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PROJECTING THE BIOLOGICAL CONDITION OF STREAMS UNDER ALTERNATIVE SCENARIOS OF HUMAN LAND USE

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Abstract. We present regression models for estimating the status of fish and aquatic invertebrate communities in all second to fourth–order streams (1:100 000 scale; total stream length = 6476 km) throughout the Willamette River Basin, Oregon (USA). The models project fish and invertebrate status as a function of physiographic, land-use/land-cover, and stream flow variables, with the latter two sets of variables subject to change under historical and alternative future scenarios of human development. Models are developed using sample data collected between 1993 and 1997 from 149 wadeable streams in the basin. Model uncertainties are propagated through model projections and into aggregated estimates of regional status. The projections show no significant change in basin-wide status in year 2050, relative to Circa 1990, for scenarios either of increased human development or continuation of current development trends, because landscape change under these scenarios is dominated by conversion of agricultural land to rural residential and urban uses, and because these changes affect only a small percentage of the basin. However, under a scenario of increased conservation, regional medians of biotic status indicators are projected to improve by 9–24% by year 2050. None of the changes projected between Circa 1990 and year 2050 is as large in magnitude as the decline in status projected to have occurred between the time of pre-European settlement and Circa 1990.

Key words: land use; model projection; riparian; scenario; stream condition; watershed; Willamette Basin.

Introduction

The ways in which altered land and water uses impact streams are well known. Water withdrawals for agriculture, municipal, and other uses reduce in-stream flows (Covich 1993, Postel 2000), leading to reduced habitat for stream biota. Conversion of lands for agricultural, residential, or urban uses is generally accompanied by higher peak flows, lower summer flows, higher stream temperatures, and increased loadings of fine sediments, nutrients, and contaminants (Karr and Schlosser 1978, Klein 1979, Schlosser 1991, Meyer 1997). These linkages between stream ecosystems and human uses of land and water are well understood in a qualitative sense, but they can be complex, difficult to observe, and highly variable over space and time. Thus, while quantitative models of the linkages have obvious value to stream management efforts, development of such models remains a major challenge.

We took up the challenge of building such models in order to estimate the effects of land use changes on the biological condition of streams in the Willamette Basin, Oregon. As a component of the Alternative Futures project (Baker et al. 2004), our task was to make spatially explicit projections for all streams in the basin's river network, and then to summarize and compare these projections over large subregions of the basin. In this paper, we describe our modeling approach and the resulting models, and we also discuss model uncertainties and their propagation into regional-scale projections of stream condition. Other project components evaluated effects of changing land use on water availability in the basin (Dole and Niemi 2004), agricultural practices (Berger and Bolte 2004), and terrestrial wildlife (Schumaker et al. 2004).

Our modeling goal was primarily that of projection. We wished to project attributes of biological communities in streams, rather than of water quality or physical habitat, because fish and macroinvertebrate communities integrate the effects of the multiple stressors that accompany human-induced changes in land use, and because they are also related more closely to desired human uses of streams (Fausch et al. 1990, Karr

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2000, National Academy of Sciences [NAS] 2001, Wang et al. 2001). Thus, we focused on assessing biological stream indicators that might be of interest to local decision makers rather than identifying and modeling those stream attributes that are particularly sensitive to land use change. Because we wished to aggregate our regional-scale assessments from explicit projections for every stream in the basin, potential driving variables for our models were restricted to those that could be estimated from digital maps having complete basin coverage.

Taken together, these problem specifications and constraints strongly suggested that we build and apply simple statistical models, rather than mechanistic models. Complex mechanistic models have been developed and used for physical or chemical attributes of stream ecosystems but few are available for biological endpoints (NAS 2001). In addition, we agree with Hilborn and Mangel (1997; see also Peters 1991 and NAS 2001) that simpler models are often more reliable for prediction in a context of limited data and incomplete process-level knowledge.

There is a substantial and growing literature based on empirical associations between landscape and stream ecosystem attributes. A few such studies (Barton et al. 1985, Porter et al. 2000) have focused on making predictions. However, most have had the more modest goals of exploring which land uses (e.g., agriculture, urbanization, or forestry) and which landscape components (e.g., riparian corridor or whole watershed) are most strongly associated either with stream water quality and physical habitat (e.g., Osborne and Wiley 1988, Hunsaker and Levine 1995, Johnson et al. 1997, Herlihy et al. 1998, Jones et al. 2001) and/or with fish and invertebrate community composition (e.g., Steedman 1988, Roth et al. 1996, Lammert and Allen 1999, Sponseller et al. 2001, Stewart et al. 2001, Tong 2001, Wang et al. 2001).

In this paper, we take association-based models to their logical extreme. We use them to project the outcomes of historical and alternative future changes in the human footprint on the landscape. In doing so, we must assume that our regression models will faithfully represent a complex web of causal relationships. In some form, this assumption is intrinsic to any predictive effort, and mechanistic models generally offer greater faith in its realism than do regressions. However, by drawing heavily on current knowledge in applied stream ecology, we have tried to formulate explanatory variables and regression equations that are the best available surrogates for the multitude of mechanisms linking human impacts on watersheds to their streams.

