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FORECASTING RELATIVE IMPACTS OF LAND USE ON ANADROMOUS FISH HABITAT TO GUIDE CONSERVATION PLANNING

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Abstract. Land use change can adversely affect water quality and freshwater ecosystems, yet our ability to predict how systems will respond to different land uses, particularly rural-residential development, is limited by data availability and our understanding of biophysical thresholds. In this study, we use spatially explicit parcel-level data to examine the influence of land use (including urban, rural-residential, and vineyard) on salmon spawning substrate quality in tributaries of the Russian River in California. We develop a land use change model to forecast the probability of losses in high-quality spawning habitat and recommend priority areas for incentive-based land conservation efforts. Ordinal logistic regression results indicate that all three land use types were negatively associated with spawning substrate quality, with urban development having the largest marginal impact. For two reasons, however, forecasted rural-residential and vineyard development have much larger influences on decreasing spawning substrate quality relative to urban development. First, the land use change model estimates 10 times greater land use conversion to both rural-residential and vineyard compared to urban. Second, forecasted urban development is concentrated in the most developed watersheds, which already have poor spawning substrate quality, such that the marginal response to future urban development is less significant. To meet the goals of protecting salmonid spawning habitat and optimizing investments in salmon recovery, we suggest investing in watersheds where future rural-residential development and vineyards threaten high-quality fish habitat, rather than the most developed watersheds, where land values are higher.

Key words: conservation targeting; ecological thresholds; exurban development; forecasting land use change; Oncorhynchus *spp.; Russian River, California; salmonid spawning habitat; urban sprawl; watershed risks.*

Introduction

Land use change is a primary driver of habitat loss and ecosystem degradation at local-to-global scales (Foley et al. 2005), yet our ability to forecast the influence of landscape attributes and future impacts on ecosystems has lagged behind other advances in environmental sciences (Harte 2001). To reduce future losses of biodiversity and ecosystem function, resource managers, decision-makers, and conservation organizations are increasingly requesting information and tools to identify where species and ecosystems are most vulnerable to future land use conversion (Newburn et al. 2005, 2006, Armsworth et al. 2006). Developing spatially explicit projections of land use changes and their consequences has thus emerged as one of the eight grand challenges in environmental science (Clark et al. 2001, National Research Council 2001). In this study, we explore nonlinear thresholds beyond which land use change will result in the degradation of aquatic ecosystems, and then forecast future land use change and its effects on these systems.

Aquatic ecosystems are particularly sensitive to land use activities within their watersheds (e.g., Roth et al. 1996, Harding et al. 1998), and rapid land use changes have contributed to disproportionately high numbers of endangered aquatic species and the decline of economically valuable fisheries, such as anadromous salmonids (Richter et al. 1997, Ricciardi and Rasmussen 1999). The mechanisms by which land use activities affect aquatic ecosystems include elevated production and delivery of fine sediment to streams, which diminish water quality, alter channel morphology, and degrade habitat conditions for organisms ranging from invertebrates to fish (ASCE Task Committee on Sediment Transport and Aquatic Habitats 1992, Soulsby et al. 2001, Greig et al. 2005). The scale of influence and relative contribution of land use activities remain debated (e.g., Strayer et al. 2003), but recent work from Pacific temperate to mediterranean climate watersheds points to watershed-scale rather than local influences driving changes in sedimentation (Pess et al. 2002, Opperman et al. 2005).

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While many factors can limit salmonid spawning and rearing habitat, embeddedness, the extent to which grains of fine sediment (particle size <2 mm) surround spawning-sized substrate, is a key attribute of spawning gravel quality (see Kondolf 2000 for review) that can be affected by watershed-scale land use patterns (e.g., Opperman et al. 2005). Successful incubation requires spawning gravels that have low concentrations of fine sediment, which can fill a redd's interstitial framework and thereby reduce exchange rates of oxygen and metabolic wastes and impede fry emergence (Phillips et al. 1975, Everest et al. 1987, Groot and Margolis 1991). Kondolf (2000) concluded from his review of the literature that salmonid survival and emergence are reduced by 50% when fines exceed 30%. Thus, research elucidating the relative impacts of different land uses on levels of fine sediment in streams can inform management of salmonid populations, and forecasts of future land use changes can be invaluable for species recovery programs. Moreover, forecasts can provide ecological support for rural land use planning (Theobald et al. 2005) and guide conservation programs and planning (Van Sickle et al. 2004, Chan et al. 2006, Newburn et al. 2006).

Forecasting the environmental consequences of land use change requires addressing several challenges, including limited data availability and resolution (Clark et al. 2001, Nilsson et al. 2003, Rindfuss et al. 2004). For example, natural scientists often rely on land-cover classifications derived from remotely sensed imagery, such as Landsat TM, to classify urban development (<1 acre per house; 1 acre = 0.405 ha) and intensive agriculture; however, this imagery cannot distinguish rural-residential development (>1 acre per house; see Plate 1) from more extensive land covers such as forest (Sutton et al. 2006). The omission of low-density development in previous studies may therefore have led to biased parameters in statistical models overestimating the effects of urban development and agriculture as the effects from rural-residential land use were incorrectly attributed to adjacent urban development and agriculture.

Assessing the specific impacts of rural-residential development is particularly important because rural-residential development is the fastest growing land use type in the United States (Heimlich and Anderson 2001, Theobald 2003, Brown et al. 2005; see Plate 1) and is expanding in Canada and Europe (Dubost 1998, Azimer and Stone 2003). Using nighttime satellite imagery, Sutton, Cova, and Elvidge (2006) found that exurban development occupies 14% of U.S. land area, whereas the urban footprint was only 1.7%. Further studies are needed evaluating the impact of rural-residential development given recent documented impacts of exurban development on wildlife abundance, including carnivores (Odell and Knight 2001) and bird communities (Merenlender et al. 1998, Odell et al. 2003, Parsons et al. 2003). More importantly, rural-residential development has recently been shown to be a fundamentally different type of growth than urban development (Newburn and Berck 2006). Specifically, urban development requires sewer and water infrastructure before higher-density development (<1 acre per house) can be built. Conversely, rural-residential development (1–40 acres per house) is almost invariably serviced by private wells and septic systems and thus not bound to existing or planned sewer and water service areas (SWSA). These differences between urban and rural-residential development extend the possible range and associated environmental impacts of rural-residential development, such as sedimentation, but also temperature and nutrient loading from septic systems, well beyond the urban fringe (Hansen et al. 2005, Newburn and Berck 2006). These findings together suggest that biophysical models must explicitly determine the relative effects of rural-residential vs. urban development, and land use change models must distinguish between these different residential densities to forecast land use development patterns.

Finally, projection of the environmental consequences of land use change requires an understanding of biophysical thresholds, the amount of disturbance that an ecosystem can withstand without changing the processes and variables that control its structure (Gunderson and Holling 2002). A growing body of theoretical and empirical research suggests that ecosystems often display nonlinear responses to stressors (Scheffer et al. 2001, Carpenter 2003, Folke et al. 2004), necessitating the use of nonlinear models and extensive data on the response variables (e.g., Yuan and Norton 2004, Donohoe et al. 2006). Understanding how responses vary with initial land use conditions is also important to minimize the marginal losses to ecological systems from expected future land use conversion.

Here we assess the impacts of existing and projected future land use on spawning-substrate quality in tributaries of the Russian River in Sonoma County, California, and discuss the implications of future land use conversions on salmonid spawning habitat. Specifically, we analyze the relative impacts of three different land uses (urban, rural-residential, and vineyard) on the levels of fine sediment in streams. In Sonoma County, almost all intensive agriculture is vineyard for premium wine production. Urban development consists mainly of single-family residences (<1 acre per house) and here also includes paved roads, commercial, and industrial uses. Rural-residential development is defined as parcels with 1–40 acres per house. We hypothesized that low-density rural-residential development is a significant predictor of elevated levels of fine sediment in streams and differs in its severity of impact on stream conditions compared to higher-density urban development.

