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Comparison of watershed disturbance predictive models for stream benthic macroinvertebrates for three distinct ecoregions in western US

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ABSTRACT

The successful use of macroinvertebrates as indicators of stream condition in bioassessments has led to heightened interest throughout the scientific community in the prediction of stream condition. For example, predictive models are increasingly being developed that use measures of watershed disturbance, including urban and agricultural land-use, as explanatory variables to predict various metrics of biological condition such as richness, tolerance, percent predators, index of biotic integrity, functional species traits, or even ordination axes scores. Our primary intent was to determine if effective models could be developed using watershed characteristics of disturbance to predict macroinvertebrate metrics among disparate and widely separated ecoregions. We aggregated macroinvertebrate data from universities and state and federal agencies in order to assemble stream data sets of high enough density appropriate for modeling in three distinct ecoregions in Oregon and California. Extensive review and quality assurance of macroinvertebrate sampling protocols, laboratory subsample counts and taxonomic resolution was completed to assure data comparability. We used widely available digital coverages of land-use and land-cover data summarized at the watershed and riparian scale as explanatory variables to predict macroinvertebrate metrics commonly used by state resource managers to assess stream condition. The "best" multiple linear regression models from each region required only two or three explanatory variables to model macroinvertebrate metrics and explained 41–74% of the variation. In each region the best model contained some measure of urban and/or agricultural land-use, yet often the model was improved by including a natural explanatory variable such as mean annual precipitation or mean watershed slope. Two macroinvertebrate metrics were common among all three regions, the metric that summarizes the richness of tolerant macroinvertebrates (RICHTOL) and some form of EPT (Ephemeroptera, Plecoptera, and Trichoptera) richness. Best models were developed for the same two invertebrate metrics even though the geographic regions reflect distinct differences in precipitation, geology, elevation, slope, population density, and land-use. With further development, models like these can be used to elicit better causal linkages to stream biological attributes or condition and can be used by researchers or managers to predict biological indicators of stream condition at unsampled sites.

1. Introduction

Modeling in ecology has increased markedly in the past decade, and major advances have been made in terrestrial landscape ecology, including forestry and plant and fire ecology (Cushman et al., 2007). While advanced mechanistic models that include spatial and temporal processes have been developed for fluvial hydrology, the application of models in stream ecology at present are primarily descriptive models and they are not as well developed as in many other research areas (Leathwick et al., 2005; Cabecinhaa et al., 2007; Turak et al., 2010). A fundamental goal of bioassessment in stream ecology is a better understanding of the effects of human land-use on stream biota and the mechanistic processes at various scales that cause these effects. However, streams are a complex spatial and temporal habitat mosaic that is directly and indirectly influenced by natural geology, climate,

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and human disturbance. Allan (2004) described the complexity of human disturbance this way, "Different disturbances will exert their influence at different spatial scales and by different pathways." Stream ecologists are trying to understand the spatial scales and processes associated with human and natural disturbances that are affecting the biota. Models provide a useful framework for testing our understanding and determining where further research is needed.

Stream bioassessments have successfully used metrics or multimetric indices of macroinvertebrates assemblages as indicators of stream condition (e.g., Davies and Jackson, 2006; Hering et al., 2006; Carlisle et al., 2008; Stoddard et al., 2008; Waite et al., 2008). Most individual metrics or aggregate indices, however, have been developed for and applied at specific local or small regional scales, and there has been considerable concern about the application of such metrics to different ecoregions or at larger spatial scales (Osborne and Suaĭrez-Seoane, 2002; Hering et al., 2006; Pont et al., 2006; Johnson et al., 2007; Ode et al., 2008; Stoddard et al., 2008). Species richness metrics for fish assemblages are known to change dramatically from river basin to river basin or when comparing between large geographic regions, such as Eastern and Western United States (Meador et al., 2005; Waite et al., 2008). There is evidence that this phenomenon also occurs for some macroinvertebrate taxa richness metrics (Herlihy et al., 2008; Ode et al., 2008) and potentially for pollution tolerance metrics (Cuffney, 2003; Cuffney et al., 2007; Stoddard et al., 2008), yet overall there is less known about the application of invertebrate metrics across a variety of spatial scales in North America.

There are many natural and human-induced factors structuring stream ecosystems. Understanding how these factors operate and over what spatial scales is of central importance in ecology and critical for better resource management (Burnett et al., 2006). Wang et al. (2006a,b) suggest that more attention is needed in developing and improving landscape models for predicting instream physiochemical and biological characteristics. Grace (2006) suggests in order to advance theory we need to branch into multivariate models that address "a progressive refinement of ideas and explanatory power, while permitting broad general comparisons." The expansion and application of multivariate models in stream ecology are helping to address these issues and hopefully will lead to better understanding of ecological and anthropogenic causal pathways and responses (Oberdorff et al., 2001; Cabecinhaa et al., 2007; Turak et al., 2010).

Much of the research documenting the effects of land-use change on stream biota indicates that as the total watershed area in agricultural and/or urban land-use increases, the biological metrics and indices decrease (Paul and Meyer, 2001; Allan, 2004; Cuffney et al., 2005; Waite et al., 2008). Though some researchers have found a threshold response (i.e., curvilinear or step function) of biological indices to individual land-use indicators (Davis and Simon, 1995; Wang et al., 2001; Walsh et al., 2005) much of the literature indicates that the response more often is a simple linear response with no initial resistance (Booth, 2005; Roy et al., 2005; Kennen et al., 2005; Morgan and Cushman, 2005; Cuffney et al., 2005; Waite et al., 2008). If biological responses to landscape measures are indeed complex and nonlinear, then newer modeling techniques such as regression classification trees (e.g., CART and random forest), machine learning techniques (e.g., multiple regression splines and neural networks), multilevel hierarchical modeling, or structural equation models (SEM) may be necessary to model these responses. However, if various biological responses to human disturbance are linear, then they should be more easily modeled via standard regression techniques, which are easier to develop and interpret.

Modeling the relations among various biological indicators and landscape measures will not only help researchers understand and rank the importance of various linkages but will also allow prediction of biological condition for unsampled streams. The latter aspect may be especially important for resource managers charged with reporting on the overall condition of all river and stream miles within their borders. Previous work on predictive models for biological indicators at unsampled streams is limited, and most of these predict fish abundance or richness (Steen et al., 2006). Until recently, macroinvertebrate data sets large enough, sampled with comparable protocols and across appropriate scales necessary for landscape modeling have likely been the limiting factor for model development.

Austin (2007) suggests that most papers on modeling do not provide the theoretical underpinnings of the model. Our conceptual model (Fig. 1) is based on the hypothesis that landscape characteristics control stream hydrogeomorphology and therefore the baseline biological assemblages (Allan, 2004; Davies and Jackson, 2006). We assume that ecoregions and watershed size provide a fundamental or baseline classification of stream types and that, in general, streams in the western U.S. are controlled more frequently by abiotic processes than biotic interactions (Hawkins et al., 2000; Waite et al., 2000). However, biotic interactions between various trophic levels may still be important even though we do not address them here (e.g., grazing by macroinvertebrates on periphyton). Human-induced changes in land-cover (i.e., agriculture, urban, roads, dams, and mining) often reduce stream riparian zones thereby increasing light and runoff into streams, reducing organic matter, and simplifying geomorphology (Allan, 2004; Utz et al., 2009). Sediment and nutrient loads and water temperature increase, and habitat complexity and volume are reduced (Waite and Carpenter, 2000; Allan, 2004). Human-induced changes may increase or decrease the magnitude and timing of flow and cause complex changes to the water chemistry including increases or decreases in dissolved oxygen and increases in ions, pesticides, and toxics (Bryant et al., 2007; Carpenter et al., 2008; Paulsen et al., 2008; Waite et al., 2008). These changes in water quality/quantity and habitat may then cause changes in biological assemblages through species additions and deletions (Fig. 1). In general, these affects can be divided into direct and indirect pathways. For example, most land-use changes can have significant impacts on streams, yet most of these impacts are mediated through an indirect pathway, such as changes in riparian shading, which then increases stream temperature. This, combined with inputs of nutrients and sediment from adjacent land-use, frequently leads to large increases in instream productivity or eutrophication resulting in a cascade of potential biological impacts. Therefore, this conceptual model suggests that watershed landscape data should be able to be used to predict biological condition in unsampled streams, assuming that the same abiotic responses occur as in the sampled streams.

Our goal in this paper is to develop predictive models for selected macroinvertebrate metrics using easily accessible watershed land-use/land-cover. We assembled macroinvertebrate data sets for the purpose of developing predictive models of stream macroinvertebrates from three disparate regions of the western coastal United States: Southern Coastal California and the Blue Mountains and Willamette Valley ecoregions, Oregon. Our overarching hypothesis was that watershed disturbance predictive models could be developed for the three distinct geographic regions using simple measures of the amount of urban, agriculture, and infrastructure within the watershed (Fig. 1) and that riparian scaled disturbance measures would largely be redundant. The development of watershed disturbance predictive models such as those presented herein will help lay a strong foundation for deriving more complex models to address the biocomplexity of causal mechanisms and disturbance pathways in landscape and aquatic ecology.