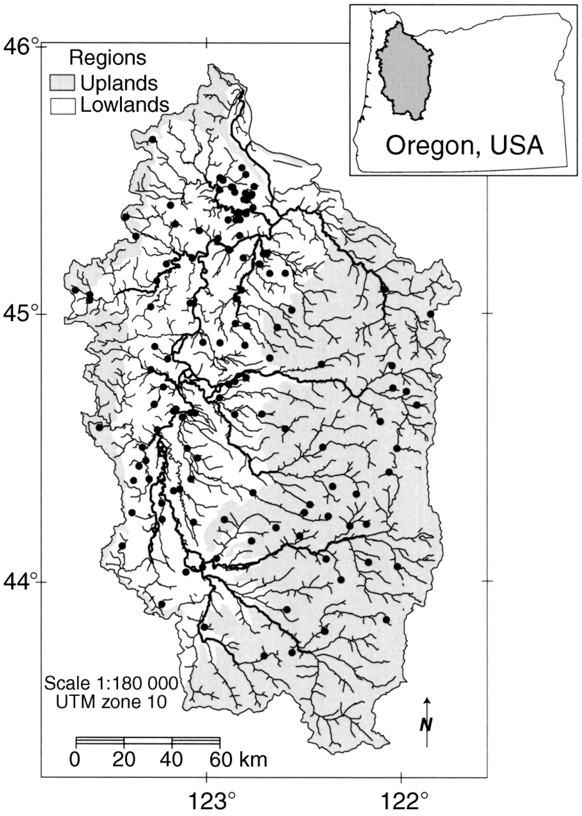

FIG. 1. The Willamette Basin stream network. Second- to fourth-order streams are thin lines, and thicker lines are fifth-order rivers or larger. Upland areas are composed of the Coast Range (to the west) and Cascades (to the east) ecoregions, and lowlands are defined as the Willamette Valley ecoregion. Points locate fish sampling sites used in model development.

After developing our regression models, we estimated the near-current status of the biota in basin streams, based on a Circa 1990 scenario of basin-wide land use and land cover. We then estimated what the biological condition of streams would have been under a historical scenario that describes the basin's land cover prior to EuroAmerican settlement (early 1800s). Finally, we projected stream conditions in year 2050 for each of three alternative scenarios of future human land and water use change from 1990 to 2050. The Plan Trend 2050 scenario assumes that present-day land and water use policies and trends continue, the Development 2050 scenario relaxes current land use restrictions to allow freer rein to market forces, and the Conservation 2050 scenario assumes more restrictive policies emphasizing ecosystem protection and restoration. All three scenarios make the realistic assumption that the 1990 human population of the basin will double by 2050. Hulse et al. (2004) provide further information on these future and historical scenarios.

METHODS

Study basin

The Willamette River drains a basin of 29 728 km^2 (Fig. 1). We focus on a subset of the basin's stream network, defined as Strahler orders 2–4 on 1:100 000 scale maps. In the Willamette Basin, these streams are generally wadeable during summer low flow, but still provide fish habitat potential. They comprise 33% of the basin's total stream length of 21 200 km. First-order streams, comprising 61% of the total network length, were too numerous, and their watersheds too small, for us to model them basin wide.

Streams of the basin vary widely, from the warmer, low-gradient systems with clay/sand substrates of the Willamette Valley, to cooler, high-gradient streams with gravel and boulder substrates of the Cascade Range on the basin's eastern rim and of the Coast Range mountains on the western rim (Fig. 1). The basin has a temperate Mediterranean climate with dry summers and wet winters, and annual precipitation ranges from ~1 m/yr in the valley to ~4.5 m/yr at the crests of both mountain ranges (Laenen and Risley 1997). Stream runoff peaks in winter and spring, with higher flows extending into summer for streams draining snow accumulations at higher elevations of the Cascade Range.

Fish communities tend to have fewer species in high-elevation cool-water streams, and more species, many of which are not native, in the warmer Valley systems (Altman et al. 1997). Basin streams support a diverse fauna of macroinvertebrates, ranging from the Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa that dominate higher-elevation forested watersheds to the more tolerant Diptera and Oligochaete taxa observed in warmer and silty streams of the Valley (Altman et al. 1997, Li et al. 2001).

Stream network, riparian corridors, and watersheds

We made model projections for each of 4045 model reaches, of Strahler orders 2, 3, and 4 and between 100 and 5000 m in length. Model reaches were defined from arc segments of the Pacific Northwest River Reach coverage, which is based on 1:100 000 scale maps (Pacific State Marine Fisheries Service 1997). Our usable model reaches totaled 6476 km in length and accounted for 93% of the basin's second- to fourth-order streams (Fig. 1).

We delineated the upstream watersheds of all model reaches using standard Arc/Info GRID operations in batch mode. Delineations were based on a whole-basin digital elevation model (DEM) of 30-m resolution that was georectified to known locations and adjusted to improve alignments between its derived drainages and the stream network (Saunders 1999, Hulse et al. 2002). Streams were classified as lowland streams if the majority of their watershed was in the Willamette Valley ecoregion, as defined by Omernik (1987), or upland streams if the majority of the watershed was in the Coastal or Cascades ecoregion (Fig. 1; Omernik 1987)

For each modeled reach, we defined three potential areas of influence for land use/land cover (LULC) effects: (1) the entire watershed, (2) a riparian corridor 120 m wide (each side) extending along all upstream first- to fourth-order reaches, and (3) a 30 m wide (each side) ''local'' riparian corridor extending upstream along all first- to fourth-order reaches that lay within a circle 10 km in radius and centered on the modeled reach. The 120 m corridor was deemed wide enough to capture all possible riparian effects from the upstream network. As an alternative, LULC within the local riparian corridor's width and extent has been shown to be strongly correlated with stream condition in Willamette Valley agricultural streams (P. D. Lattin, P. J. Wigington, Jr., T. J. Moser, B. E. Peniston, D. R. Lindeman, and D. R. Oetter, *unpublished manuscript*). Riparian corridors were constructed using Arc/Info buffering functions on the vector network.

Indicators of stream condition: fish and invertebrate communities

Indicators.—We selected five key indicators of stream condition, based on fish and macroinvertebrate communities, as model response variables. Native fish species richness reflects the overall biodiversity of the system, and one or more native species can be lost when human disturbances result in higher temperatures, siltation, toxic contaminants, introductions of non-native fish species, or other changes in stream habitats (Hughes et al. 1998). Second, we modeled an index of biotic integrity (IBI), designed to assess the alteration in composition and functional organization of a fish community, relative to that expected in the absence of human disturbance (Karr 1981, Hughes et al. 1998). The IBI, which has so far been developed only for lowland streams in the basin, is expressed on a scale of 0 to 100 with low values representing greater alteration relative to undisturbed communities (Hughes et al. 1998). We also modeled coastal cutthroat trout (*Oncorhynchus clarkii*) abundance because this species is the most widely distributed salmonid in the basin. Although several anadromous salmonids do reproduce and rear in basin streams, they appeared in only 15% of our stream samples, and we did not attempt to model them.