Our analysis integrated several modeling improvements for the first time. First, we developed an ordinal logistic response model to estimate the relative impact of each land use type on the probability distribution of levels of fine sediment in these watersheds. Ordinal logistic regression is designed to detect nonlinear threshold responses (Neter et al. 1996): in this case, the

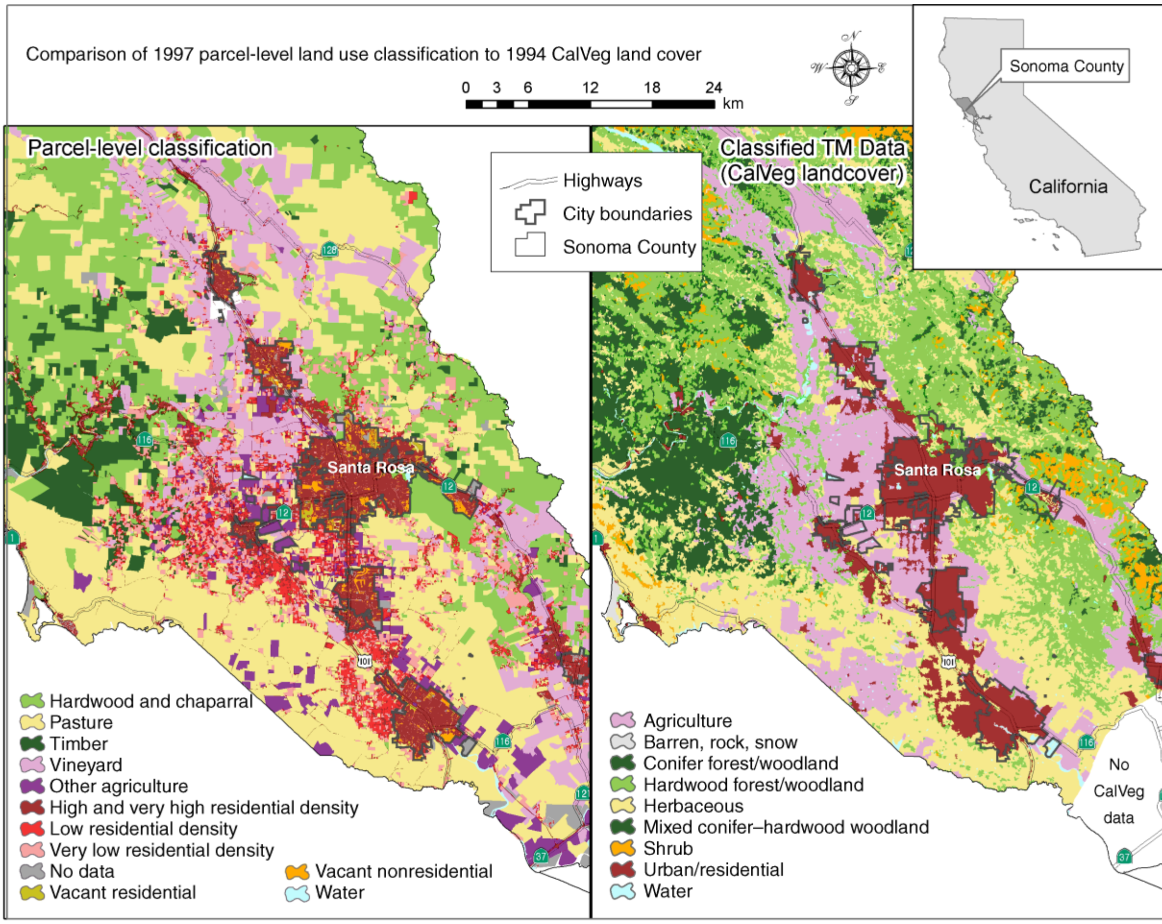

FIG. 1. Comparison of parcel-level and LANDSAT TM imagery land use (based on CalVeg classification) in the study region in Sonoma County, California. Parcel-based land use classification for 1997 shows rural-residential development (1–40 acres per structure; 1 acre ≈ 0.4 ha) and urban development (<1 acre per structure). Residential densities were based on parcel records obtained from the Sonoma County tax assessment office. Vineyard land use was digitized from aerial photographs in 1997.

probability of a spawning site within a given reach declining in spawning-substrate quality with increases in different land uses. Second, we develop a spatially explicit land use change (LUC) model using individual owner land use conversion decisions (including rural-residential, urban, and vineyard development) as a function of the parcel-level characteristics. The LUC model was used to calculate the expected probability of future conversion for each land use type on all remaining developable parcels, which was then integrated with the biophysical model to forecast the expected loss in substrate quality in each watershed. We performed the last critical step of forecasting land use change and its impacts on future levels of fine sediment to aid planners and other decision-makers in preventing further damage to salmonid spawning sites in the Russian River Basin. After combining our forecasts on the expected impacts to spawning habitat with hedonic models for estimating land costs, we conclude with recommendations of priority areas for land conservation efforts and for future development.

METHODS

Study basin

The Russian River basin is 3850 km^2, and is located in Sonoma and Mendocino Counties in northern California. The basin is underlain primarily by the Jurassic-Cretaceous age Franciscan Formation and experiences a mediterranean climate, with cool, wet winters and hot, dry summers; mean annual rainfall ranges from 69 to 216 cm. Natural vegetation consists mostly of mixed-hardwood forests, oak savannas, and grassland, with conifer-dominated forests occurring near the coast and on north-facing slopes throughout the basin. Primary land uses include vineyards, orchards, and other agriculture, sheep and cattle grazing, timber harvest, and urban and residential development.

We focused our studies on tributaries of the Russian River in Sonoma County that (1) support anadromous salmonid spawning habitat, and (2) where stream habitat and digital parcel-level land use data were available (Fig. 1). Focal tributaries included Green

Valley, Mill, Willow, Mark West, Dutch Bill, Maacama, Atascadero, Ward, and Austin Creeks. In the Russian River, three species of anadromous salmonids, including the Central California Coast steelhead (*Oncorhynchus mykiss*), Central California Coast coho (*Oncorhynchus kisutch*), and California Coastal chinook (*Oncorhynchus tshawytscha*), have been listed as threatened under the Federal Endangered Species Act.

Indicator of spawning gravel quality

We used a database from the California Department of Fish and Game (CDFG) for spawning streams in the Russian River Basin to characterize the levels of fine sediment in salmonid spawning habitat. Field crews working for CDFG evaluated the degree of embeddedness of spawning habitat in surveys conducted from 1994 to 2002. Embeddedness was defined as the extent to which fine sediment (particle size $<$2 mm) surrounded spawning-sized substrate (i.e., gravel and cobbles). Each potential spawning site in a stream reach was ranked for the level of fine sediment surrounding the appropriate spawning substrate, using a four-level ordinal system. Rank 1 indicates low levels of fine sediment (0–25%) surrounding spawning-sized substrate, and Rank 4 indicates very high levels of fine sediment (75–100%) surrounding the substrate. We estimated the distribution of substrate quality for each reach surveyed from 1994 to 1997, and used the rank level of each spawning site as our dependent variable. We employed a geographic information system (GIS) to segment these data by stream reach (Byrne 1996, Radko 1997). We restricted our analyses to depositional reaches (gradient $<$0.03) most likely to be impacted by sediment. This data set included 93 stream reaches with an average of 54 spawning sites per reach.