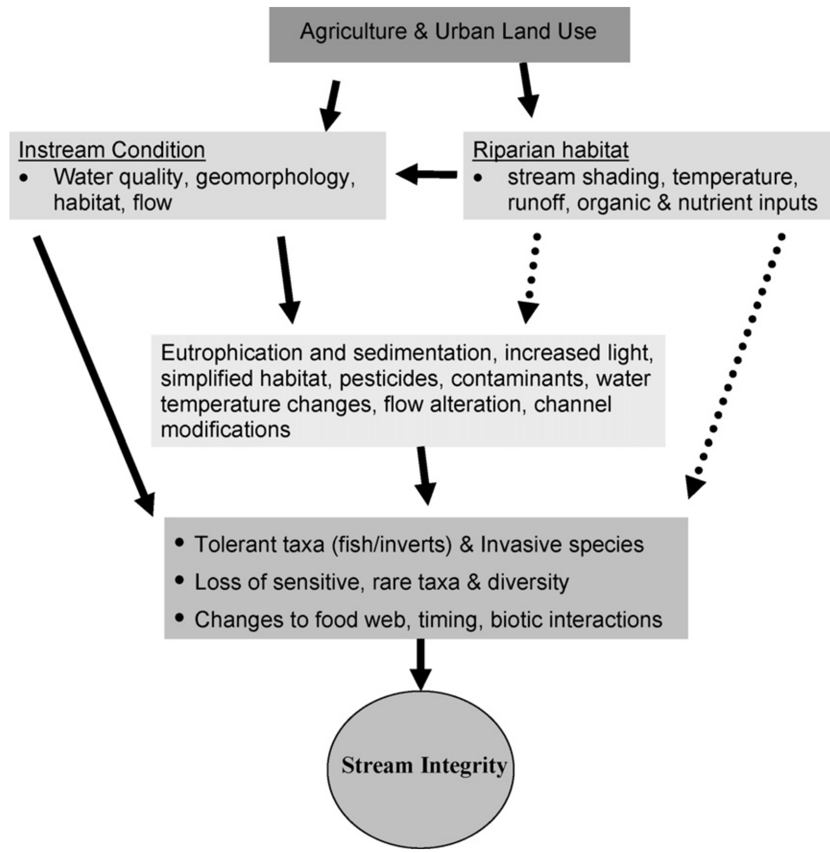

Fig. 1. Conceptual model relating the influence of agricultural and urban land-use on factors that affect stream condition. Solid arrows indicate direct pathways, dashed arrows indirect pathways. *Note:* Direction of response may be positive or negative even within one conceptual box.

2. Methods

2.1. Data aggregation and landscape analysis

We evaluated multiple data sets for inclusion in our study. We gathered a list of all possible watersheds with macroinvertebrate data for wadeable streams in non-forest dominated landscapes in order to focus on the affects of agricultural and urban land-use in the states of Washington, Oregon, and California. Site location data were obtained from both Federal and state agencies, including the U.S. Geological Survey, the U.S. Environmental Protection Agency, Oregon State University, the Oregon Department of Environmental Quality, and the California Department of Fish and Game. Combined, these datasets contained nearly 3000 sampling sites. The sites were then evaluated on the following criteria: invertebrate data sampled with comparable methods; upstream watershed area of between 13 and 259 km^2; and sites could not be nested watersheds (i.e., no spatial autocorrelation) The sites meeting the criteria resulted in three principal study areas: Coastal Southern California (55 sites), the Blue Mountains ecoregion of eastern Oregon (148 sites), and the Willamette Valley ecoregion in north-central Oregon (96 sites) (Fig. 2).

Watersheds were delineated for the selected sampling sites within the three study areas using USGS 7.5-min quadrangle digital raster graphics (DRG) as base layers. The DRGs were displayed on-screen along with National Hydrography Dataset (NHD) high resolution stream lines for each region (U.S. Geological Survey, 2007). Watershed boundaries were digitized on-screen at a scale of 1:10,000 or larger. Adjacent watershed polygons were edge matched to eliminate all overlaps and gaps. All work was conducted using ArcGIS, ArcMap 9.2 (Environmental Systems Research Institute, Redlands, CA) GIS software.

Riparian zone buffer polygons were created within each watershed, extending 2 km upstream from the outlet of each watershed along the main stem and all tributaries and 90 m on either side of the stream centerlines. The buffers were created by selecting the appropriate NHD stream lines within each watershed and creating routes along each main stem and tributary flow path. The routes were then clipped to a distance of 2 km from the basin outlet and buffered.

Spatial datasets representing landscape metrics of watershed disturbance were created for each watershed and riparian zone buffer from available national and regional datasets (Appendix 1) and included elevation, slope, land-cover (1992 and 2001), population density, road networks, soil infiltration capacity, hydrography, pollution point sources, dams, and precipitation. Land-use summaries were based on either 1992 or 2001 spatial data, depending on which data source was closer to the macroinvertebrate sample date for that watershed. The landscape metric data were of two types (raster and vector), which were processed differently to obtain summary statistics for each watershed and riparian zone buffer. Landscape metric data in vector format were processed by intersecting the watershed and riparian zone polygons with each landscape dataset. Summary statistics for each watershed and riparian zone buffer were then calculated from the intersect results. Landscape metric data in raster format were processed using the Spatial Analyst extension and the zonal statistics tool in ArcMap. Watersheds and riparian zone buffers were used to define zones for analysis and calculate summary statistics. The 1992 and 2001 land-cover datasets used slightly different classification schemes. Uniform codes based on the 2001 classification scheme

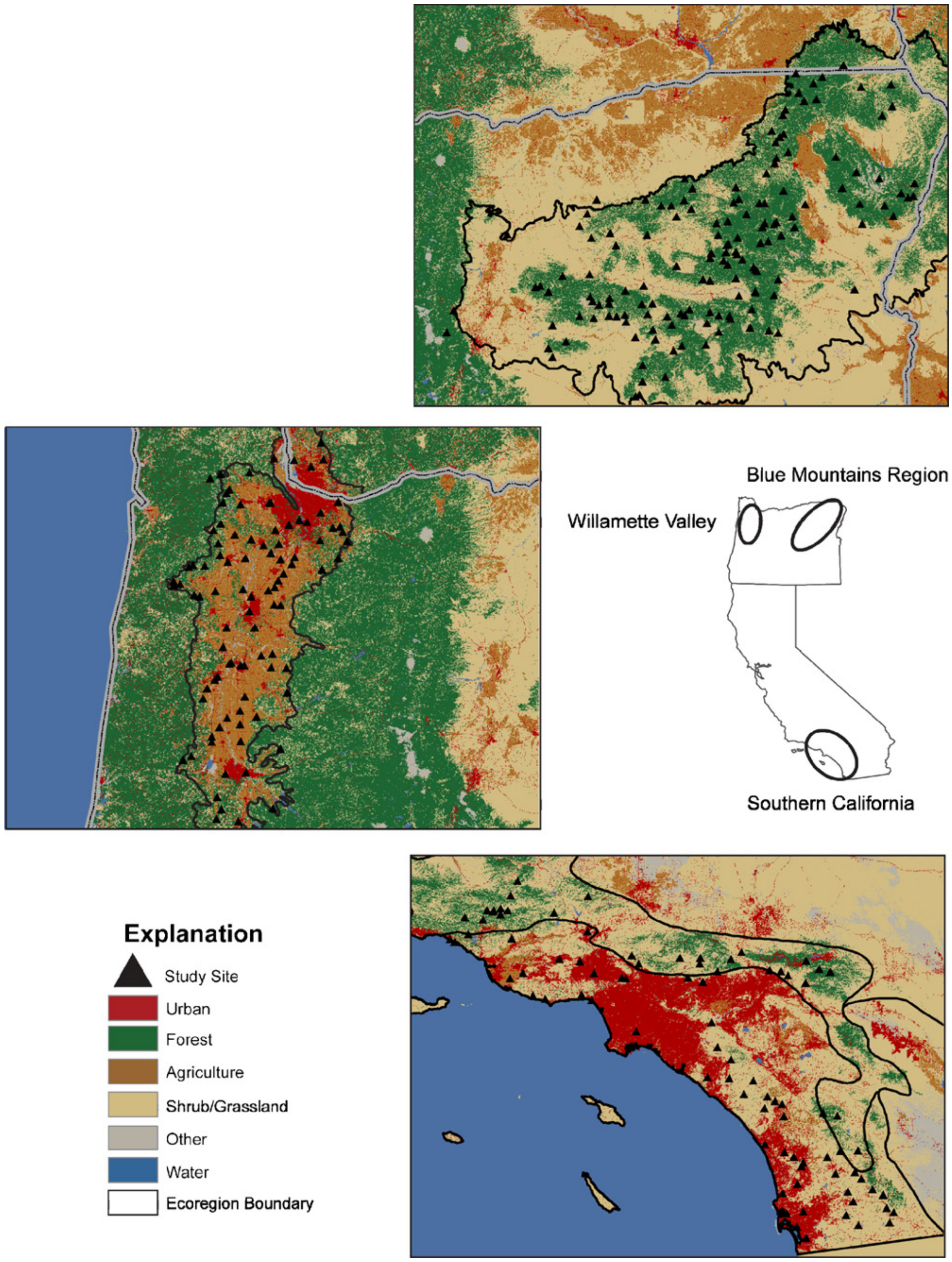

Fig. 2. Map showing land-use and land-cover for the three modeling regions: Blue Mountains and Willamette Valley, Oregon and Southern California.

were assigned to all land-cover classes in the final summary statistics table.