Fourth, we developed a model for EPT richness, defined as the total number of Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies) genera in the macroinvertebrate community, an indicator widely used in biomonitoring because EPT taxa are generally intolerant of silt, warm temperatures, and water quality degradation (Barbour et al. 1999). And finally, we modeled the Willamette invertebrate observed/expected (WINOE) index, defined as the percentage of macroinvertebrate taxa at a site that were also found at two or more minimally disturbed reference sites. Indices comparing observed taxa lists to those expected at physiographically similar reference sites are used as the basis for a widely applied inver-

TABLE 1. Fixed and scenario variables for stream condition models.

Variable	Description
Fixed variables (constant across scenarios)	
WSAREA	watershed area (ha)
ELEV	mean reach elevation (m)
LENGTH	reach length (m)
GRADIENT	mean reach gradient (%)
ORDER	Strahler order, 1:100,000 scale
PRECIP	long-term mean annual precipitation (mm)
RIV5DIS	network distance (km) to nearest fifth-order river
DIVDIS	distance (km) to watershed divide along stream network
LAT, LON	latitude, longitude (degrees)
QMEAN	mean annual discharge (m^3/s)
STRMPOW	stream power index, QMEAN × GRADIENT
Scenario variables (changing across scenarios)	
AGRC	all agriculture: row and field crops, orchards, berries, vineyards, pasture, fallow, Christmas trees
DVLP	‘‘developed’’: urban and rural residential, commercial, industrial, roads
CFOR	closed forest: closed-canopy conifer and hardwood stands, including plantations and woodlots
CONM	mature conifer stands >80 yr old
HDWD	hardwoods, closed or semi-closed stands
QSUM80	80% exceedence flow (m^3/s), mean of July and August

Note: LULC variables are areal percentages, estimated upstream of each reach for the 120-m riparian corridor, 30-m local corridor, and whole watershed.

tebrate assessment process (Moss et al. 1987, Wright et al. 1993, Hawkins et al. 2000).

Although these five indicators are not entirely independent, each was chosen to emphasize a different aspect of stream biotic condition and was expected to respond somewhat differently to disturbance-related explanatory variables. We developed a different model for each indicator, and we jointly interpret the projections of all five in overall assessments of stream condition.

Data sources.—To develop our models, we combined fish and invertebrate samples from six separate studies in order to obtain adequate spatial coverage and a large enough sample size for multiple regression analysis (Fig. 1; Friesen and Ward 1996, Herlihy et al. 1997, Waite and Carpenter 1999, Herger and Hayslip 2000; P. D. Lattin, P. J. Wigington, Jr., T. J. Moser, B. E. Peniston, D. R. Lindeman, and D. R. Oetter, *unpublished manuscript*). Samples were collected between 1993 and 1997 from 149 first- to fourth-order stream sites. Variance components analysis (Urquhart et al. 1998) showed that between-site variances of all indicators were at least 10 times greater than between-year variances, so we concluded that combining data across the five sampling years spanned by the six studies added relatively little uncontrolled temporal variation to our data and models.

All six studies sampled fish communities using backpack electroshocking during the summer (July through September) low-flow season. Sampling protocols specified by EPA’s Environmental Monitoring and Assessment Program (Lazorchak et al. 1998) were followed at 99 sites. At an additional 30 sites, electroshocked surface areas were within a factor of two of EPA specifications. These combined data sets (129 sites) were used to develop models of native fish richness and fish IBI. Eighty-two of the sites were lowland streams, while the remaining 47 were upland (Fig. 1). An additional 20 sites (total 149 sites) were used for cutthroat trout abundance modeling by employing the catchability model of Bayley and Dowling (1993) to estimate trout density from number of fish caught, sampling effort and stream physical features.

Benthic macroinvertebrate communities were sampled during summer low flow at 55 lowland and 50 upland sites using either kick net or Surber samples passed through a 500 μm sieve. Because the number of individual samples taken per reach varied across studies, we simulated a consistent sampling effort by compositing multiple samples at each site to approximate a 500-organism count.

Explanatory variables: land use/land cover, physiography, and stream flow

We restricted our candidate explanatory variables to those that could be derived from spatial databases having basin-wide coverage, thus ensuring the availability of predictor data for every modeled reach. These candidates fell into two broad groups (Table 1). Land use/land cover (LULC) and summer stream flow variables were used to represent, either directly or indirectly, all human impacts on streams that have occurred since the time of pre-European settlement. In making our model projections, these ‘‘scenario’’ variables were assumed to change among alternative scenarios as described by Hulse et al. (2004). A second group of ‘‘fixed’’ candidate variables described the physiographic and annual stream flow characteristics of each reach and were assumed to remain fixed for each model reach across all scenarios.

Scenario variables.—We aggregated the 65 specific LULC classes identified by Hulse et al. (2002; see also Oetter et al. 2000) into five broad categories of land use that might be expected to have distinctly different effects on stream biota (Table 1). Areal percentages for each LULC category in Table 1 were estimated for each of the three potential areas of influence (120-m riparian corridor, local 30-m corridor, and whole watershed).

We also evaluated whether more complex expressions of LULC would produce stronger models. We calculated cumulative areas of influence as weighted averages of LULC percentages in the local 30-m corridor, in the area between the local 30-m and the larger 120-m corridors, and in the watershed beyond the 120-m corridor. Three different weightings were considered: 1:1:1, 3:2:1, and 7.5:1.5:1. In addition, the developed LULC class (DVLP) was subdivided into low- and high-intensity uses, and the agricultural LULC class (AGRC) into three subgroups expected to have relatively small, moderate, and large effects on stream condition. Composite agriculture and developed LULC percentages were then estimated by weighting their respective subgroups according to the severity of their expected effects. We also estimated a composite ‘‘natural vegetation’’ variable which weighted older forest classes more heavily than younger classes, which in turn were more heavily weighted than non-forest classes of woody vegetation and natural grasslands.