To examine the relationship between land use and embeddedness as a measure of spawning habitat quality, we used a 10-m Digital Elevation Model (DEM) and the ArcView extension FlowZones (ESRI 2002) to delineate watersheds above the downstream end of each surveyed reach that had a minimum of five spawning sites. Ten spawning sites per reach, representing the actual distribution of rankings observed at each reach, were used in model development to avoid overrepresentation of sites in particularly long reaches. For example, if a reach had 100 spawning sites and 70, 20, 10, and 0% of the spawning sites were Rank 1, 2, 3, and 4, respectively, then we represented this distribution in the model as 7, 2, 1, and 0 spawning sites (10 total) with Rank 1, 2, 3, and 4, respectively, for that given reach. No more than five reaches nested in the same drainage area were used to reduce overrepresentation of any given watershed and to minimize spatial autocorrelation. Watersheds ranged in size from 500 to 18 165 ha. Finally, we excluded those few watersheds in the study area that currently or historically supported extensive timber harvesting to avoid problems associated with the land use legacies (Harding et al. 1998). Other extensive uses such as historic livestock grazing, orchards, and other agriculture were treated as baseline land uses. In total, 93 watersheds were used for model development; 58 reaches were excluded to reduce overrepresentation of different watersheds and/or land use legacies, resulting in a model based on 922 spawning sites.

Parcel-based land use classification

For land use classifications, we used tax assessment parcel-level data linked to a digital parcel map within a GIS to provide information on residential development density classes. This approach provides more accurate residential classification than LANDSAT TM imagery, which was used in our previous work in the Russian River basin (Opperman et al. 2005), because tax assessment parcel data provide information on residential density. Specifically, the Sonoma County tax assessment data contain information on the number of housing units and lot size for each landowner, and therefore they can be used to determine housing density. By comparison, LANDSAT data do not indicate residential density; they only classify areas as either urban, or extensive uses such as agriculture or hardwood forest. We note to planners and managers that LANDSAT still has better spatial resolution and accuracy for vegetation cover than parcel level data.

For this study, residential development was categorized into four density classes: very high density ($<$0.25 acres per structure), high density (0.25–1 acres per structure), low density (1–5 acres per structure), and very low density (5–40 acres per structure). These four residential density classes were used in the land use change model described below. For the biophysical model, however, very low and low classes were later combined into the rural-residential class for the ordinal logistic regression in order to reduce multicollinearity, because these two classes were highly correlated within watersheds ($r^2 = 0.68$). Similarly, very high and high-density classes were combined into urban development. The urban classification also included paved roads, parking lots, and commercial uses (industrial uses were relatively uncommon within the CDFG-surveyed watersheds). The specific distinction between urban ($<$1 acre per structure) and rural-residential (1–40 acres per structure) was made at 1 acre per structure because this density is the typical limit on residential development serviced by septic systems (Newburn and Berck 2006). To obtain the amount of vineyard land use in each watershed, we digitized vineyard boundaries from 1997 aerial photographs. Vineyard parcels were classified as vineyard if the parcel had $\geq$10% vineyard or $\geq$5 ha of vineyard, based on the intersection of the parcel and aerial photo vineyard classification. A comparison of land use classification by parcel-level data and LANDSAT TM imagery is provided in Fig. 1.

Model development

We developed ordinal logistic response models (cumulative proportional odds) using the rank level of substrate quality at each spawning site as our response variable (Hosmer and Lemeshow 2000). Explanatory variables included existing areal percentages of vineyard, urban, and rural-residential land use in 1997 within each watershed and biophysical watershed variables as controls (Hosmer and Lemeshow 2000). These watershed variables included continuous variables such as stream-power index (product of stream gradient and watershed size), road density, soil particle size, a hillslope stability index from a shallow landslide model, SHALSTAB (Dietrich et al. 2001) (*available online*)[5] as well as categorical variables including channel type, dominant geology type (Franciscan mélange, volcanic, and sedimentary), and bank substrate material (bedrock, boulder, silt/clay, cobble). Other extensive land uses including historic livestock grazing, orchards, and other agriculture were thus treated as baseline uses in our model; the impact of an additional 1% of specified land use (e.g., vineyard, urban, rural-residential) is the amount of impact above the baseline impact of extensive uses.

Given the response variable y taking on ordinal values from 1 to J and the $1 \times K$ vector of explanatory variables X^i for watershed i, the proportional odds model is expressed as

$$\log(P_j^i/1 - P_j^i) = \alpha_j + \beta X^i, \quad j = 1, 2, \ldots, (J-1)$$

where $\beta X^i = \beta_1 X_1^i + \beta_2 X_2^i \cdots \beta_k X_k^i$ and P_j^i denotes the probability that a spawning site in watershed i falls into rank category j or lower. The cumulative proportion odds specification indicates a nonlinear relationship between the probability of each rank level and the explanatory variables. Furthermore, α_j provides the threshold parameters between the rank categories j and $j + 1$. The models were constructed such that Rank 1 corresponded to the highest substrate quality and Rank 4 corresponded to the lowest. Therefore, a negative sign in the parameter estimates indicates reduced substrate quality, because in this case, a marginal change in the variable would lower the probability of observing a high-quality spawning site with Rank 1.

Log-likelihood (LL) ratio tests were used to test the difference between a given model and any nested model and decide which variables to drop from or add to the model. Chi-square is the difference in log-likelihood ratios (−2LL) for the two models. If the computed chi-square was equal to or greater than the critical value of chi-square for the given degree of freedom, then the models were significantly different and the dropped variable in the nested model was considered significant in predicting the dependent. For category variables (dominant geology and bank substrate quality), we assessed the significance of these variables by comparing the chi-square difference of the full model and a model with all the variables in a dummy set dropped (e.g., bedrock, boulder, cobble/gravel, and silt/clay). Thus we treated the dummy variables associated with the categorical variable as a block (Hosmer and Lemeshow 2000).

We evaluated the goodness of fit and performance of the biophysical model on an additional data set of watersheds not used previously for model building. First, we refitted the model including the additional data set. Second, the full model, which included all variables, was compared with a partial model that excluded rural residential development. The partial and full models were used to predict substrate quality based on additional streams surveyed from 1998 to 2002 ($n = 45$ reaches) and updated 2002 parcel-level data and aerial photos of vineyard. We evaluated the capability of both the partial and full model to predict the values observed in the validation set of watersheds using the mean square prediction error (sum of squared errors/number of watersheds in the validation set) (Neter et al. 1996).

Land use change model

A parcel-level LUC model was constructed for the period 1994–2002, using the tax assessment data to determine residential development and aerial photos to determine vineyard development. The data were initially compiled to determine the set of developable parcels in 1994, and then used to assess whether the developable parcels were converted to either vineyard or one of several housing densities from 1994 to 2002. A parcel was considered developable if there was no vineyard use in 1994 and the existing housing density in 1994 was less than one structure per 40 acres. Hence, the set of developable parcels excluded those parcels protected in parks and reserves and already converted to vineyard or residential development before 1994. Residential development was categorized into the four density classes described above. Land use conversion was defined as transitions from developable parcels into vineyard development or one of the four residential density classes during the period 1994–2002.

A multinomial logit model was developed to explain land use transitions as a function of parcel-site characteristics, including average slope, growing degree-days (microclimate), 100-year floodplain, accessibility to major employment centers, designated sewer and water services, and minimum lot size zoning. The 1989 General Plan was used because it was in effect as the planning document during 1994–2002 and therefore guided new development location and type. An indicator variable was used to specify whether a given parcel is located outside the existing 1989 sewer and water service area. Urban development is expected to be less likely in places without access to public water and sewer service. However, it should be noted that rural-residential homes built in the unincorporated areas are often privately serviced by groundwater wells and septic systems, and thus are still likely to occur outside the sewer service area. Zoned minimum lot size is included as another

[5] ⟨http://socrates.berkeley.edu/geomorph/⟩

proxy for potential residential development, represented in natural log form.

Average percentage slope and elevation in meters were calculated for each parcel. Growing degree-days, summed over the April to October vineyard growing season, served as a proxy for microclimate. A dummy variable was used to represent whether a given parcel was situated within the 100-year floodplain. An optimal routing algorithm within the GIS was used to calculate the minimum travel time in minutes between each parcel and San Francisco along the road network, utilizing weighted travel speeds of 55 mph (88 km/h) on major highways and 25 mph (40 km/h) on county roads. The distance in kilometers from each parcel centroid to the nearest major highway was calculated. This variable represents access to local employment centers within Sonoma County, because all incorporated cities are located along these transportation corridors.