2.2. Description of modeling regions

The Coastal Southern California (SoCal; Southern and Central California Chaparral and Oak Woodlands Ecoregion) region has a Mediterranean climate of hot dry summers and cool moist winters (Ode et al., 2005). Precipitation averages 25–50 cm/year (Fig. 3). The geology of the ecoregion is dominated by recently uplifted and poorly consolidated marine sediments. Vegetative cover in this region consists mainly of chaparral and oak woodlands, though grasslands occur in some lower elevations and patches of pine are found at higher elevations (open low mountains or foothills). The landscape is currently dominated by urban development; the human population is approximately 19 million and is projected to exceed 28 million by 2025 (Ode et al., 2005). Outside the urban centers, much of this region was historically grazed by domestic livestock or cultivated for fruits and vegetables, but most of this was converted to urban starting many decades ago.

The Blue Mountains (Blue_Mt) are the westernmost range of the Middle Rocky Mountains and, like the Cascade Range, are largely volcanic with fertile plateaus and deeply fissured river valleys. Carved by two rivers (the John Day and Grande Ronde Rivers) the landscape has steep hillsides, bluffs and rimrock faces. Temperature and precipitation are highly correlated with elevation. Precipitation ranges from 22 to 45 cm/year along the river valleys and greater than 250 cm/year in the nearby mountains. This region is dominated by coniferous forests in mid- to higher elevations and shrub and grassland in lower elevations, though much of the latter has been displaced by agriculture and grazing. The region has no large cities and urbanization is limited to scattered smaller cities and small towns.

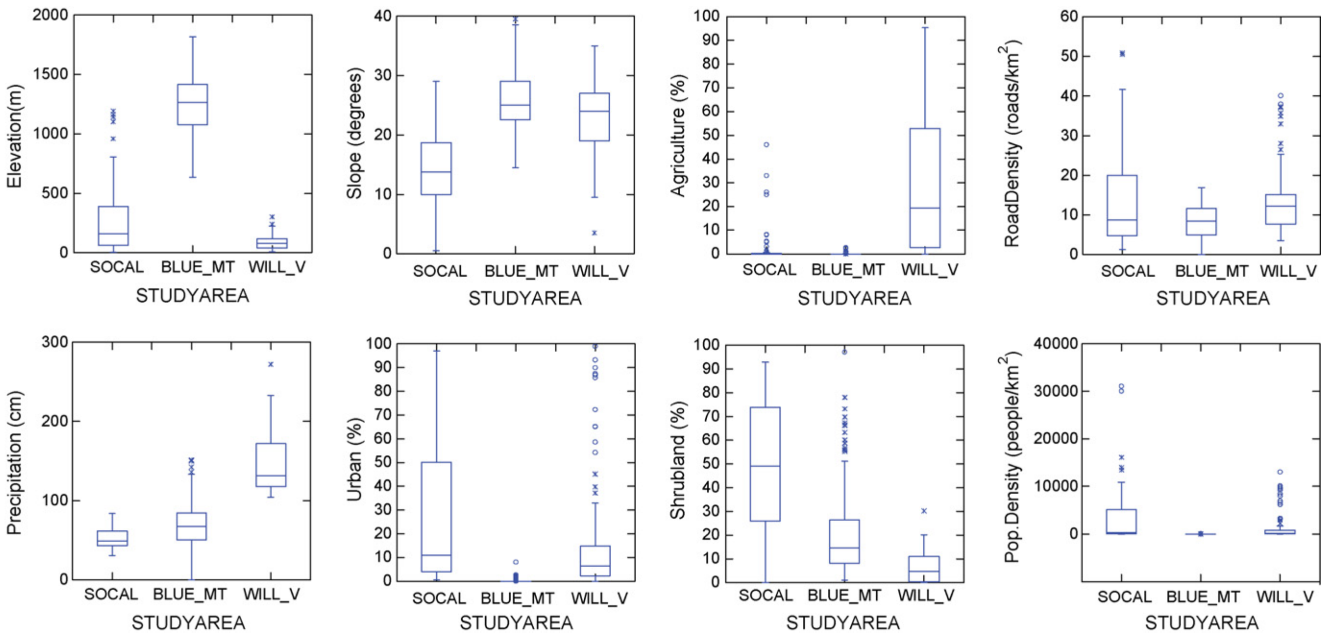

Fig. 3. Box plots of selected land-use and land-cover variables for the three modeling regions summarized separately. See text for description of variables.

The Willamette Valley (Will_V) ecoregion contains a mixture of rolling prairies, mixed forests, and extensive lowland valley wetlands. With temperate, dry summers and cool, wet winters, the Willamette River basin and surrounding area is characteristic of the Pacific Northwest climate. About 90% of the annual precipitation (100–130 cm/year) occurs during October through May (Uhrich and Wentz, 1999), falling as rain in the valley and snow in the mountains. The land-use/land-cover in the valley plains and foothills is primarily cultivated crops, pasture, and grasslands. Urbanization ranges from minimal to extensive (U.S. Geological Survey, 2005). Centered on the confluence of the Columbia and Willamette Rivers, Portland is the most populous city in Oregon, with 539,000 people in city limits and nearly 3 million people in the Portland metropolitan area (U.S. Census Bureau, 2000). The population in the metropolitan area increased almost 30% from 1990 to 2000, with some suburban populations increasing more than 80% during the same period (U.S. Census Bureau, 2000). The drainage network in the Willamette Valley combines natural tributaries, complex networks of canals in agricultural areas, and stormwater canals and groundwater infiltration wells in cities.

As a result, the three geographic regions modeled in this study have distinct natural settings and the extent of human disturbances. SoCal had the driest climate, intermediate mean stream site elevation (Min_Elev) and percent agriculture, and the highest population density (Fig. 3). Blue_Mt had the highest mean site elevation and mean watershed slope, intermediate mean precipitation, and the lowest population density, percent urban, and percent agriculture. Will_V had the greatest precipitation, lowest mean site elevation, and the highest percent agriculture.

2.3. Macroinvertebrate data

Macroinvertebrate data from 1994 to 2005 assembled for this study were considered to be comparable in terms of sampling protocols (sampled habitat, number of composite samples and total sampled area) and laboratory procedures, including sorting, subsample count level, and taxonomic resolution (pers. commun. state agency personnel, 2005; Waite et al., 2004). Extensive review of the data was completed to make sure aggregated data from separate sources included the same taxonomic groups, followed the same spelling and abbreviation procedures, and had appropriate taxonomic resolution before data analysis was attempted. The Invertebrate Data Analysis System (IDAS) software (Cuffney, 2003) was used to resolve by region all taxonomic issues (taxonomic identification level and nomenclature), to remove ambiguous taxa, and to randomly subsample raw counts to an equal specimen count by region of either 300 or 500 count. In general, data for dominant aquatic insect orders were resolved at genus level. Less common orders were often aggregated to family level. Rare organisms or those with difficult taxonomy were sometimes aggregated to order or higher. The dipteran family, Chironomidae, is considered an important bioindicator group, yet historically a difficult group to identify to genus or species. As a result, data for this group were assigned to six taxa levels (five subfamilies plus Chironomidae) from the various family to genus level identifications that occurred within the original data. After data preparation, the IDAS program was used to calculate 137 invertebrate metrics, many of which are commonly used in stream bioassessment (Rosenberg and Resh, 1993; Davis and Simon, 1995; Barbour et al., 1999). Tolerance and functional group metrics were calculated using values from Barbour et al. (1999), supplemented with values from Wisseman's tolerances for the Pacific Northwest (Wisseman, 2004; pers. commun.). Tolerances were calculated on the basis of richness (average of tolerance values assigned to each taxon) and density (density-weighted tolerances; Cuffney, 2003). In addition to individual macroinvertebrate metrics described above, ordination axes scores from nonmetric multidimensional scaling ordinations run on each full macroinvertebrate Bray-Curtis resemblance matrix using all taxa were also used as bioindicator variables.

2.4. Model development

Scatter plots and correlation matrices were used to examine data distributions and to detect potential outliers. Response variables and landscape variables with a limited range of response were removed from consideration ($r < 0.50$). Remaining metrics and ordination axes scores were correlated (Spearman rank correlation) against each other to examine redundancy, as were the landscape

Table 1
Description, variable code and definition of explanatory (landscape) and predictor (invertebrate metrics) variables used for model development.