Finally, we estimated the expected stream flow during dry summer conditions (QSUM80; Table 1). We first estimated the ‘‘natural’’ flow for 32 gauged watersheds (<250 km^2 in area) in the basin as the average of their long-term observed 80% exceedance flows during summer, minus estimates of current water consumption for their watersheds (Dole and Niemi 2004). These estimates were used to develop a linear regression model ($R^2 = 0.82$) for log(natural flow) as a function of log(WSAREA) and PRECIP (Table 1), which was assumed to remain fixed across all scenarios. Actual dry-year summer flows were then estimated for all reaches and scenarios by subtracting their scenario-specific watershed consumption estimates (Dole and Niemi 2004) from their regression-estimated natural flows.

Fixed variables.—Variables describing watershed size, steepness, elevation, and network location (Table 1) were estimated from appropriate overlays of the delineated watershed, DEM, and vector stream network. Long-term mean annual precipitation for each watershed was estimated by spatially averaging PRISM model estimates (4-km grid resolution) within the watershed boundary (Taylor et al. 1993, Daly et al. 1994). Long-term annual mean flow (QMEAN) was estimated from a linear regression ($R^2 = 0.98$) of log(QMEAN) on log(WSAREA), PRECIP, and stream gauge elevation. An index of stream power (STRMPOW = QMEAN × GRADIENT) was also estimated to represent the overall potential for streambed alteration.

Model development

We developed regression models using each of our five indicators as responses. For each indicator, separate models were initially developed for upland and lowland streams. Where possible, models for the two regions were then replaced by a single basin-wide model through the inclusion of physiographic variables representing major differences between the regions. Exploratory models showed that linear regression was adequate to model all endpoints except cutthroat trout abundance. The variance of cutthroat trout abundance increased rapidly with increasing projected mean abundance in initial models, so we formulated a negative binomial generalized linear model to represent an overdispersed Poisson error structure for this indicator (McCullagh and Nelder 1989, Venables and Ripley 1997).

Taken together, the large number of available explanatory variables (Table 1), their intercorrelations, and options for modeling effects (additive and/or interactive) all made it hazardous to rely solely on automated methods for variable selection. Instead, we applied best-subsets variable selection (RSQUARE option; SAS 1989) to a random two-thirds subset of the data using the candidates of Table 1 (Myers 1990, Ramsey and Schafer 1997). This effort produced short lists of low-order models that differed little in their quality of fit. We also explored many special-interest models such as those involving complex LULC and area-of-influence explanatory variables. To reduce our lists to a few best models, we discounted models with ‘‘wrong’’ signs induced by collinearity of explanatory variables (Myers 1990), and also examined residual plots, as well as the qualities of predictive fit (as measured by bias and mean-squared error) on the remaining one-third of the data. Two or more ‘‘best’’ models for each indicator were refitted to the entire data set. Because we explored a large number of models for each indicator, the significance of individual model terms is exaggerated by standard tests (Harrell 2001), and we retained individual terms in our best models only if their coefficient magnitudes were at least twice the coefficient standard errors. In this paper we report, for each indicator, the structure and complete projection results only for a single slightly preferred model, but we also illustrate the sensitivity of our projections to selected variations in model structure.

Model projections and uncertainty propagation

For each of the 4045 model reaches, we used the models to project each stream condition indicator under each of the five scenarios. Each reach was viewed as a homogeneous unit, so that a single projected value of stream condition was attributed to the entire reach.

TABLE 2. Final models used for projection of stream condition indicators under alternative scenarios.

Indicator	Region	Model	R^2	N
Fish IBI	lowland	$\underset{(4.2)}{67.86} - \underset{(0.07)}{0.45} \times \text{AGRC} - \underset{(0.07)}{0.40} \times \text{DVLP}$	37	82
Native fish richness†	lowland + upland	$\underset{(0.41)}{0.36} + \underset{(0.24)}{0.52} \times \text{ORDER} + \text{LDIS} \times [\underset{(0.66)}{4.85} - \underset{(1.33)}{8.52} \times \text{LEL300}$ $- \underset{(0.09)}{0.18} \times \text{GRADIENT} - \underset{(0.006)}{0.038} \times \text{AGRC} - \underset{(0.007)}{0.026} \times \text{DVLP}]$	70	129
WINOE‡	lowland	$100 \times [\underset{(11.52)}{42.79} - \underset{(0.09)}{0.34} \times \text{LON} + \underset{(0.04)}{0.11} \times \text{SPOW}$ $- \underset{(0.0008)}{0.0042} \times \text{AGRC} - \underset{(0.0009)}{0.0034} \times \text{DVLP}]$	52	55
Invertebrate EPT‡	lowland	$\underset{(1.32)}{0.29} + \text{SPOW} \times [\underset{(0.82)}{6.51} - \underset{(0.012)}{0.069} \times \text{AGRC} - \underset{(0.014)}{0.062} \times \text{DVLP}]$	61	55
Cutthroat trout abundance	lowland + upland	$\exp[\underset{(0.47)}{7.59} + \underset{(0.007)}{0.027} \times \text{WSAREA} - \underset{(0.010)}{0.059} \times \text{AGRC} - \underset{(0.010)}{0.040} \times \text{DVLP}]$	⋯	149

Notes: AGRC and DVLP in all models are percentages of agriculture and developed land, respectively, in a 120-m riparian corridor along the entire upstream network. Other explanatory variables are defined in Table 1. N = number of sites used for final model fit, and R^2 = percentage of indicator variance explained by each model (not available for negative binomial cutthroat trout model). IBI = index of biotic integrity, WINOE = Willamette invertebrate observed/expected index, and EPT = Ephemeroptera, Plecoptera, Trichoptera. Standard errors of coefficients are in parentheses under each coefficient. Footnotes identify transformed variables.