We used the estimated coefficients from the multinomial logistic regression to predict the site-specific conversion probabilities for each land use type on each developable parcel remaining in 2002, given that the site characteristics were already known for all parcels within the GIS. Zoning variables and sewer water service area boundaries were updated to the 2001 General Plan. We note that although the county had a relatively high population growth rate, 2–3% annually, the zoning and sewer and water service area boundaries changed by a very small amount from 1989 to 2001. We then used the LUC model to simulate the expected amount and location of development for each land use type within each watershed. According to the site-specific conversion probabilities, each parcel may remain developable or become converted to one of the five developed land use types in a given simulation. We repeated the simulations 1000 times to obtain average expected watershed area converted to each land use type. The amount of future development from the LUC model spanned an eight-year period, 2002–2010, because the LUC model was calibrated over an eight-year development period, 1994–2002. Over this short planning horizon period, we assumed no additional changes in urban zoning and boundaries. Hence, the forecasted amounts of land use change from 2002 to 2010 represent a "business-as-usual" scenario. The two rural residential classes were then grouped, and two urban classes were also grouped, to simplify the ordinal logistic model on spawning-substrate quality. We then calculated the percentages of the three land uses in each watershed (percentage of total watershed area) for 2002–2010. To obtain the forecasted land use in 1997–2010, the amount of forecasted change in 2002–2010 was added to the actual extent of land use change measured from aerial photos and tax assessment data.

Hedonic price model for estimating land values

We used a hedonic price model to determine the market value for developable land as a function of the site-specific characteristics. Specifically, recent property transactions of developable parcels were used to estimate the actual sales price as a function of the parcel land characteristics. The Sonoma County Tax Assessor's database provides the necessary information on individual parcels for the land value, current land use, and other property characteristics. Using the GIS, we used a similar set of explanatory variables for each parcel, including characteristics for land quality (slope, elevation, microclimate, 100-year floodplain), accessibility (travel times to urban centers, sewer and water service), neighboring land use externalities (percentage of protected open space and urban), and zoning (land use designations, minimum lot size).

Coefficients in the hedonic equation are interpreted as the marginal implicit value of a unit change in the explanatory variable. For example, the hedonic coefficient on travel time to San Francisco estimates the gradient in land values as one travels away from the urban center. We are then able to estimate the value of developable land for each developable parcel, since key site characteristics are known within the GIS. The predicted value of developable land was observed to range over several orders of magnitude. The large degree of variation in land prices highlights why priority setting should include the spatial heterogeneity in land values. See Newburn et al. (2006: Table 2) for more details on the hedonic model used here to estimate the land value of developable parcels in Sonoma County.

Forecasting environmental consequences of land use change

We forecasted the probability distribution of spawning-substrate quality based on the expected percentages of each land use type in 2010 and the estimated parameters in the ordinal logistic model. To estimate the relative impact of each land use type in 2010, we calculated the change in the probability distribution of substrate quality in response to each land use type in 2010, conditional on holding the other two land use types at the existing amount in 1997. Furthermore, in order to demonstrate how nonlinear responses to future land use development is sensitive to the initial levels of land use in each watershed, we categorized watersheds into quartiles (most developed, moderate, less, least developed) based on the summed percentages of all three types of existing development in 1997 (87 watersheds with forecasts).

A targeting rule was used to identify priority areas for protection based on the expected loss of high-quality spawning substrate from future land use conversion and the average land costs in each watershed. Hence, we maximized conservation goals based on the objective of minimizing the expected loss in environmental benefit per unit cost (Newburn et al. 2006). Applying this targeting rule to our results, we identified priority areas by summing the relative probabilities of loss of Ranks 1

TABLE 1. Average existing development (1997) and forecasted changes in land use (1997–2010) in the least to most developed watersheds (as a percentage of the watershed) and across all watersheds ($n = 87$ watersheds).

Variable	Land use	Land use in watershed (%)				
		Least	Less	Moderate	Most	All watersheds
Existing development, 1997	urban	0.06	0.48	0.64	5.05	1.56
	rural-residential	0.10	1.74	6.43	22.59	7.71
	vineyard	0.36	1.07	4.29	2.41	2.03
	total	0.52	3.28	11.36	30.05	11.30
Change 1997–2010	urban	0.10	0.05	0.10	0.21	0.11
	rural-residential	1.66	1.71	1.14	1.64	1.54
	vineyard	1.58	1.98	2.85	2.82	2.31
	total	3.35	3.73	4.08	4.67	3.96

and 2 and dividing by the average cost per acre for that watershed.

RESULTS

The parcel-level land use classification in Sonoma County revealed that urban (<1 acre per structure) and vineyard land use represented only 1.56% and 2.03% of the land area in 1997 within the CDFG-surveyed watersheds, respectively, while rural-residential development (1–40 acres per structure) represented 7.71% (Table 1). Indeed, rural-residential development constituted >80% of the total land area developed for residential use, although it only represented <20% of the total population in the area. The spatial distribution of these land uses was extremely variable among the study watersheds (Fig. 1). On average, the most-developed watersheds had an order of magnitude more development than the least-developed watersheds (Table 1).

Ordinal logistic regression models (cumulative proportional odds) were used to estimate the probabilities for observing each of the four spawning-site quality levels within a given reach as a function of the percentages of watershed-scale land uses in 1997 and biophysical variables. Thus, each reach had a unique set of four probabilities, corresponding to the watershed characteristics for the specific reach. The best ordinal logistic regression model on spawning-substrate quality included land use variables for the percentages of urban, rural-residential, and vineyard use within each watershed and biophysical watershed variables for stream power index, geology, and bank substrate material (Table 2). The model results showed that all three land use variables were negatively and significantly associated with spawning-substrate quality. Partial likelihood ratio tests excluding rural-residential indicated that this land use type significantly improved the model fit ($G = 16.55$, $P < 0.0001$), supporting the hypothesis that increased rural-residential development is a significant predictor of elevated levels of fine sediment in streams. An index of stream power, the product of watershed size and stream gradient, and stream bank substrate material were the only significant biophysical watershed variables. Strict adherence to conventional levels of statistical significance would have dictated that we consider a smaller model deleting dominant geology. However, due to the fact that geology is an important control variable on

TABLE 2. Final model for projection of spawning habitat quality under land use change.

Term	Estimate	SE	Lower 95% confidence limit	Upper 95% confidence limit	Chi-square	P*
Intercept [1]†	−0.859	0.313			7.53	0.0061
Intercept [2]†	1.268	0.314			16.27	<0.0001
Intercept [3]†	2.524	0.323			61.19	<0.0001
Stream power index	−1.764	0.617	−2.925	−0.608	8.18	**0.0042**
Urban 1997 (%)	−0.120	0.033	−0.189	−0.059	12.96	**0.0003**
Rural-residential 1997 (%)	−0.034	0.008	−0.051	−0.018	17.01	**<0.0001**
Vineyard 1997 (%)	−0.055	0.022	−0.099	−0.013	6.38	**0.0115**
Substrate [bedrock]	−0.173	0.231	−0.651	0.296	0.56	0.4541
Substrate [boulder]	1.169	0.431	0.278	2.124	7.36	**0.0067**
Substrate [cobble/gravel]	−0.226	0.210	−0.668	0.206	1.16	0.2819
Geology [Franciscan]	0.398	0.260	−0.058	0.935	2.34	0.1260
Geology [sedimentary]	−0.167	0.271	−0.647	0.384	0.38	0.5381
Geology [volcanic]	0.381	0.265	−0.084	0.923	2.07	0.1501

Notes: Estimated ordinal logistic regression terms, coefficients and standard errors (SE), and confidence limits are reported. Chi-square is the likelihood-ratio chi-square test for the hypothesis that all regression parameters are zero, and P value is the probability of obtaining a greater chi-square value by chance alone if the specified model fits no better than the model that includes only intercepts. $N = 922$ pools; −2 log-likelihood = 199.9.