Explanatory variables: landscape		Definition
Description	Variable code	
Watershed Scale Variables		
Percent Urban Land-use	WS_Urban	Percent watershed area in urban land-use (NLCD 2000 categories 21, 22, 23, and 24)
Percent Agricultural Land-use	WS_Ag	Percent watershed area in agricultural land-use (NLCD 2000 category 82)
Sum of Percent Ag + Urban	WS_Ag+Urb	Sum of percent watershed area in urban (NLCD 2000 categories 21, 22, 23, and 24) and agricultural (NLCD 82) land-use
Percent Forest	WS_Forest	Percent watershed area in forest land-use (NLCD 2000 categories 41, 42, 43)
Percent Pasture	WS_Pasture	Percent watershed area in pasture land-use (NLCD 2000 category 81)
Percent Shrub/Scrub	WS_Shrub	Percent watershed area in Shrubland, Shrub/Scrub (NLCD 2000 category 52)
Road Density	WS_RdDens	Road density in watershed = road length (km)/watershed area (km^2)
Mean Population Density	WS_PopDen	Watershed mean population density based on 2000 census (persons/km^2)
Mean Elevation	WS_Mn-Elev	Mean watershed elevation (m)
Mean Slope Percent	WS_Slope	Mean percent watershed slope
Manmade Stream Density	WS_MmStreams	Manmade stream density in watershed = manmade stream length (km)/watershed area (km^2)
Mean Annual Precipitation	WS_MnAnnPrecip	Mean annual precipitation (cm)
Soil Infiltration Rate	Soil_Mod-Infil	Hydrologic soil group B, moderate infiltration rate (min. infiltration rate 4–8 mm/h)
Riparian Scale Variables		
Percent Urban Land-use	Rip_Urban	Percent buffer area in urban land-use (NLCD 2000 categories 21, 22, 23, and 24)
Percent Agricultural Land-use	Rip_Ag	Percent buffer area in agricultural land-use (NLCD 2000 category 82)
Sum of Percent Ag + Urban	Rip_Ag+Urb	Sum of percent buffer area in urban (NLCD 2000 categories 21, 22, 23, and 24) and agricultural (NLCD 82) land-use
Percent Forest	Rip_Forest	Percent buffer area in forest land-use (NLCD 2000 categories 41, 42, 43)
Percent Pasture	Rip_Pasture	Percent buffer area in pasture land-use (NLCD 2000 category 81)
Percent Shrub/Scrub	Rip_Shrub	Percent buffer area in Shrubland, Shrub/Scrub (NLCD 2000 category 52)
Road Density	Rip_RdDens	Road density in buffer = road length (km)/watershed area (km^2)
Mean Population Density	Rip_PopDens	Buffer area mean population density based on 2000 census (persons/km^2)
Mean Slope Percent	Rip_Slope	Mean percent buffer slope
Maximum Elevation	Rip_Max-Elev	Maximum buffer elevation (m)
Response Variables: Invertebrate Metrics		
Total Taxa Richness	RICH	Total richness (number of non-ambiguous taxa)
EPT richness	EPTR	Richness composed of mayflies, stoneflies, and caddisflies
EPT percent richness	EPTRp	Percentage of total richness composed of mayflies, stoneflies, and caddisflies
EPT/chironomid ratio	EPT_CHR	Ratio of EPT richness to midge richness
PLECO percent richness	PLECORp	Percentage of total richness composed of stoneflies
Intolerant abundance percent	Intol_abundp	Percent abundance-weighted USEPA tolerance value for intolerant taxa
Tolerant richness	RICHTOL	Average USEPA tolerance values for sample based on richness
Tolerant percent richness	RICHTOLp	Average USEPA tolerance values for sample based on percent richness
Noninsect percent richness	NONINSRp	Percentage of total richness composed of noninsects
NMDS Axis1 score	nMDS axis 1	Axis 1 values from a bi-plot of two-dimensional distribution based on multivariate similarities

variables. Surrogate variables were selected to represent intercorrelated ($r > 0.70$) groups of variables. If all quantitative factors were equal between two variables, we considered the general applicability of the variables to other geographic areas, regional or national acceptance, and ease of measurement. We then examined correlations of macroinvertebrate metrics with landscape variables and deleted variables that had no correlations greater than 0.70. All analyses were completed using a combination of Primer v6 (Clarke and Gorley, 2006), SAS (version 9.2) and R statistical program (R Development Core Team, version 2.7.2).

The remaining variables were used to develop multiple linear regression (MLR) models (see Table 1 for final variable list, definitions and codes). If necessary, variables were transformed to improve their distributions. Models were developed for each geographic region separately. We assessed model performance using a variety of statistics, including adjusted mean sum of squares (R^2), root mean squared error (RMSE), Akaike Information Criterion (AIC), predicted sum of squares (PRESS), and regression coefficients. We adopted a model fitting approach for each response variable. We used a step-wise selection based on AIC for all models ranging from 1 to 5 environmental variables, as appropriate by region. Model residuals, potential outliers and interaction terms were evaluated. When selecting the final or best model for each region, consideration was given to the number of explanatory variables and whether an interaction term was needed. Models were ranked in order of adjusted R^2 value with higher ranking for models with the lowest number of variables and/or no interaction term. To help evaluate the relative importance of each variable within the final models, partial R^2 values were determined for each variable. For brevity, only plots of observed versus fitted points (predicted) for the metric RICHTOL will be presented for each region. A 1:1 line is added to the plot to help visual interpretation of the observed and fitted points; ideally, points should cluster close to the 1:1 line with equal points above and below. To allow better interpretation of the model coefficients (predictors), all variables were standardized in the final model development to a mean of zero using the 'scale' function in *R*.

3. Results

3.1. Southern California

Three macroinvertebrate response variables were retained for final model development: EPT taxa richness (EPTR), total taxa richness (RICH), and average tolerance value of taxa present (RICHTOL). Eight environmental predictor variables were retained: two riparian variables, mean road density, and mean slope (Rip_RdDens, Rip_Slope) (Appendix 1) and six watershed variables, percent forest and shrub landcover, percent manmade streams, mean population density, mean annual precipitation, and mean slope (WS_Forest {arcsine}, WS_Shrub {arcsine}, WS_MmStreams

Table 2
Multiple linear regression models for the Southern California (SoCal), Blue Mountains (Blue_Mt) and Willamette Valley (Will_V) ecoregions; regression equation parameters provided—intercept and standardized regression coefficients (in parentheses), partial R^2, as well as four statistical "goodness-of-fit" measures, R^2 and adjusted R^2 (Adj-R^2), root mean squared error (RMSE) and predicted residual sum of squares (PRESS). Regression coefficients and intercept are statistically significant at $P < 0.05$.

Response variable	Regression model	Partial R^2	AIC	R^2	Adj-R^2	RMSE	PRESS
SoCal							
RICHTOL	Intercept (6.419)		−95	0.68	0.67	0.424	10.7
	WS_PopDen_L (0.511)	0.404					
	Rip_RdDens_L (0.174)	0.274					
EPTR	Intercept (5.702)		120	0.59	0.58	2.789	454.9
	WS_PopDen_L (−2.106)	0.523					
	Rip_Slope_L (1.510)	0.069					
RICH	Intercept (21.729)		223	0.55	0.52	7.038	3007.6
	WS_PopDen_L (−8.581)	0.341					
	WS_MmStreams_A (−2.624)	0.118					
	WS_Shrub_A (−4.691)	0.087					
Blue_Mt							
RICHTOL	Intercept (3.98)		−219	0.45	0.44	0.446	29.3
	WS_Shrub (0.20)	0.262					
	WS_Ag (0.11)	0.108					
	WS_MnAnnPrecip (−0.02)	0.085					
EPTRp	Intercept (48.155)		629	0.41	0.40	8.996	30.3
	WS_Shrub (−4.956)	0.217					
	WS_Pasture (−3.212)	0.140					
	WS_Slope (0.2.874)	0.057					
Will_V							
RICHTOL	Intercept (5.960)		−124	0.75	0.74	0.380	14.3
	WS_Ag+Urb_SQ (0.327)	0.676					
	WS_MnAnnPrecip_SQ (−0.258)	0.053					
	Rip_Ag+Urb_SQ (0.124)	0.017					
EPTR	Intercept (7.917)		−115	0.72	0.71	3.343	1110.5
	WS_Ag+Urb_SQ (−2.836)	0.647					
	WS_MnAnnPrecip_SQ (2.731)	0.071					
NONINSRp_SQ	Intercept (5.246)		−116	0.72	0.71	0.834	69.4
	WS_Ag+Urb_SQ (0.698)	0.682					
	WS_MnAnnPrecip_SQ (−0.422)	0.028					
	Rip_Max-Elev_SQ (−0312)	0.013					
PLECORp	Intercept (8.252)		−107	0.69	0.68	4.403	1946.9
	WS_Ag+Urb (−4.896)	0.644					
	Soil_Mod-Infil (2.206)	0.047					

L: log 10(X+1) transformed; A: arcsine transformed; SQ: square root transformed.

{arcsine}, WS_MnAnnPrecip, WS_PopDen, and WS_Slope, respectively) (Table 2). All models included watershed population density, which was the best single explanatory variable (Table 2). For RICHTOL, the best model included the log of watershed population density and the log of riparian road density (Table 2). Increases in these two variables resulted in an increased mean tolerance of the taxa present at a site. Additional environmental variables provided little or no reduction in AIC. The observed versus fitted plot for RICHTOL showed a slight bias for overestimation of fitted points at low values (Fig. 4).