† LDIS = $\log_{10}$(DIVDIS). LEL300 = $\log_{10}$(ELEV) − $\log_{10}$(300), if ELEV > 300 m. Otherwise LEL300 = 0.

‡ SPOW = $(\text{STRMPOW} + 0.01)^{0.25}$.

For multiple linear regression models, the variance of an individual prediction has a component due to the model error term, as represented by the residual mean squared error, as well as a component due to the estimation uncertainty of the regression coefficients, as represented by their estimated covariance matrix (Myers 1990). Using a Monte Carlo approach, we added both sources of uncertainty to each reach projection and then propagated the uncertainties into the distributions and summary statistics of the projections across all reaches in a region for both the lowland region (1408 reaches, totaling 2389 km) and the upland region (2637 reaches, totaling 4087 km).

In each Monte Carlo trial, we made projections for all 4045 reaches under all five scenarios. For each trial, we randomly drew a single set of model coefficients from their estimated multinormal distribution and employed that set for all projections. Separate randomly drawn model errors were then added to each individual projection in the trial. This approach emulates prediction variance formulae for functions of multiple predictions (Miller 1981). Still within one trial, for each scenario we then computed the cumulative distribution function (CDF) of the projected indicator across all reaches in a region, where each reach is weighted by its length (Särndal et al. 1992). The process was repeated for 1000 such trials, generating a set of 1000 CDFs for each scenario.

For each indicator, projected CDFs had very similar shapes across all scenarios. Thus, the weighted median, defined as the 50th percentile of the weighted CDF, is an adequate regional summary statistic for a scenario outcome. To compare an alternative scenario's projected distribution to that of the baseline Circa 1990 scenario, we computed the difference in weighted medians of the two scenarios within each Monte Carlo trial. We then report the mean of these differences across the 1000 trials, along with their fifth and 95th percentiles as 90% confidence limits.

RESULTS AND DISCUSSION

Best models

The ''best'' projection models contained from two to five explanatory variables (Table 2). Variance inflation factors (Myers 1990) were less than 2.5 for all coefficients on model terms involving scenario variables. In addition, product–moment correlations between explanatory terms involving scenario variables in the Table 2 models were all <0.65 in magnitude. Thus, although multicollinearity inhibited the selection of a single best model, we concluded that collinearity within each of the Table 2 models did not seriously impair either their coefficient uncertainties or our assumptions of shifts in covariance structure that are a consequence of alternative scenarios.

In the fish IBI model, no fixed variables added noticeable explanatory power to that obtained from riparian agriculture and development (Table 2). The model thus supports the original design of this IBI, in which the index scoring itself has been adjusted for variation across major natural gradients (Hughes et al. 1998).

Exploratory scatterplots suggested that an upper limit to native fish richness could be modeled as a linearly increasing function of watershed size for our sites. As a result, we used interference-interaction expressions of the form $\beta_1 X - \beta_2 ZX$ to model the combined effects of limiting (watershed size index; X) and nonlimiting (other variables; Z) factors on native fish richness (Table 2; Neter et al. 1996, Cade et al. 1999). In the Table 2 model, log-transformed distance to the divide (DIVDIS) acts as an index of watershed size that provides a better-fitting model than does watershed area itself. The positive coefficient β_1 is the net effect of multiple size-related factors, including an underlying positive species–area relation, the effects of the larger habitat volumes that were sampled in larger streams, and the probable decrease in catchabilities and resultant species detectabilities within those larger volumes (Bayley and Peterson 2001). Estimated coefficients on the interaction terms were negative, supporting the interference concept. Inclusion of elevation and gradient terms gave a single fish richness model suitable for both upland and lowland streams. The elevation term in this model uses a threshold transformation to express the sudden decline in richness as stream elevation increased beyond 300 m, a pattern we observed in scatterplots of richness vs. elevation.

An interference–interaction model, this time using the stream power index as the limiting factor, also produced a strong model for EPT richness (Table 2). Stream power is a major factor controlling streambed composition (Leopold et al. 1964) and thus is expected to greatly influence the benthic invertebrate community.

Like fish IBI, indices of the WINOE type are intended to be preadjusted for natural gradients, if they can be developed from an adequate spectrum of minimally disturbed reference sites (Hawkins et al. 2000). But because nearly all watersheds on the valley floor are dominated by agriculture and developed uses, our only available minimally disturbed lowland reference sites were on steeper foothill streams having higher stream power. We were not surprised, therefore, to see a positive stream power effect in our WINOE model (Table 2). This example illustrates our experience that some degree of confounding between ‘‘natural’’ and ‘‘disturbance’’ effects appears inevitable when one is developing regression models from real landscapes.

In upland streams, we failed to find any significant correlations between either WINOE or EPT richness and any of our LULC or summer stream flow variables, after accounting for stream gradient, elevation and other physiographic effects. Thus we did not develop predictive invertebrate models for upland streams.

We obtained reasonable terms and coefficients for the cutthroat trout abundance model (Table 2). However, our data had a high percentage of zero abundances at lowland sites and, although trout were common at upland sites, their abundances varied greatly. As a result, the fitted model's estimated standard deviation of abundance in a reach exceeded the predicted mean by a factor of at least three, for all feasible settings of the explanatory variables. Propagation of uncertainties this large into regional medians produced confidence bounds so wide that scenario comparisons for cutthroat trout had little meaning, and we do not report them here.