* The values in boldface type indicate significance at the $P < 0.05$ level.

† The ordinal logistic model fits a different intercept, but the same slope, for each of $r - 1$ cumulative logistic comparisons, where r is the number of response levels. There are three intercept parameters because there are four response categories.

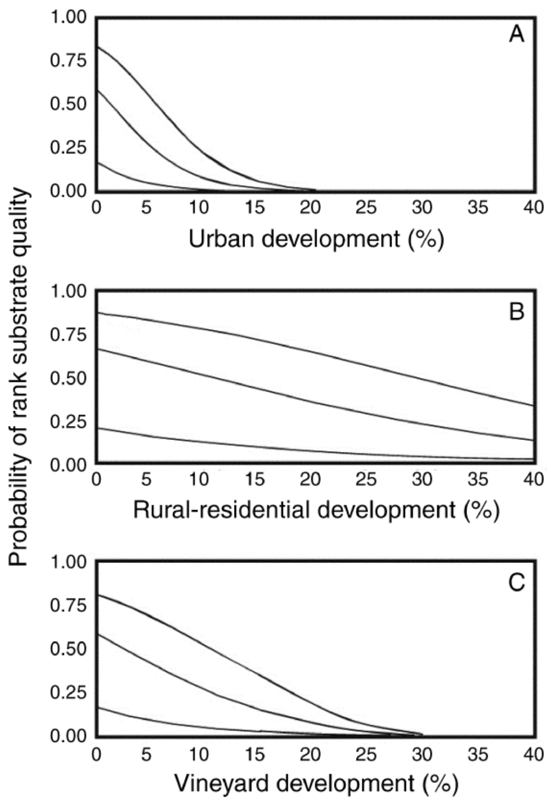

FIG. 2. Ordinal response regression models for (A) the percentage of urban development, (B) the percentage of rural-residential development, and (C) the percentage of vineyard development in the watershed.

sediment production and delivery, dominant geology was retained to control for this factor across watersheds (Hosmer and Lemeshow 2000). Significance of stream bank substrate material indicated more local-scale influences on spawning gravel quality.

The probability of observing low levels of fine sediment in spawning gravels decreased as the percentage of different types of development increased in the watershed (Fig. 2). The marginal effects of urban development (i.e., the change in the probability of substrate quality with 1% increase in urban development) were larger than either vineyard or rural-residential development in lesser-developed watersheds (Fig. 2). However, the marginal effect of urban land use decreased when there was already a high percentage of existing development. In the least-developed watersheds, >65% of spawning sites were high quality (Ranks 1 and 2), whereas >70% of the sites in the most-developed watersheds were highly embedded with sediment (Ranks 3 and 4) (Fig. 3). Thus, prior development had already impacted the majority of spawning sites in the most-developed watersheds.

Estimating the model with all the data (1994–2002) did not significantly alter the coefficient estimates in the final model indicating goodness of fit. Results from projecting the effects of land use change from 1997 to 2002 on stream conditions on the test set of watersheds ($n = 45$) showed that the mean prediction error only decreased 7% with the full model compared to the partial model. Biased parameter estimates for urban and vineyard could help to explain why there were only minor differences in the mean squared prediction errors between the models; the partial model overestimated the effects from urban and vineyard because it had mistakenly attributed the effect from the omitted exurban variable to urban and vineyard.

Forecasting land use change

The estimation results from the LUC model indicated that urban and rural-residential development responded very differently to land use regulations. Designation of sewer and water service area boundaries was the most important determinant of urban development (Table 3). Calculating the odds ratios for the two urban classes showed that very high and high-density development were respectively 44.5 and 4.5 times less likely to occur outside of sewer and water service area boundaries compared to areas with existing and planned sewer service. In contrast, designation of sewer and water service areas did not affect rural-residential development, as development at this density only requires the installation of private groundwater wells and septic systems. The odds ratios for the two rural-residential classes show that very low and low-density development are actually 5.9 and 2.7 times more likely outside of sewer and water service area boundaries. Hence, because of these different responses to land use controls, the LUC model showed that rural-residential development actually leapfrogged into less-developed areas well beyond sewer and water service area boundaries. Furthermore, urban development at high and very high densities was less likely on steeper slopes, within the 100-

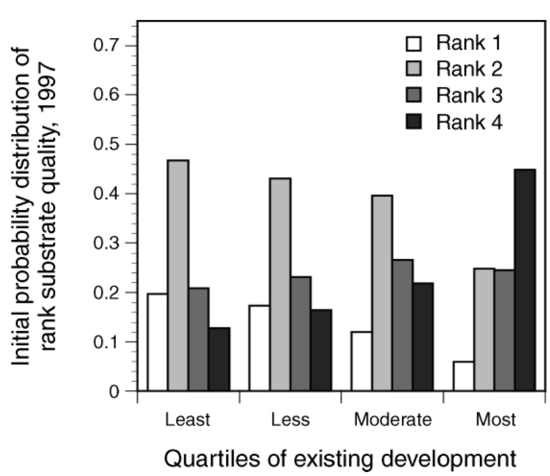

FIG. 3. Estimated probability distribution of quality levels of spawning habitat within stream reaches, grouped according to the quartiles of existing land use development in 1997 (least, less, moderate, and most developed).

TABLE 3. Estimated coefficients of multinomial logit model for land use conversion (to very high, high, low, and very low housing density, or vineyard) during 1994–2002 on undeveloped parcels in Sonoma County, California.

Variable	Housing density classes: Very high	High	Low	Very low	Vineyard
Outside sewer service areas	−3.797**	−1.510**	1.006**	1.781**	2.469**
	(0.199)	(0.153)	(0.176)	(0.372)	(0.324)
Travel time to San Francisco	−0.015**	0.008*	−0.022**	−0.0294**	0.011**
	(0.003)	(0.003)	(0.004)	(0.006)	(0.003)
Distance to nearest highway	−0.304**	−0.146**	−0.041	0.004	−0.112**
	(0.055)	(0.047)	(0.031)	(0.030)	(0.018)
Slope	−0.053**	−0.052**	−0.036**	0.001	−0.049**
	(0.006)	(0.005)	(0.005)	(0.005)	(0.004)
Growing degree-days	0.198	−0.059	−0.154	0.696**	1.796**
	(0.144)	(0.152)	(0.156)	(0.198)	(0.115)
Floodplain	−1.111**	−1.811**	−1.116**	−1.066	−0.500*
	(0.252)	(0.416)	(0.345)	(0.589)	(0.199)
Elevation	−0.008**	0.0026**	0.002**	0.002**	−0.001
	(0.002)	(0.001)	(0.001)	(0.001)	(0.001)
ln(zoned minimum lot size)	0.089**	−0.177**	−0.112**	0.085	0.539**
	(0.029)	(0.0379)	(0.038)	(0.049)	(0.034)
Constant	−0.603	−2.092**	−2.672**	−7.282**	−11.669**
	(0.494)	(0.552)	(0.568)	(0.755)	(0.506)

Notes: "Remain undeveloped" is the baseline alternative. Standard errors are in parentheses. For the ordinal logistic model in Table 2, the very high and high-density classes were combined into urban development, while the very low and low-density classes were combined into rural residential development. $N = 20\,487$ parcels; log likelihood $= -8732.04$.

* $P < 0.05$; ** $P < 0.01$.

year floodplain, and farther from major highways. (See Newburn and Berck [2006] for more details on differences between urban and rural-residential development.) Finally, vineyard development was more likely on areas with lower slope and higher growing degree-days (warmer microclimate).