The model for EPTR included log of riparian slope in addition to log of population density (Table 2). Including additional environmental variables decreased AIC by three or four points, but R^2 was only improved by about 10%, and the additional variables were not significant at $P < 0.05$ in the regression models. For these reasons we chose the two variable model as the best. The model indicates that EPTR declines with increasing watershed population density but that steeper riparian slopes tend to ameliorate the effect.

The model for the invertebrate metric RICH was the most complex, it included three variables—log of population density,

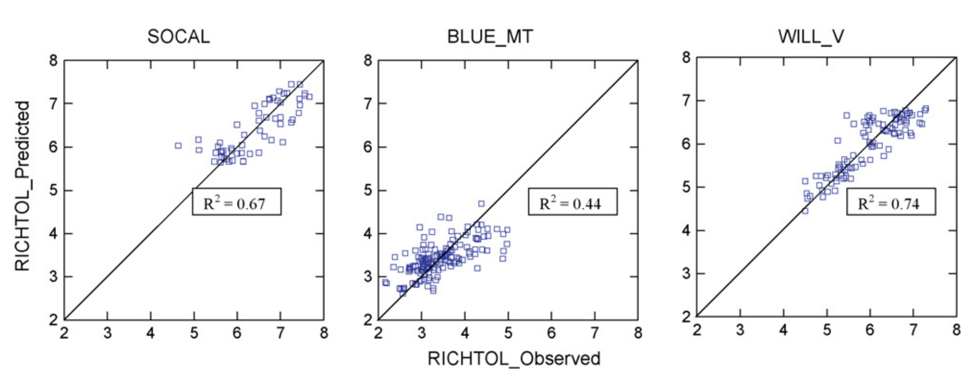

Fig. 4. Predicted vs. observed richness weighted tolerance values (RICHTOL) from MLR models developed for Southern California (SoCal), Blue Mountains (Blue_Mt) and Willamette Valley (Will_V).

percentage of manmade channels (arcsine) and percentage of shrubland (arcsine) in the watershed (Table 2). Similar to that found with RICHTOL, additional environmental variables provided little or no reduction in AIC for RICH metric. Total taxa richness declined as the environmental variables increased.

3.2. Blue mountains

Two macroinvertebrate response variables were retained for model development in Blue Mountains, percent EPT richness (EPTRp) and RICHTOL, along with six watershed explanatory variables including percent pasture (WS_Pasture); shrub, agriculture, and forest landcovers; and mean annual precipitation and mean slope. The model for RICHTOL included percent shrub, percent agriculture, and mean annual precipitation (Table 2). As watershed area in shrub and agricultural land increased, the number of tolerant taxa increased. The response was dampened by the amount of annual precipitation. Watersheds with higher annual rainfall had lower numbers of tolerant taxa. Precipitation was positively correlated with percent forest and elevation. The observed versus fitted plot for RICHTOL showed a relatively high degree of departure from the 1:1 line, with significant scatter at higher values of RICHTOL (Fig. 4). The best model for EPTRp included percent shrub and pasture and mean slope (Table 2). Increases in shrub and pasture within a watershed resulted in lower percent EPT richness. The response was dampened by increases in watershed slope.

3.3. Willamette valley

Four macroinvertebrate response variables were retained for model development in Willamette Valley: RICHTOL, EPTR, the square root (sqrt) of percent noninsect richness (NONINSRp) and percent Plecoptera richness (PLECORp). There were six watershed scale and three riparian scale environmental explanatory variables retained. The watershed variables were percent agriculture plus urban land-use (WS_Ag + Urb), percent forest (WS_Forest), mean annual precipitation, mean slope, mean elevation (WS_Mn-Elev) and mean moderate soil infiltration rate (Soil_Mod-Infil). The three riparian scaled variables were percent agriculture plus urban land-use (Rip_Ag + Urb), percent forest (Rip_Forest) and maximum elevation (Rip_Max-Elev).

The best model for RICHTOL included watershed scale percent agriculture plus urban (sqrt), mean annual precipitation (sqrt), and riparian scaled agriculture plus urban (sqrt) (Table 2). As the total agriculture plus urban land-use increased at both the watershed and riparian scales, the number of tolerant taxa increased. The response was reduced with an increase in the mean annual precipitation. The observed vs. fitted points for tolerant taxa richness (RICHTOL) was tightly clustered along the 1:1 line, perhaps with a slight underestimate bias at high values (Fig. 4).

For PLECORp, the best model included WS_Ag + Urb and Soil_Mod-Infil suggesting that as the total percent watershed area of agriculture plus urban land-use increases the percent richness of stoneflies decreases (Table 2). This relationship was ameliorated by watersheds having higher mean moderate soil infiltration rates. As expected, the model for EPTR was similar to the PLECORp model since Plecoptera is the "P" in EPT; the EPTR model included the same land-use types (WS_Ag + Urb) and mean annual precipitation was substituted in place of soil infiltration rate. Both models were able to explain similar amounts of variation, 68–71%. The EPTR model suggests that as the amount of total area of agricultural plus urban land-use increases the number of EPT taxa decreases. The response was reduced in watersheds with higher mean annual precipitation.

The best model for percent noninsect richness (sqrt) included watershed agriculture plus urban land-use and mean annual precipitation as found in two of the other models but also included riparian maximum elevation (sqrt) (Table 2). This model suggests that as the amount of total agriculture plus urban land-use increases the percentage of noninsect taxa increases. The response was reduced in watersheds with higher precipitation and higher riparian elevation.

4. Discussion

Considering the differences in the natural environmental settings among regions and that we started model development with 120 potential macroinvertebrate metrics, there was remarkable commonality in the macroinvertebrate response metrics that were selected in the best models within each region (Table 3). The response variables for each region included richness of tolerant taxa (RICHTOL) and total EPT taxa (richness or percent richness). Tolerant taxa and EPT richness are commonly used metrics in bioassessment and have been shown to be sensitive to disturbance in a variety of geographic regions. Cuffney et al. (2005) found RICHTOL to have a strong consistent correlation (R^2 = 0.60–0.85) to an index of urban intensity in three distinct metropolitan regions with contrasting climates and topography (Boston, MA; Birmingham, Alabama; Salt Lake City, UT). Across these three metropolitan regions there was a decrease in EPT taxa richness of over 67% when comparing low urban sites to high urban sites. Waite et al. (2008) found that EPTR had one of the highest correlations (R^2 > 0.72) of all variables to a variety of land-use measures (population density, impervious surface, urban + agriculture and urban intensity index) in the Willamette Valley and it was also highly correlated (R^2 > 0.75) to various water quality measures of human disturbance (e.g., total pesticides, pesticide toxicity index, toxic equivalents (TEQ) index and total phosphorus). In addition to tolerant taxa and EPT richness, best models were developed for three other macroinvertebrate metrics. Southern California was the only region that created a significant model for total invertebrate richness (RICH) and Willamette Valley the only region for noninsect richness (NONINSRp) and stonefly richness (PLECORp).

Land-use variables were significant predictors in all three regions, although the specific variables selected within each model differed between regions (Tables 2 and 3). Southern California had the largest range of population density and road density compared to the other two regions, the maximum population density in Southern California was over twice the maximum of the other two

Table 3
List of dependent variables (macroinvertebrate metrics) for models for each region and model R^2 values. Values in parentheses = number of significant explanatory variables retained in the model.

	SoCal	Blue_Mt	Will_V	Response variables		
				SoCal	Blue_Mt	Will_V
Model R^2	0.67 (2)	0.44 (3)	0.74 (3)	RICHTOL	RICHTOL	RICHTOL
Model 2 R^2	0.58 (2)	0.40 (3)	0.71 (2)	EPTR	EPTRp	EPTR
Model 3 R^2	0.52 (3)	–	0.71 (3)	RICH	–	NONINSRp
Model 4 R^2	–	–	0.68 (2)	–	–	PLECORp

regions (Fig. 3). Therefore, it was not surprising that these two variables were dominant explanatory variables in all three of the best models developed for Southern California. Similarly, Willamette Valley had higher ranges in percent agriculture and percent agriculture plus urban than the other two regions and the latter variable was the dominant variable in all of the Willamette Valley models.

Blue Mountains also showed a response due to land-use/land-cover (shrub and pasture); although the amount of variation in invertebrate metrics explained was much lower than either of the other two regions. The Blue Mountains data set had little agriculture or urban land-use, but according to Hubler (2007) this was partly due to a relatively high rate of denied access to stream sites by land owners in many of the highly agricultural areas, reducing the number of sites with higher potential disturbance. Though the 147 sites used within this study were randomly selected, the high rate of denied access limited our ability to model the macroinvertebrate response over the complete disturbance gradient. This reduced disturbance gradient is reflected in the narrow range of macroinvertebrate tolerance values (RICHTOL) seen in Blue Mountains compared to either Southern California or Willamette Valley (Fig. 4). Therefore, it is somewhat surprising that any significant models were developed for Blue Mountains given the truncated disturbance gradient. We believe this is evidence of the robust sensitivity of watershed models developed using macroinvertebrates as response variables.