LULC effects.—All of the models in Table 2 project stream condition as a function of agriculture and development in the 120-m riparian corridor. Models based on LULC within the 120-m riparian corridor fit consistently better than did corresponding models based on whole-watershed LULC and also fit better in most cases than models based on local riparian LULC. In all cases, model R^2 differed by <0.10 units across the three areas of influence. Ultimately, we employed the 120-m rather than local riparian corridor LULC estimates for our Table 2 models and baseline projections, in part because of our concern for the accuracy of our thematic-mapper-based LULC estimates within the narrower 30-m corridor. Our cumulatively weighted estimates of LULC also did not measurably improve, and sometimes decreased, model fits relative to 120-m corridor LULC, thus giving little justification for using this more complex area of influence.

Agricultural and developed LULC were negatively associated with stream condition, as expected, but model responses were not strong (Table 2). For example, with all physiographic variables held fixed at their regional mean values, an increase in riparian-corridor agriculture from 25% to 60%, accompanied by an increase in developed land use from 5% to 10%, yielded predicted IBI decreasing from 54.6 to 45.9, native fish species richness from 2.4 to 1.8, WINOE from 100 to 92, and EPT species richness from 7.1 to 5.1.

Forested LULC classes and summer stream flow (Table 1) all had substantially weaker associations with our indicators than did agricultural and developed LULC, for all areas of influence. In particular, we were unable to see any significant correlations between forest LULC classes and any of our indicators in upland streams. This may be partly due to the relative rarity of watershed-scale deforestation in the Cascades and Coast Range. Ninety percent of our upland sampled sites had at least 55% coverage of closed forest (CFOR) within their upstream watersheds and riparian corridors, and the majority of sites had at least 80% coverage. Models using composite indices of LULC, differentially weighted for different types of vegetation, agriculture or development, had comparable or lower R^2 than models based on the aggregate AGRC and DVLP variables. Thus, we used the simpler AGRC and DVLP variables in our Table 2 models in favor of the more complex composite LULC variables, although we compare model projections for the two below.

Our estimates of LULC effects differ in some ways from those reported by other investigators. For example, Wang et al. (2001) concluded that development

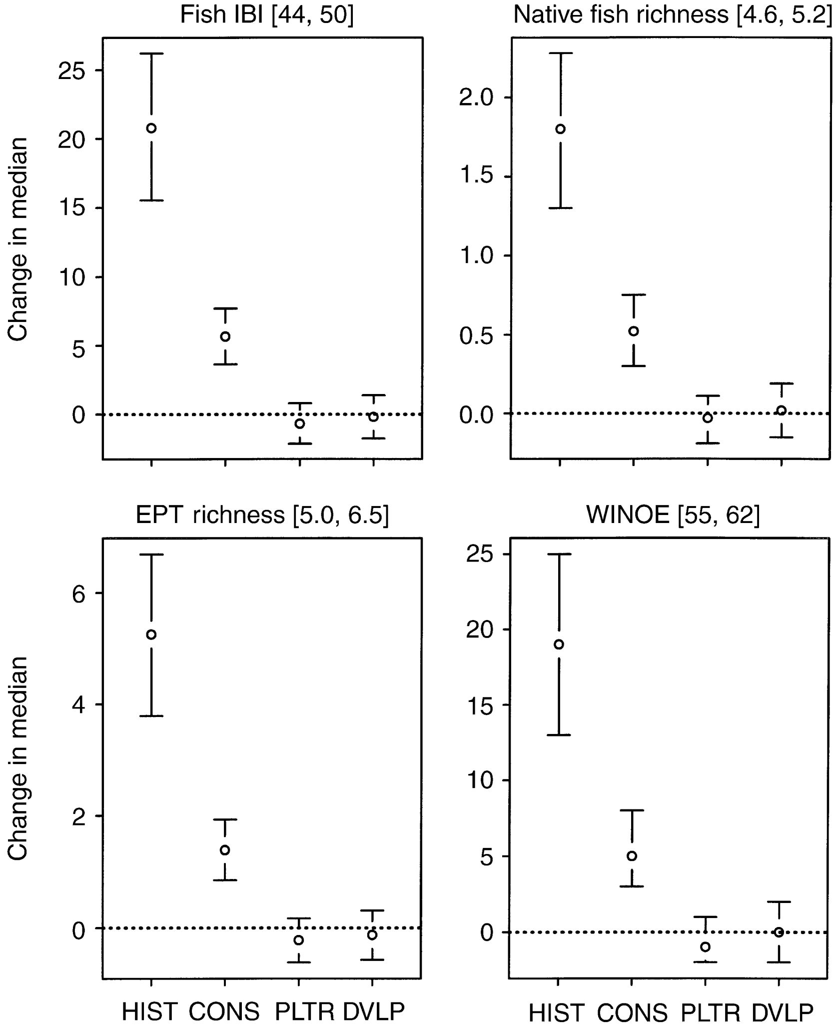

FIG. 2. Projected change in lowland stream condition for Historical (HIST), Conservation 2050 (CONS), Plan Trend 2050 (PLTR), and Development 2050 (DVLP) scenarios, relative to the baseline Circa 1990 scenario. Stream condition is represented by fish IBI (index of biotic integrity), native fish richness, EPT (Ephemeroptera, Plecoptera, Trichoptera) richness, and WINOE (Willamette invertebrate observed/expected index). Mean and 90% CLS of the change in median, based on 1000 Monte Carlo trials, are plotted for four indicators of fish and invertebrate communities. Brackets enclose 90% CLS for the Circa 1990 median, and dotted lines denote zero change.

effects were stronger than agricultural effects in Wisconsin streams. In contrast, for each of our models, coefficients on the agriculture and development terms are not different, within the uncertainty bounds expressed by coefficient standard errors (Table 2). Regional differences in biophysical setting as well as in the nature of the agriculture and development in the two areas may account for these different results. In addition, the studies cited in the *Introduction* show no consistent pattern for the relative associational strengths between stream attributes and land use near a sampled stream site and/or in riparian corridors, versus land use at greater distances from sites. Differences in results among these studies may be due to their differing sets of sampled streams and watersheds, to differences in their configurations for areas of influence, and to the statistical difficulties of assessing relative importance among highly intercorrelated variables. Such ambiguities emphasize that alternative models should be considered in any assessment of LULC impacts on streams.