We used the LUC model to forecast development for the period 1997–2010. Although urban development resulted in the largest marginal change in probability in substrate quality per unit increase in development (Fig. 2), the amount of future urban development was relatively small, largely due to no changes in urban zoning and boundaries. For the forecast period 1997–2010, the area developed as urban in CDFG watersheds was estimated to increase only 0.11%, whereas rural-residential and vineyard development were estimated to increase by 1.54% and 2.31%, respectively (Table 1).

Forecasting land use impacts on spawning-substrate quality

Future vineyard and rural-residential development had larger relative impacts on spawning-substrate quality than future urban development across all watersheds (Fig. 4). Initial conditions of the watersheds largely determined which watersheds had the most to lose with respect to good-quality spawning substrate (Ranks 1 and 2) (Fig. 5). The amount and type of expected land use change also factored into which watersheds were expected to lose good spawning habitat (decreases in Ranks 1 and 2) and to be impaired by sedimentation (increases in Ranks 3 vs. 4) (See Fig. 6, but also the Appendix for forecasts for all watersheds.) The interplay between these two factors, initial conditions and expected land use change, was observed across the watersheds in Sonoma County. Specifically, watersheds near Cloverdale, farthest from the San Francisco Bay area, were less disturbed and generally responded to expected land use change with declines in the probability of observing high-quality spawning sites (declines in Rank 1; Fig. 6a). In watersheds near Healdsburg, particularly to the east near Napa County, high amounts of projected vineyard development and, to a lesser extent, rural-residential development, led to large expected losses of Rank 1 and Rank 2 sites and large increases in Rank 4 sites (Fig. 6b). Whereas the southern most-developed watersheds near Santa Rosa showed little change in the probable loss in Rank 1 spawning sites because spawning-substrate quality was already low, watersheds showed large probable gains in Rank 4 sites from expected losses of Ranks 2 and 3 sites (Fig. 6c).

The average land cost per acre varied widely across watersheds in the study area and generally decreased from south to north (Fig. 5). Based upon land costs and the likelihood of future development, watersheds in the northern and central part of the study area (shaded in red and orange, Fig. 6) had the highest probability of loss of good substrate quality per unit land cost. Watersheds colored red represent the highest benefit-cost option for conserving habitat. In contrast, watersheds in the south (yellow watersheds, Fig. 6) had relatively low probable loss of good substrate quality per unit land cost.

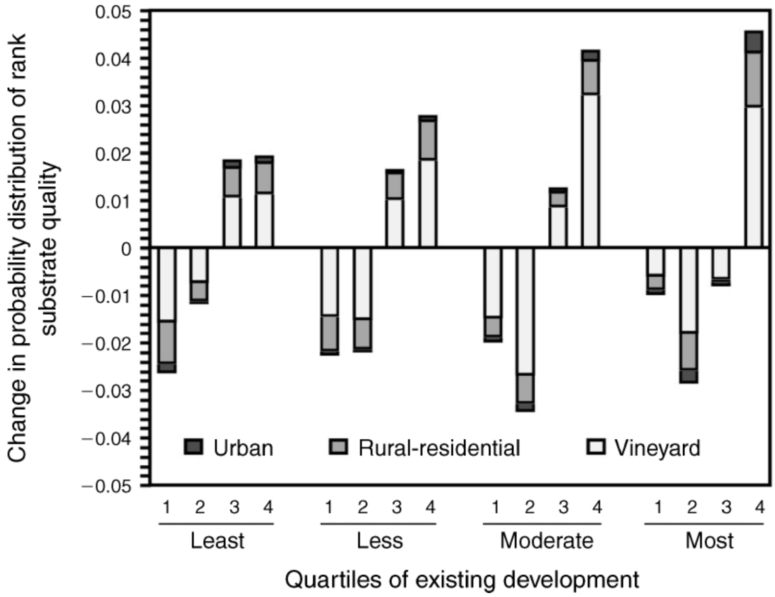

FIG. 4. Average change in the probability distribution of spawning site quality (Rank 1–4) in least to most developed watersheds. Shading in bars indicates the relative impacts of forecasted rural-residential, urban, and vineyard development on the change in spawning site quality.

DISCUSSION

We quantified nonlinear relationships between land use (including low-density residential development) and relative levels of fine sediment in streams and then forecasted the expected impacts of land use change on spawning habitat for endangered salmon. Elevated inputs of fine sediment from land use conversion can negatively impact salmonid populations through the degradation of both spawning and rearing habitat (Reiser and White 1988, O'Connor and Andrew 1998, Kondolf 2000, Suttle et al. 2004), aggradation of pools (McIntosh et al. 2000), simplification of habitat (McIntosh et al. 2000), and suppression of invertebrate prey base for juvenile fish (Osmundson et al. 2002, Suttle et al. 2004). Taken together, results presented here and the linkages between fine sediment and salmonid population decline suggest that steelhead trout and coho salmon, already listed as threatened, are vulnerable to future increases in fine sediment loads due to expected land use conversions.

In this study, urban and vineyard land use were significant predictors of in-stream levels of fine sediment, consistent with our previous work (Opperman et al. 2005) and other studies (Wang et al. 2001, Pess et al. 2002, Morse et al. 2003, Donohoe et al. 2006). Unlike previous studies, however, we were able to distinguish and evaluate the effects of rural-residential development based on a spatially explicit, parcel-level land use change model. We found that the proportion of high-quality spawning sites decreased significantly with the percentage of rural-residential development in the watershed (see Plate 1). Findings suggest that previous studies relying on Landsat TM for land-cover data likely have omitted an important type of development that adversely impacts aquatic ecosystems (Fig. 1). As the amounts of urban and rural-residential development were more likely to occur within the same watershed (correlation coefficient = 0.52 in our watersheds), omission of the rural-residential variable in the regression model would have mistakenly attributed much of its effect to urban development. As a result, decision-makers might adopt policies to curb or redirect urban development, such as urban-growth boundaries (UGB) on sewer infrastructure expansion, while allowing rural-residential development to continue unabated (Newburn and Berck 2006). While our findings point to the previously omitted impacts of rural-residential development, the use of parcels as the spatial reporting unit likely overestimated the percentage of the watershed impacted by this type of land use because the entire parcel may not be impacted by the developed area. More research is needed to quantify the actual area of development associated with low-density residential development. We have begun to use pixel-based and object-based remote sensing to calculate the development footprint around existing rural residences, and have found that these methods effectively delineate the developed areas as long as tree cover does not hide structures and roads. Beyond the actual developed area, indirect impacts associated with the presence and use of roads for rural-residential development remain poorly characterized and likely extend the disturbance footprint of rural-residential development (Havlick 2002, Forman et al. 2003). Research in this area is underway to calculate the development areas for a large number of parcels, as