Models developed for the three regions were able to explain from 41 to 74% of the variation in macroinvertebrate metrics due to changes in some measure of land-use and natural factors (Table 2). A number of studies using fish metrics (i.e., IBI, index of biotic integrity) as response variables were able to explain similar amounts of variation (Kennen et al., 2005; Kaufmann and Hughes, 2006) based on various combinations of watershed and riparian scaled land-use. Steen et al. (2006) developed an MLR model that was able to predict the presence of brook trout at sites throughout the lower peninsula of Michigan with an accuracy of 86% and absence of brook trout at sites with 72% accuracy. The three explanatory variables were July air temperature, stream size, and percent forest, the converse of percent agriculture plus urban. The database they used to develop these models included 900 sites spanning 22 years and an independent database with 628 sites over a geographic area larger than the majority of states in the U.S. This suggests that a very large n (i.e., the total number of stream sites) is likely needed to have a high degree of predictive power or explain a large amount of biotic variability over a relatively large geographic area. Nevertheless, in the Willamette Valley, with a much smaller number of sites ($n = 96$) covering a smaller region, we were able to explain over 70% of the variation of several macroinvertebrate metrics with only two or three explanatory variables. However, because there is no known independent data set in any of these regions, we have not been able to test our prediction accuracy. Van Sickle et al. (2004) also modeled fish and macroinvertebrates as a function of watershed land-use/land-cover, physiographic and stream flow variables in the Willamette River Basin. They developed regression models with two to five explanatory variables for fish IBI and invertebrate EPT richness. All models developed had the amount of agricultural and urban land-use within the watershed as separate measures of human disturbance. Some models also included measures such as stream power, stream order, stream gradient, or watershed area. Invertebrate models were based on 55 sampled streams within the Willamette Valley Ecoregion and were able to explain 0.52 and 0.61% of the variance (R^2) for invertebrate O/E (observed/expected, 4 variable model) and EPT richness (3 variable model) indicators, respectively. Many of the sites used by Van Sickle et al. (2004) were also included in the data set used in this study.

The spatial scale for optimal model development is an important consideration with practical implications. Ideally, researchers and managers would like models to be highly parsimonious and applicable over large geographic areas; however, the large variation in natural physiographic and biotic conditions often makes this unrealistic (Hawkins et al., 2008; Ode et al., 2008; Paulsen et al., 2008; Utz et al., 2009). In this study we used ecoregions as our primary blocking variable. Comparisons made between two bordering ecoregions in Michigan by Diana et al. (2006) indicated that when the two ecoregions were modeled together, MLR models using instream habitat variables were better predictors of fish IBIs than models using land-use variables. However, when the two watersheds were modeled separately, urban and agricultural land-use variables became more important explanatory factors. Using percent wetland in riparian buffer and percent urban and agriculture in the watershed, they were able to predict fish IBI scores with an adjusted R^2 of 0.79 in the Raisin River basin. In the Huron River basin, the combination of agriculture plus urban performed better than each land-use variable individually ($R^2 = 0.76$) (Diana et al., 2006). Kaufmann and Hughes (2006) also found that models for predicting fish IBI were better when stream sites within the Coast Range of Oregon were broken up by geology (sedimentary and volcanic) and catchment size (< or >15 km^2). Important explanatory variables included road density and an index of riparian anthropogenic land-use and instream variables of percent bedrock and summer discharge.

Many studies have shown that watershed or stream size is an important natural determinate of biological assemblages (Waite et al., 2000; Allan, 2004; Infante et al., 2006; Kaufman and Hughes 2006; Ode et al., 2008). For this reason we selected only sites from watersheds ranging from 13 to 259 km^2 (corresponds approximately to second to fourth order streams in the western United States) to focus more on land-use disturbance than natural gradients. A standard axiom in building models is that there are inherent tradeoffs in the ability of models to reflect reality, precision, and generality. When models are developed for larger spatial areas (i.e., generality) the precision and reality of models often decline (Ode et al., 2008). The research described above and results from this study suggest that as the modeled spatial scale increases, natural environmental setting variables become more important and likely swamp differences in anthropogenic impacts, and therefore it is important to block or classify sites by natural variables with large variation across spatial scales (e.g., elevation, basin size, physiographic provinces, climate). Because of the large gaps in distribution of sites between the three regions and the large differences in natural variables, we did not attempt to develop one model across all three regions. However, there is enough commonality in the response metrics and explanatory variables that future evaluation of model error structure and causal links is warranted through the application of more advanced modeling methods.

In Willamette Valley, combining agriculture and urban land-use into one variable performed better than entering each variable individually. For EPTR the variance explained increased from 59 to 65%. The combined variable likely provides more information on general watershed disturbance and possibly smoothes out the distribution of data by filling in uneven gaps in the land-use data. Waite et al. (2008) found that they could not distinguish the effects of agricultural land-use from urbanization for three biotic assemblage measures (algae, macroinvertebrates, and fish) in the Willamette Valley. Wang et al. (2001) found larger negative effects of urbanization than agriculture on fish IBIs in Wisconsin streams, and Moerke and Lamberti (2006) suggested that even low percentages of urban land-use (<40%) had similar effects on fish and water quality as higher amounts of agricultural land-use (>50%). Other researchers have found similar negative influences of the two land-use types (Van Sickle et al., 2004; Diana et al., 2006; Waite et al., 2008). Stanfield and Kilgour (2006) suggest that "there is value in developing an overall metric of catchment disturbance" such as the combination of agriculture plus urban land-use. For Southern California and Blue Mountains, combining agriculture and urban land-use did not improve the respective models because those regions were dominated by a single human disturbance. In Willamette Valley, combining these variables into a “catchment disturbance” variable did show considerable improvement in all four of the models because both agriculture and urban land-uses are large.

In another Willamette Valley model (RICHTOL), the amount of agriculture plus urban land-use within the riparian corridor was added as a significant explanatory variable even though watershed scaled agriculture plus urban was already contained within the model. This suggests that land-use disturbance within the riparian buffer helps explain variation in macroinvertebrates above and beyond the watershed measure of land-use disturbance. The effects of riparian land-use on streams may be more direct or at least have a shorter causal pathway. Wang et al. (2006a,b) found that watershed characteristics had more influence on fish assemblages in disturbed systems and local instream factors greater influence in undisturbed systems. They suggested that in minimally disturbed streams, watershed, riparian, and instream conditions are in dynamic equilibrium, providing a stable ecosystem with the natural biotic communities adapted to this dynamic interplay of causal scales. When human disturbance alters this equilibrium, the stream establishes a new equilibrium, forcing the resident organisms to adapt or respond to the change in the environment. Results from our study suggest that watershed and local riparian disturbances both have influences on biota that are not necessarily mutually exclusive. In addition, although watershed variables tended to be better predictors than riparian scaled predictors in this study, this may be due more to the fact that the riparian data was generated from the same large remote-sensing NLCD data collected at a coarse resolution (minimum pixel scale of 30 m × 30 m) and less due to the inherent influence of riparian zones on water quality and biological integrity in streams. We suggest that assessment of riparian land-use/land-cover data at finer resolution should be considered in future watershed modeling efforts.

In addition to the watershed and riparian variables describing land-use disturbance, natural factors were also important explanatory variables in the three regions (Table 3). Mean annual precipitation and mean watershed slope occurred in at least one model from all regions. In Willamette Valley, natural factors related to maximum riparian elevation and moderate soil infiltration rate (Soil_Mod-Infil) were also important. Around the world, land-use development for urban and agriculture generally follows natural physiographic gradients, therefore these natural factors are intertwined with gradients of human disturbance (Allan, 2004; Cuffney et al., 2005). Urban and agricultural watershed development in the Willamette River basin and surrounding area has occurred in the flat valley lowlands rather than in the higher elevation foothills and mountains (Uhrich and Wentz, 1999; Waite et al., 2008). However, precipitation and channel slope also follow this natural topography, resulting in more precipitation and higher slopes in the higher elevation foothills. When the 20 highest elevation sites were removed from the Willamette Valley database and the models rerun, mean precipitation still was a significant explanatory variable and the amount of overall variation explained went down. The intertwining of these natural and human gradients are often complex, yet this type of covariance can affect comparison of results and application of models to different regions affected by unique natural factors.

In summary, we were able to use widely available digital coverages of land-use and land-cover data summarized at the watershed and riparian scale as explanatory variables to predict commonly used macroinvertebrate metrics. MLR models with only two to three explanatory variables were able to explain between 41 and 74% of the variation in macroinvertebrate metrics. In each region, the best model contained some land-use measure of urban and/or agriculture, yet often the model was improved by including a natural explanatory variable such as mean annual precipitation or mean watershed slope. Two macroinvertebrate metrics were common among all three regions: the metric that summarizes the richness of tolerant macroinvertebrates (RICHTOL) and some form of EPT richness (the combination of the aquatic insect orders Ephemeroptera, Plecoptera and Trichoptera). Best models were developed for the same two invertebrate metrics even though the geographic regions have distinct differences in precipitation, geology, elevation, slope, population density, and land-use. With further development, models like these can be used to better understand causal linkages between environmental drivers and stream biological attributes or condition. Further, such models not only represent the foundation of more complex mechanistic models but may also be highly useful tools for researchers or managers for predicting biological indicators of stream condition at unsampled sites.