Model projections for alternative scenarios

Lowlands.—Our biological indicators all responded in a similar fashion to the alternative scenarios (Fig. 2) because our final models (Table 2) are all driven by agricultural and developed LULC within the 120 m wide riparian corridor. Projected medians of all indicators showed no significant change by 2050, relative to Circa 1990, for either the Development or the Plan

TABLE 3. Net percentages of aggregated land use classes within 120-m (each side) riparian corridors of all first- to fourth-order streams in the lowlands (Willamette Valley ecoregion) of the Willamette River Basin, under five alternative scenarios.

Scenario	Land use: Agriculture	Development	Forest
Historical	0	0	55
Circa 1990	42	10	33
Conservation 2050	27	12	37
Plan Trend 2050	41	13	32
Development 2050	37	16	31

Notes: ''Forest'' includes all hardwood, coniferous and mixed stand types. Not included: native grass and shrublands, wetlands, barren lands and water.

Trend future scenarios (Fig. 2). This result occurred for two reasons. First of all, the changes in agricultural and developed LULC between Circa 1990 and these two scenarios were relatively small—less than 7 percentage points in each case (Table 3). Secondly, LULC changes between Circa 1990 and these two scenarios were dominated by transformations from agricultural to developed LULC, with the total of the two uses altered by fewer than 3 percentage points (Table 3). Because our models have nearly the same coefficients for agricultural and developed LULC (Table 2), they respond to the combined areas of these two land uses, but not to exchanges between them.

In contrast, the Conservation 2050 scenario assumed a net decrease of 13 percentage points in the combined agricultural and developed LULC within riparian corridors, relative to Circa 1990 (Table 3). As a result, significant improvements in Lowland stream condition were projected for Conservation 2050, as judged by increases in median fish and EPT taxa richness, IBI, and WINOE, with confidence intervals being bounded away from zero (Fig. 2). These increases in median stream condition ranged between 9% (for WINOE) and 24% (for EPT richness) of Circa 1990 medians.

For all indicators, projected medians under the Historical scenario are substantially higher than those for Circa 1990 (Fig. 2). The differences between Historical and Circa 1990 medians are also greater than those between Conservation 2050 and Circa 1990, suggesting that only partial restoration of pre-European conditions is possible under the Conservation 2050 scenario. The Historical scenario assumes that agricultural and developed land uses were zero everywhere in the landscape, representing basin conditions prior to the arrival of European settlers (Table 3). Under these idealized Historical assumptions of ''no human impact,'' our models still project some variability in stream condition across streams, rather than an unrealistic, single, optimal condition attained in all streams.

Uplands.—In developing our models, we failed to find significant relationships in Upland streams between our biological indicators and any of our formulations of the forested LULC that dominates upland areas (Table 1 and the composite natural vegetation variable). Our only available model for making upland projections was the native fish richness model of Table 2, which adequately expresses observed physiographic associations with upland richness, but includes only agricultural and developed land uses as predictors. These two land uses together make up <2% of upland riparian corridor areas under all scenarios. As a result, all alternative scenarios were projected to have nearly the same median native fish richness (4.8 to 4.9 species) in the uplands, with a 90% CI on each median of about 4.4 to 5.2 species.

We believe that relationships between upland stream condition and riparian/watershed forest cover do in fact exist, but our data-driven modeling approach and remotely sensed forest estimates at the scale of the Willamette Basin were not sensitive enough to detect them. Elsewhere, we have presented projections of trout habitat suitability that are based on an expert-judgment model and do respond to the relatively minor changes in upland forests seen under the alternative scenarios (Hulse et al. 2002). The suitability model is a weighted sum, with weights assigned by expert judgment, of riparian land use factors, such as forest stand type and recruitment potential for in-stream large wood, that are known to influence trout habitat. The model projects between-scenario differences for upland streams that are similar to, although smaller in magnitude than, the differences seen for other indicators in lowland streams (Hulse et al. 2002).

Uncertainty in model choice

We are uncertain that the models in Table 2 are the most reliable and accurate obtainable from our data. As described earlier, models based on alternative areas of influence fit our data nearly as well as the models in Table 2. Pearson correlations consistently exceeded 0.8 between variables of the same LULC class but different areas of influence, providing more evidence that different areas of influence would make approximately the same explanatory contributions to a model. Because patterns of LULC naturally tend to be similar throughout a small watershed and its riparian areas, such high correlations are difficult to avoid in observational studies and have constrained previous empirical modeling efforts (Richards et al. 1996, Roth et al. 1996, Wang et al. 2001).

Unfortunately, models based on alternative areas of influence do not always give nearly equivalent model projections. To illustrate, we compare lowland projections of native fish richness from the Table 2 model to those obtained from three alternative models (Fig. 3). The four models have R^2 ranging from 0.674 to 0.713 and all coefficients in each model exceed twice their standard errors. In Fig. 3, the ''local'' model is identical to the Table 2 model except that it employs local ri-

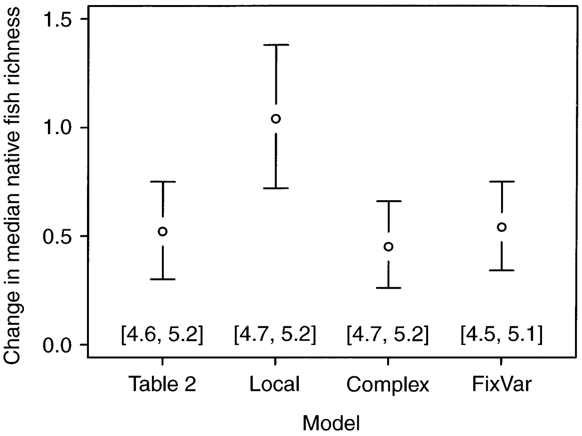

FIG. 3. Change in median lowland native fish richness (mean change with 90% confidence limits), from the Circa 1990 to the Conservation 2050 scenario, projected by four alternate models (for model descriptions, see *Results and discussion: Uncertainty in model choice*). Brackets enclose 90% confidence limits for the Circa 1990 median.

parian (30 m) percentages of agricultural and developed LULC rather than those within the 120 m riparian corridor. The ''complex'' model is also identical to the Table 2 model, except that it employs weighted composite agricultural and developed percentages and a 1:1:1-weighted cumulative area of influence. Finally, in the ''FixVar'' model the two weakest fixed variables (ORDER and GRADIENT) are dropped from the Table 2 model.