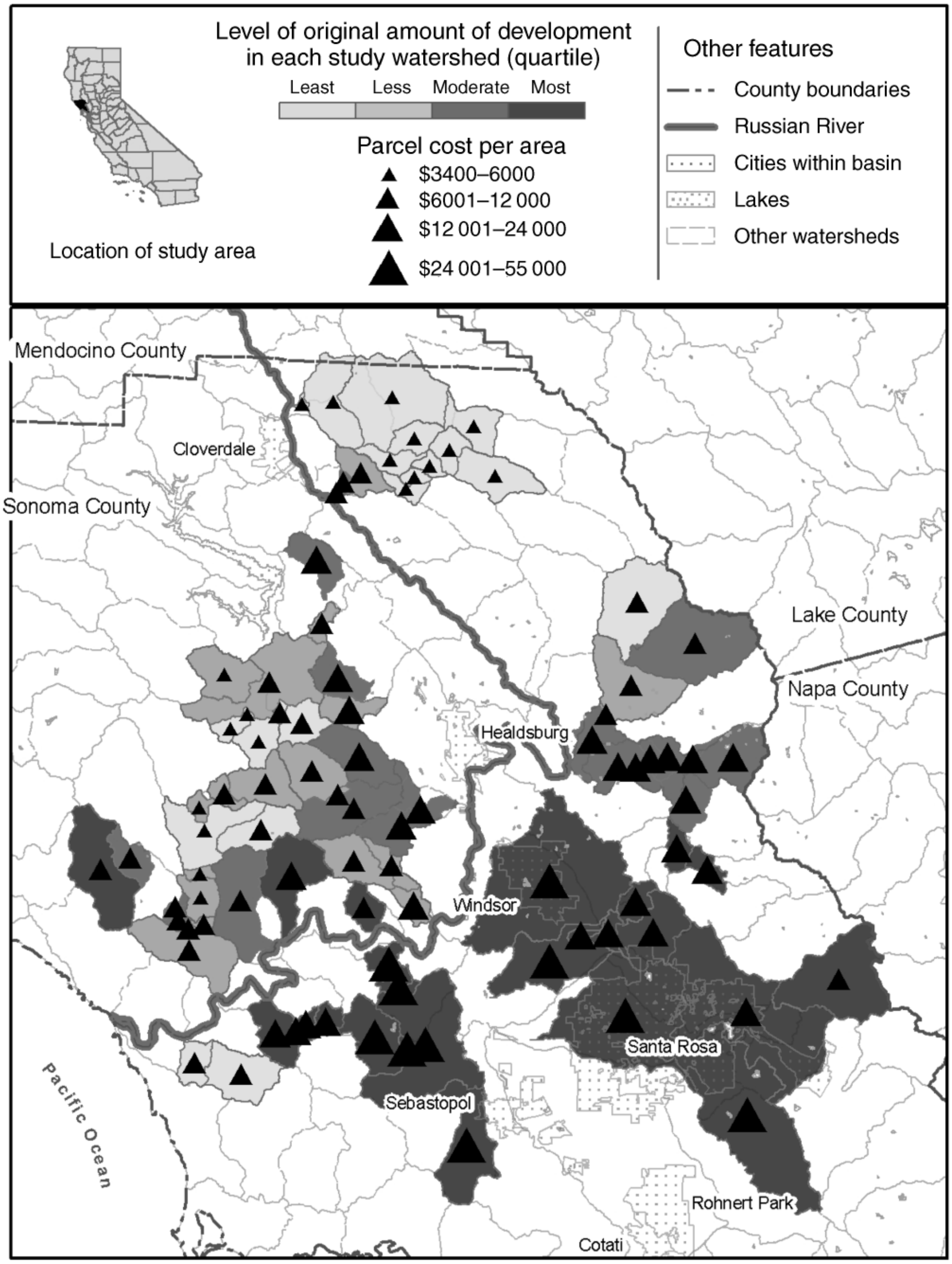

FIG. 5. Initial conditions of land use development in the study watersheds and cost per parcel area (see *Methods: Hedonic price model* for description of estimating land values from tax assessor's database on parcels).

there appears to be a high level of variability that can in part be explained by parcel size.

Our results also indicate that urban, rural-residential, and vineyard development differed in their severity of impact on streams. While urban development had the largest marginal effects (greatest response per unit of land use change), our data suggest that future rural-residential may have a greater overall impact than urban development on spawning-substrate quality. We expect this greater impact because the LUC model predicts 10 times as much land to be converted to rural-residential compared to urban development. In addition, the model projects rural-residential development to occur in watersheds ranging from the least to the most developed, and thus will affect reaches that currently have suitable habitat to support salmon reproduction. In contrast, the LUC model predicts future urban development to be more likely in areas that already have high levels of urban land use and low-quality spawning habitat (Fig. 6c). Finally, our results indicate that future

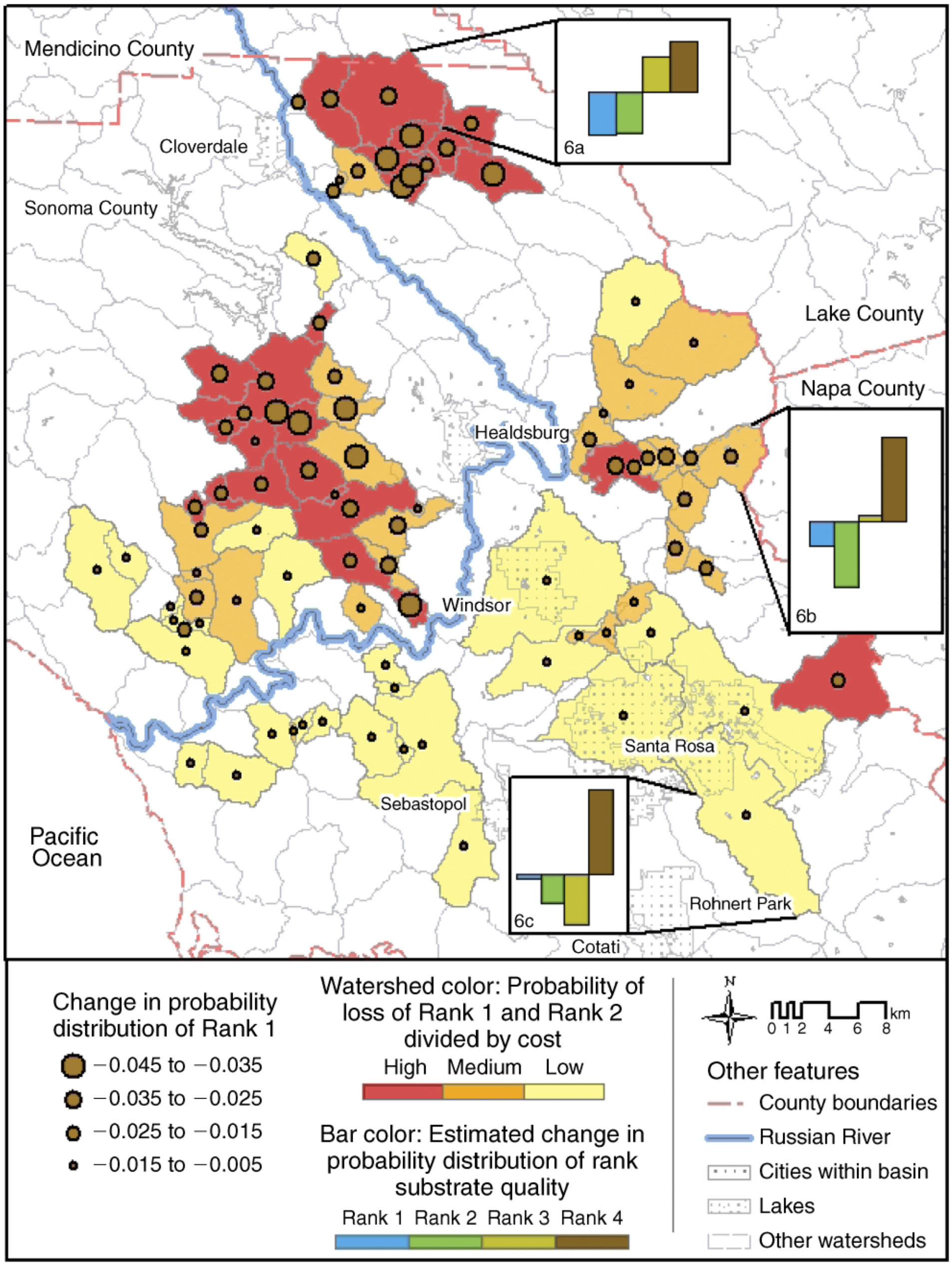

FIG. 6. Change in probability distribution of high-quality spawning sites (Rank 1) with forecasted land use change (key with circles) and probability of loss of high-quality substrate ÷ land cost in least to most developed watersheds in the Russian River Basin (watershed color). The watersheds colored red represent the lowest cost option for conserving high-quality spawning habitat. Inset bar color graphs show examples of estimated change in probability distribution of substrate quality within that rank for (6a) least, (6b) moderate, and (6c) most developed watersheds.

vineyard conversion could lead to high levels of sedimentation, and hence have a larger relative impact than urban development. Together, our findings suggest that fundamentally different land use types should not be aggregated in risk-assessment models.