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Appendix 1. Sources of geographical information system (GIS) and digital data used in model development

Spatial dataset	Data source	Source data format	Processing format	Resolution/scale	Reference
Hydrography	National Hydrography Dataset (NHD)	Vector	Vector	1:24,000	U.S. Geological Survey, National Hydrography Dataset, Digital data, Accessed January 2007 at http://nhd.usgs.gov/data.html
Land-cover 1992	National Land-Cover Dataset 1992 (NLCD)	Raster	Vector	30 m	U.S. Geological Survey, National Land-Cover Dataset 1992, Digital data, Accessed March 2003 at http://landcover.usgs.gov/natllandcover.php
Land-cover 2001	National Land-Cover Dataset 2001 (NLCD)	Raster	Vector	30 m	U.S. Geological Survey, National Land-Cover Dataset 2001, Digital data, Accessed January 2007 at http://www.mrlc.gov/
Elevation	National Elevation Dataset (NED)	Raster	Raster	10 m	U.S. Geological Survey, National Elevation Dataset, Digital data, Accessed May 2007 at http://seamless.usgs.gov/

Appendix 1 (*Continued*)

Spatial dataset	Data source	Source data format	Processing format	Resolution/scale	Reference
Slope	National Elevation Dataset (NED)	Raster	Raster	10 m	U.S. Geological Survey, National Elevation Dataset, Digital data, Accessed May 2007 at http://seamless.usgs.gov/
Road Networks	U.S. Census Bureau Tiger	Vector	Vector	1:100,000	U.S. Census Bureau, TIGER line data, Digital data, Accessed May 2007 at http://www.census.gov/geo/www/tiger/
	Ground Transportation Roads Publications Arc	Vector	Vector	1:24,000	Oregon BLM, Ground Transportation Roads Publication Arc, Digital data, Accessed July 2007 at http://www.blm.gov/or/gis/
Soil Infiltration Capacity	USDA NRCS STATSGO	Vector	Vector	1:250,000	Natural Resource Conservation Service, STATSGO soils data, Digital data, Accessed May 2007 at http://datagateway.nrcs.usda.gov/
Population Density	U.S. Census Bureau Census 2000	Vector	Raster	30 m	U.S. Census Bureau, Census 2000, Digital data, Accessed May 2007 at http://www.census.gov/main/www/cen2000.html
Precipitation	Oregon State University PRISM	Raster	Raster	30 arc-second	PRISM Group, Oregon State University, Precipitation data for the U.S., Digital data, Accessed May 2007 at http://www.prismclimate.org
Dams	National Inventory of Dams	Vector	Vector	Various	U.S. Army Corps of Engineers, National Inventory of Dams, Digital data, Not publicly available

References

Allan, J.D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annu. Rev. Ecol. Evol. Syst. 35, 257–284.

Austin, M., 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. Ecol. Model. 200, 1–19.

Barbour, M.T., Gerritsen, J., Snyder, B.D., Stribling, J.B., 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates, and fish. 2nd ed., U.S. Environmental Protection Agency, Office of Water, EPA Report 841-B-99-002, Washington, DC.

Booth, D.B., 2005. Challenges and prospects for restoring urban streams: a perspective from the Pacific Northwest of North America. J. N. Am. Benthol. Soc. 24, 724–737.

Bryant, W.L., Goodbred, S.L., Leiker, T.L., Inuoye, L., Johnson, B.T., 2007. Use of chemical analysis and assays of semi-permeable membrane devices extracts to assess the response of bioavailable organic pollutants in streams to urbanization in six metropolitan areas of the United States. U.S. Geological Survey Scientific Investigations Report 2007-5113, 46 p., 2 app., accessed May 17, 2007, at http://pubs.water.usgs.gov/sir2007-5113.

Burnett, K.M., Reeves, G.H., Clarke, S.E., Christiansen, K.R., 2006. Comparing riparian and catchment influences on stream habitat in a forested, montane landscape. In: R.M. Hughes, L. Wang, P.W. Seelbach, (Eds.), Landscape influences on stream habitats and biological assemblages. Am. Fish. Soc., Symp. 48, 175–198.

Cabecinhaa, E., Silva-Santosa, P., Cortesb, R., Cabral, J., 2007. Applying a stochastic-dynamic methodology (StDM) to facilitate ecological monitoring of running waters, using selected trophic and taxonomic metrics as state variables. Ecol. Modeling: 4787 (19 p). Available at www.sciencedirect.com.

Carlisle, D.M., Falcone, J., Meador, M.R., 2008. Predicting the biological condition of streams: use of geospatial indicators of natural and anthropogenic characteristics of watersheds. Environ. Monit. Assess., 1–18, doi:10.1007/s10661-008-0256-z.

Carpenter, K.D., Sobieszczyk, S., Arnsberg, A.J., Rinella, F.A., 2008. Pesticide occurrence and distribution in the lower Clackamas River basin, Oregon, 2000–2005. U.S. Geological Survey Scientific Investigation Report 2008-5027. 98 p.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: Users Manual/Tutorial PRIMER-E: Plymouth, England, 190 p.

Cuffney, T.F., 2003. User's manual for the National Water-Quality Assessment Program Invertebrate Data Analysis System (IDAS) software: Version 3. U.S. Geological Survey Open-File Report 03-172, Raleigh, North Carolina. Available at: ftp://ftpext.usgs.gov/pub/er/nc/raleigh/tfc/IDAS/.

Cuffney, T.F., Zappia, H., Giddings, E.M.P., Coles, J.F., 2005. Urbanization effects on benthic macroinvertebrate assemblages in contrasting environmental settings: Boston, Birmingham, and Salt Lake City. In: L.R. Brown, R.H. Gray, R.M. Hughes, M.R. Meador (Eds.). Effects of urbanization on stream ecosystems. Am. Fish. Soc., Symp. 47, 361–408.

Cuffney, T.F., Bilger, M.D., Haigler, A.M., 2007. Ambiguous taxa: effects on the characterization and interpretation of invertebrate assemblages. J. N. Am. Benthol. Soc. 26, 286–307.

Cushman, S.A., McKenzie, D., Peterson, D.L., Littell, J., McKelvey, K.S., 2007. Research agenda for integrated landscape modeling. Gen. Tech. Rep. RMRS-GTR-194. Fort Collins, CO: U.S. Department of Ag, Forest Service, Rocky Mountain Research Station. 50 p.

Davies, S.P., Jackson, S.K., 2006. The biological condition gradient: a descriptive model for interpreting change in aquatic ecosystems. Ecol. Appl. 16, 1251–1266.

Davis, W.S., Simon, T.P. (Eds.), 1995. Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making. Lewis Publishers, Boca Raton, FL.

Diana, M.J., Allan, J.D., Infante, D., 2006. The influence of physical habitat and land use on stream fish assemblages in southeastern Michigan. In: R.M. Hughes, L.Wang, P.W. Seelbach, (Eds.), Landscape influences on stream habitats and biological assemblages. Am. Fish. Soc., Symp. 48, 359–374.

Grace, J.B., 2006. Structural Equation Modeling and Natural Systems. Cambridge University Press, New York, 365 p.

Hawkins, C.P., Norris, R.H., Gerritsen, J., Hughes, R.M., Jackson, S.K., Johnson, R.K., Stevenson, R.J., 2000. Evaluation of the use of landscape classifications for the prediction of freshwater biota: synthesis and recommendations. J. N. Am. Benthol. Soc. 19, 541–556.

Hawkins, C.P., Paulsen, S.G., Van Sickle, J., Yuan, L.L., 2008. Regional assessments of stream ecological condition: scientific challenges associated with the USA's national Wadeable Streams Assessment. J. N. Am. Benthol. Soc. 27, 805–807.

Hering, D., Johnson, R., Kramm, S., Schmutz, S., Szoszkiewicz, K., Verdonschot, P., 2006. Assessment of European streams with diatoms, macrophytes, macroinvertebrates and fish: a comparative metric-based analysis of organism response to stress. Fresh. Biol. 51, 1757–1785.

Herlihy, A.T., Paulsen, S.G., Van Sickle, J., Stoddard, J.L., Hawkins, C.P., Yuan, L.L., 2008. Striving for consistency in a national assessment: the challenges of applying a reference-condition approach at a continental scale. J. N. Am. Benthol. Soc. 27, 860–877.

Hubler, S., 2007. Wadeable Stream Conditions in Oregon. Oregon Department of Environmental Quality Laboratory Division—Watershed Assessment Section. DEQ07-LAB-0081-TR.

Infante, D.M., Wiley, M.J., Seelbach, P.W., 2006. Relationships among channel shape, catchment characteristics, and fish in lower Michigan streams. In: R.M. Hughes, L.Wang, P.W. Seelbach, (Eds.), Landscape influences on stream habitats and biological assemblages. Am. Fish. Soc., Symp. 48, 359–374.

