.3	2.36	0.158	0.066

Table A5. Fitted parameter values for habitat models in confidence sets for eight species. Model variables are defined in Table A3. Parameters are defined in equations 1–2. Parameter values are listed for each model in the confidence set for a given species.

Species	Model ^a	Constant	β_1	β_2
<i>Coniferous Species</i>				
Golden-crowned Kinglet	VOL+IJI	0.4359	0.0005	-0.0609
Winter Wren	DECID+ IJI	0.6223	-0.0077	-0.0243
<i>Deciduous Species</i>				
Song Sparrow	VOL+IJI	-4.0540	-0.0009	0.0748
	DECID+PA	-1.8444	0.0140	-0.0160
Swainson's Thrush	VOL+DECID	-1.4178	-0.0004	0.0111
	VOL+IJI	-2.2051	-0.0006	0.0356
	DECID	-1.9730	0.0150	—
Warbling Vireo	DECID+PA	-1.4932	0.0153	-0.0054
	DECID+EDGE	-1.8524	0.0150	-0.0086
	VOL+DECID	-1.2206	0.0005	0.0145
	DECID+PROP	-1.0915	0.0121	-0.0226
<i>Generalist Species</i>				
American Robin	VOL+IJI	-0.7309	-0.0007	0.0198
Chestnut-backed Chickadee	PROP	-0.4991	0.0142	—
	DECID	0.0296	-0.0050	—
	DECID+IJI	0.3475	-0.0037	-0.0091
	IJI	0.4146	-0.0150	—
	DECID+EDGE	0.0383	-0.0038	-0.0033
Dark-eyed Junco	VOL+DECID	0.4025	-0.0008	-0.0060
	VOL+IJI	0.6536	-0.0007	-0.0153
	VOL	-0.0819	-0.0006	—

^aVariables are defined in Table 1.

Table A6. Relative importance of nine habitat variables to habitat selection by eight bird species. Relative importance is the Akaike weight (w_i) of the univariate model containing the specified variable, where w_i were calculated over the candidate set of nine univariate models. Variables are defined in Table A3. Species codes: Golden-crowned Kinglet (GCKI), Winter Wren (WIWR), Song Sparrow (SOSP), Swainson's Thrush (SWTH), Warbling Vireo (WAVI), American Robin (AMRO), Chestnut-backed Chickadee (CBCH), Dark-eyed Junco (DEJU).

Species	CC	VOL	DECID	PA	PARA	EDGE	PROP	PR	IJI
GCKI	0.000	0.673	0.000	0.000	0.000	0.000	0.000	0.010	0.318
WIWR	0.001	0.008	0.525	0.001	0.000	0.006	0.050	0.020	0.389
SOSP	0.000	0.001	0.039	0.062	0.000	0.000	0.068	0.000	0.830
SWTH	0.000	0.061	0.709	0.005	0.000	0.001	0.096	0.004	0.123
WAVI	0.000	0.001	0.837	0.000	0.000	0.001	0.161	0.000	0.000
AMRO	0.000	0.992	0.000	0.000	0.000	0.000	0.003	0.000	0.004
CBCH	0.026	0.042	0.220	0.016	0.099	0.016	0.422	0.013	0.115
DEJU	0.004	0.991	0.000	0.000	0.001	0.000	0.000	0.001	0.000