All four models projected very similar median richness under the Circa 1990 scenario (Fig. 3) as well as the Plan Trend 2050 and Development 2050 scenarios (not shown). However, the ''local'' model projected a substantially greater change in richness under the Conservation 2050 scenario than did the other three models (Fig. 3). This occurs because, unlike the other scenarios, Conservation 2050 assumes extensive riparian protection and restoration on private agricultural lands within 30 m of streams, while freely allowing agricultural uses outside the 30 m corridor (Hulse et al. 2002).

The ambiguity in projected species richness for Conservation 2050 is a consequence of model structural uncertainty (Beck 1987, Draper 1995), an uncertainty that appears unavoidable because we can make no clear theoretical or empirical arguments for land use within either riparian corridor width (30 m or 120 m) providing superior projections of fish species richness. By reporting projected extremes from a set of approximately coequal model structures, Fig. 3 illustrates a ''bounding'' strategy for structural uncertainty (Norton 1996, Church and Van Sickle 1999). Alternatively, one could average the projection results from a set of nearly equal models (Draper 1995, Burnham and Anderson 1998). With either strategy, the central challenge is to specify a set of models that captures the full range of structural uncertainty, but is still compact enough for practical application.

Estimating between-scenario differences from a chosen model

Even if the Table 2 models are the most reliable expressions of scenario effects, they still fail to account for substantial portions of the observed variances in our stream indicators. Sources of model residual error variance include model structural error, important excluded variables, errors in map-based estimates of model predictors, and sampling variation in measures of stream condition indicators. The combined effects of all these error sources are incorporated into our uncertainty estimates for between-scenario differences in regional medians (Figs. 2 and 3) and the regional CDFs from which they were derived.

We would have preferred to compare scenarios by computing between-scenario differences separately for each reach. Such an approach recognizes that each individual modeling unit (reach) and its physiographic features is assumed to be fixed over all scenarios, and it would allow explicit basin-wide mapping of scenario effects. Reach-specific differences between scenarios could then be aggregated to produce regional summaries (CDFs or medians) similar to Fig. 2.

However, we were unable to specify a realistic error variance for the projected between-scenario difference of any given reach. When regression predictions are made for each of two scenarios, the errors for the two predictions can be assumed independent, and the error variance for the difference between the predictions will then be the sum of the individual prediction variances (Rice 1988). For the Table 2 models, an independence assumption yields standard errors for between-scenario differences in a given reach that are much greater than the differences themselves.

But full independence of model errors within one reach does not seem realistic, because some of these sources would likely be constant across scenarios within the same reach, thereby reducing the error variance of a between-scenario difference in projected condition. For example, model inadequacy is partly due to factors affecting stream condition that were not included in the models. Some of these excluded factors, such as the magnitude of groundwater inflows, would not be expected to change appreciably among scenarios for a given reach. Thus, the error variance of a between-scenario difference is likely greater than zero, but it is also likely to be smaller, to an unknown degree, than the sum of error variances for the two projections. Because we could not extract from the overall model error only those components that affect between-scenario differences, we did not estimate reach-by-reach differences between scenarios in projected stream condition.

SUMMARY AND CONCLUSIONS

Our models projected clear and reasonable decreases in lowland stream condition between Historical and Circa 1990 scenarios. In other words, the models suggest that the biological condition of stream biota has declined markedly due to the widespread urban and agricultural transformation of the lowland landscape over the past 150 years. Under a Conservation scenario, some of this decline may be reversed over the next 50 years, even with a doubling of the human population. Alternatively, if no new conservation measures are implemented over the next 50 years, and the only major landscape transformation is the loss of agricultural land converted into rural residential and urban development at the current pace (Plan Trend scenario), or an accelerated pace (Development scenario), our models project no further declines in the condition of invertebrate and fish communities, on a region-wide basis. Baker et al. (2004) and Hulse et al. (2002) discuss, in a broad context, the utility and implications of these results for policymakers and citizens contemplating the future of the Willamette Basin.

Based on our model projections, it would be risky to conclude that the landscape transformations assumed under the Plan Trend and Development scenarios would have no effect whatsoever on streams. In the first place, our model projections are highly uncertain for any individual stream reach, and major, localized changes in riparian corridor land use could have deleterious effects in particular watersheds. Such localized impacts are rarely visible when assessments are made at regional scales. Second, urban and residential development in watersheds is likely to impact peak flow, water chemistry and sediment loads in streams. Such impacts are clearly relevant to flood control and human health, and also can affect the physical habitats of fish and macroinvertebrates. In our data and modeling, however, we did not find evidence that these probable impacts were ultimately more serious for fish and invertebrates in developed watersheds than in agricultural watersheds.

Our results suggest possible shifts in emphasis for future research and management activities in the basin's streams. In the past, researchers in the basin, and throughout the Pacific Northwest, have focused on streams in forest-dominated landscapes and their responses to forest management practices. But on a landscape scale, our data and models suggest that current riparian land uses in Lowland agricultural and developed watersheds of the basin have had a more discernible impact on stream biota than they have in upland forested watersheds. Moreover, our models could not detect a clear difference between the effects of agriculture and development on stream biota, at the same time as future scenarios project that exchanges between these two land uses may dominate landscape dynamics in the basin over the next 50 years. These conclusions all point to a need for a better understanding of stream ecology in agricultural and urban watersheds of the Willamette River Basin.

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