Johnson, R.K., Furse, M.T., Hering, D., Sandin, L., 2007. Ecological relationships between stream communities and spatial scale: implications for designing catchment-level monitoring programmes. Fresh. Biol. 52, 939–958.

Kaufmann, P.R., Hughes, R.M., 2006. Geomorphic and anthropogenic influences on fish and amphibians in Pacific Northwest coastal streams. In: R.M. Hughes, L.Wang, P.W. Seelbach, (Eds.), Landscape influences on stream habitats and biological assemblages. Am. Fish. Soc., Symp. 48, 429–456.

Kennen, J.G., Chang, M., Tracy, B.H., 2005. Effects of landscape change on fish assemblage structure in a rapidly growing metropolitan area in North Carolina, USA. In: L.R. Brown, R.H. Gray, R.M. Hughes, M.R. Meador, (Eds.), Effects of urbanization on stream ecosystems. Am. Fish. Soc., Symp. 47, 39–52.

Leathwick, J.R., Rowe, D., Richardson, J., Elith, J., Hastie, T., 2005. Using multivariate adaptive regression splines to predict the distributions of New Zealand's freshwater diadromous fish. Fresh. Biol. 50, 2034–2052.

Meador, M.R., Coles, J.F., Zappia, H., 2005. Fish assemblage responses to urban intensity gradients in contrasting metropolitan areas—Birmingham, Alabama and Boston, Massachusetts. Am. Fish. Soc. Symp. 47, 409–423.

Moerke, A.H., Lamberti, G.A., 2006. Relationships between land use and stream ecosystems: a multistream assessment in Southwestern Michigan. In: R.M. Hughes, L.Wang, P.W. Seelbach, (Eds.), Landscape influences on stream habitats and biological assemblages. Am. Fish. Soc., Symp. 48, 323–338.

Morgan, R.P., Cushman, S.F., 2005. Urbanization effects on stream fish assemblages in Maryland, USA. J. N. Am. Benthol. Soc. 24, 643–655.

Oberdorff, T., Pont, D., Hugueny, B., Chessel, D., 2001. A probabilistic model characterizing fish assemblages of French rivers: a framework for environmental assessment. Fresh. Biol. 46, 399–415.
Ode, P.R., Hawkins, C.P., Mazor, R.D., 2008. Comparability of biological assessments derived from predictive models and multimetric indices of increasing geographic scope. J. N. Am. Benthol. Soc. 27, 967–985.
Ode, P.R., Rehn, A.C., May, J.T., 2005. A quantitative tool for assessing the integrity of southern coastal California streams. Environ. Manage. 35, 493–504.
Osborne, P.E., Suaŕez-Seoane, S., 2002. Should data be partitioned spatially before building large-scale distribution models? Ecol. Model. 157, 249–259.
Paul, M.J., Meyer, J.L., 2001. Streams in the urban landscape. Annu. Rev. Ecol. Syst. 32, 333–365.
Paulsen, S.G., Mayio, A., Peck, D.V., Stoddard, J.L., Tarquinio, E., Holdsworth, S.M., Van Sickle, J., Yuan, L.L., Hawkins, C.P., Herlihy, A.T., Kaufmann, P.R., Barbour, M.T., Larsen, D.R., Olsen, A.R., 2008. Condition of stream ecosystems in the US: an overview of the first national assessment. J. N. Am. Benthol. Soc. 27, 812–821.
Pont, D., Hugueny, B., Beier, U., Goffaux, D., Melcher, A., Noble, R., Rogers, C., Roset, N., Schmutz, S., 2006. Assessing river biotic condition at a continental scale: a European approach using functional metrics and fish assemblages. J. Appl. Ecol. 43, 70–80.
R Development Core Team., 2007. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (Available from: http://www.R-project.org).
Rosenberg, D.M., Resh, V.H. (Eds.), 1993. Freshwater Biomonitoring and Benthic Macroinvertebrates. Routledge, Chapman and Hall, Inc., New York.
Roy, A.H., Freeman, M.C., Freeman, B.J., Wenger, S.J., Ensign, W.E., Meyer, J.L., 2005. Investigating hydrologic alteration as a mechanism of fish assemblage shifts in urbanizing streams. J. N. Am. Benthol. Soc. 24, 656–678.
SAS (Statistical Analysis Software), 2006. Stat user's guide, version 9.2, 4th ed., volume 2, SAS Institute, Cary, NC.
Stanfield, L.W., Kilgour, B.W., 2006. Effects of percent impervious cover on fish and benthos assemblages and instream habitats in Lake Ontario tributaries. In: R.M. Hughes, L.Wang, P.W. Seelbach, (Eds.), Landscape influences on stream habitats and biological assemblages. Am. Fish. Soc., Symp. 48, 577–600.
Steen, P.J., Passino-Reader, D.R., Wiley, M.J., 2006. Modeling brook trout presence and absence from landscape variables using four different analytical methods. In: R.M. Hughes, L. Wang, P.W. Seelbach, (Eds.), Landscape influences on stream habitats and biological assemblages. Am. Fish. Soc., Symp. 48, 513–532.
Stoddard, J.L., Herlihy, A.T., Peck, D.V., Hughes, R.M., Whittier, T.R., Tarquinio, E., 2008. A process for creating multimetric indices for large-scale aquatic surveys. J. N. Am. Benthol. Soc. 27, 878–891.
Turak, E., Ferrier, S., Barrett, T., Mesley, E., Drielsma, M., Manion, G., Doyle, G., Stein, J., Gordon, G., 2010. Planning for the persistence of river biodiversity: exploring alternative futures using process-based models. Fresh. Biol., doi:10.1111/j.1365-2427.2009.02394.x.
Uhrich, M.A., Wentz, D.A., 1999. Environmental setting of the Willamette Basin, Oregon. U.S. Geological Survey Water-Resources Investigations Report 97-4082-A. 20 p.
U.S. Census Bureau, 2000. Census 2000 redistricting data summary file: U.S. Census Bureau Technical Documentation Public Law 94–171, 223 p.
U.S. Geological Survey, 2005. National land cover database 2001 (NLCD 2001): U.S. Geological Survey database, accessed 2007 at http://www.mrlc.gov/.
U.S. Geological Survey, 2007. National Hydrography Dataset (High Resolution), Digital data, Accessed November, 2007 at URL: http://nhd.usgs.gov/data.html.
Utz, R.M., Hilderbrand, R.H., Boward, D.M., 2009. Identifying regional differences in threshold responses of aquatic invertebrates to land cover gradients. Ecol. Indic. 9 (3), 556–567.
Van Sickle, J., Baker, J., Herlihy, A., Bayley, P., Gregory, S., Haggerty, P., 2004. Projecting the biological condition of streams under alternative scenarios of human land use. Ecol. Appl. 14, 368–380.
Waite, I.R., Herlihy, A.T., Larsen, D.P., Klemm, D.J., 2000. Comparing strengths of geographic and nongeographic classifications of stream benthic macroinvertebrates in the Mid-Atlantic Highlands, USA. J. N. Am. Benthol. Soc. 19, 429–441.
Waite, I.R., Carpenter, K.D., 2000. Associations among fish assemblage structure and environmental variables in Willamette Basin streams, Oregon. Trans. Am. Fish. Soc. 129, 754–770.
Waite, I.R., Herlihy, A.T., Larsen, D.P., Urquhart, N.S., Klemm, D.J., 2004. The effects of macroinvertebrate taxonomic resolution in large landscape bioassessments: an example from the Mid-Atlantic Highlands. USA. Fresh. Biol. 49, 474–489.
Waite, I.R., Sobieszczyk, S., Carpenter, K.D., Arnsberg, A.J., Johnson, H.M., Hughes, C.A., Sarantou, M.J., Rinella, F.A., 2008. Effects of urbanization on stream ecosystems in the Willamette River Basin and surrounding area, Oregon and Washington. Chapter D of "Effects of urbanization on stream ecosystems in six metropolitan areas of the United States. Scientific Investigations Report 2006-5101-D. 62p.
Walsh, C.J., Fletcher, T.D., Ladson, A.R., 2005. Stream restoration in urban catchments through redesignin stormwater systems: looking to the catchment to save the stream. J. N. Am. Benthol. Soc. 24, 690–705.
Wang, L.J., Lyons, J., Kanehl, P., Bannerman, R., 2001. Impacts of urbanization on stream habitat and fish across multiple scales. Environ. Manage. 28, 255–266.
Wang, L., Seelbach, P.W., Hughes, R.M., 2006. Introduction to landscape influences on stream habitats and biological assemblages. In: R.M. Hughes, L. Wang, P.W. Seelbach, (Eds.). Landscape influences on stream habitats and biological assemblages. Am. Fish. Soc., Symp. 48, 1–24.
Wang, L., Seelbach, P.W., Lyons, J., 2006. Effects of levels of human disturbance on the influence of catchment, riparian, and reach-scale factors on fish assemblages. In: R.M. Hughes, L. Wang, P.W. Seelbach, (Eds.). Landscape influences on stream habitats and biological assemblages. Am. Fish. Soc., Symp. 48, 199–220.
Wisseman, B., 2004. Aquatic Biology Associates, Corvallis, OR (pers. commun.).