Due to the nonlinearity of the responses, watersheds that differed in their level of initial development conditions had varying vulnerability to degradation of spawning habitats from future development. Based on the forecasting model, watersheds with lower percentages of existing development showed relatively large declines in the probability of high-quality spawning habitat (Ranks 1 and 2) (Fig. 6a). This sensitivity declined within the most-developed watersheds largely because these reaches initially had a small proportion of high-quality spawning habitat (Fig. 6c). Watersheds with large amounts of expected land use change (particularly agriculture) also showed large gains in the

PLATE 1. Example of rural-residential development in Sonoma County, California, USA. Photo credit: A. M. Merelender.

highest sediment levels (Fig. 6b). High sensitivity to development emphasizes the need to protect salmon habitat very early in the development process (or trajectory), often before many regulations designed to protect water from land use activities are triggered.

In this study, we forecasted changes over a short planning horizon (only about a decade) because the LUC model was calibrated over an eight-year development period, 1994–2002. Over longer planning horizons, market forces and urban service boundaries may change, making land use change projections more uncertain and assumptions underlying the models invalid. In a detailed study of exurban and urban development scenarios, Newburn and Berck (2006) showed that the probability of urban development increased 10-fold if they extended a sewer and water service area boundary, but rural-residential development did not change. We expect that the impacts of urban development in our model results would have been larger if sewer and water service areas were extended. Nonetheless, the impacts would still have been felt mostly in watersheds of already low-quality habitat. Thus, altered urban boundaries would not have likely changed the priority of conservation targets. Over a longer time frame (25–50 years), we expect the projected losses of habitat quality would be much larger due to urban expansion but also to rural-residential development in lesser-developed watersheds. Again, we expect conservation priorities would be similar to our short-term forecasts because priorities are based on relative rankings, in this case, the relative probabilities of loss of good spawning substrate divided by the average cost per acre for that watershed. Longer range forecasts are a topic of ongoing research.

The nonlinear relationships between various land uses and fine sediment described here can provide decision-makers with information on vulnerability of high-quality spawning habitat to different development pressures. Because resources for land conservation are limited, this forecasting approach can be used to prioritize areas for conservation efforts intended to reduce sediment loading to streams, such as purchasing conservation easements, reconnecting streams to flood-plains, and reducing the sediment production from road networks. Funding for land conservation will likely be more fiscally efficient if areas with low-to-moderate threat to land use conversion are targeted rather than land at the urban fringe with the highest threat. Land costs at the urban fringe are several orders of magnitude higher than low-threat areas, making compensation to landowners for forgoing development far more costly (Fig. 5) (Newburn et al. 2005, 2006). Such a process will also identify locations where existing land use development may overwhelm the future efficacy or marginal benefit of conservation programs.

Through local zoning and other land use policies, decision-makers can work to influence the density and location of future residential development. Transfer of development rights (TDR) programs, for example, can be used to create a market between properties with existing rural-residential development rights located in environmentally sensitive areas (sending areas) and regions that are already serviced for denser urban development (receiving areas). For instance, local planners in Montgomery County, Maryland downzoned properties with 5-acre minimum lot sizes and credited the landowners with the development rights. These development rights were then sold to developers who wanted to build urban housing at high densities within areas that already had SWSAs (Johnston and Madison 1997). In the context of our study, we recommend that a TDR program be implemented to curtail lower-density rural-residential development within moderate- and less-developed watersheds (sending areas in red and orange, Fig. 6), while encouraging higher-density infill urban development to take place in areas already highly disturbed (receiving areas in yellow watersheds, Fig. 6) (Johnston and Madison 1997, Nilsson et al. 2003, Merenlender et al. 2004).

In concert with these more transformative planning tools, effective runoff and construction control techniques can be employed when development does occur in sensitive watersheds. Best management practices for road construction and maintenance include guides for environmentally sensitive maintenance of dirt and gravel roads, as well as basic road design elements (Roads, Highways, Bridges–NPS categories) (*available online*).[6] Other low-impact development (LID) strategies for storm water management are also available to use at a local scale (Low-Impact Development) (*available online*).[7] The next research steps in spatial targeting include spatial prioritization within targeted watersheds that will begin to meet the needs of conservation groups who require finer scale spatial information on the relative value of individual parcels. On this research front, Newburn et al. (2006) have taken the first step toward parcel-level targeting within these watersheds, but had the simplicity of a linear benefit function in their model. Our future research will work toward integration of a dynamic optimization of the economic and land use change model with our biophysical model encompassing cumulative and nonlinear threshold effects.

While we effectively assessed the nonlinear response of spawning habitat to land use change, we still need a better understanding of hysteresis, as the conditions under which spawning sites shift to higher fine-sediment levels may differ from those that will shift the system back to lower levels. Reductions in fine sediment may occur through punctuated changes in stream flow or shifts in stream geomorphology. In general, a better understanding of the mechanism of sediment transport in these watersheds is desirable; we need to address questions about how water extraction and channel incision and other changes to stream geomorphology associated with development influence sediment dynamics. This increased understanding would inform management efforts to improve the quality of stream habitat where existing conditions fall below desired thresholds.

[6] ⟨http://www.epa.gov/owow/nps/roadshwys.html⟩
[7] ⟨www.EPA.gov/owow/nps/lid/⟩

Conclusions

It is well recognized that urban development and intensive agriculture can increase sediment production and delivery to downstream stream reaches, rendering them unsuitable for successful fish spawning. In this study, we were also able to examine the impacts of exurban land use and found that increases in the percentage of total exurban development in a watershed significantly reduced the probability of observing high-quality stream habitat. In fact, results from this study suggest that exurban development may have a greater relative impact than urban development on stream conditions in the next decade because 10 times as much land is expected to be developed in exurban than urban areas, and exurban development has the ability to leapfrog into less-developed watersheds, which contain high-quality habitat, compared to urban development, which is typically constrained by urban growth boundaries. As exurban development now takes up 15 times the area of higher-density development (Brown et al. 2005) and is the fastest-growing type of land use in the United States (Theobald 2001), these findings raise concern for other areas where low-density residential development is on the rise.

Results from our study also demonstrate that urban and rural residential development are fundamentally different and thus require different land use policies to reduce their impacts on stream ecosystems and upland areas. Future urban development will tend to be clustered in areas that already have high levels of urban development and little high-quality spawning habitat. In contrast, exurban development is more likely to leapfrog into remote areas well beyond sewer water service areas and impact watersheds with good habitat quality. Hence, limits on the sewer service extension, a key objective of an urban growth boundary, will likely be effective in curbing urban expansion. However, it would have little or no influence on rural residential development. The application of our findings demonstrates the need to target conservation efforts in watersheds with the lowest cost option for protecting high-quality habitat. This approach directs resources away from those watersheds with the greatest threat of future development, which tend to have the highest land costs, and toward watersheds with low to moderate threat of future development. These watersheds contain high-quality habitat and have significantly lower land costs and are still at risk of low-density development in the near future. We recommend that local governments implement purchase and transfer of development rights programs as a primary strategy for influencing patterns of rural-residential development. In addition, we need to inform planners about the potential impacts of this type of land use and its consequence for environmental degradation because few existing policies, regulations, and incentive-based conservation programs are in place to adequately address the problem.

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LITERATURE CITED

Armsworth, P., G. C. Daily, P. Kareiva, and J. N. Sanchirico. 2006. Land market effects can undermine conservation efforts. Proceedings of the National Academy of Sciences (USA) 103:5403–5408.

ASCE (American Society of Civil Engineers) Task Committee on Sediment Transport and Aquatic Habitats. 1992. Sediment and aquatic habitat in river systems. Journal of Hydraulic Engineering 118:669–687.

Azimer, J., and L. Stone. 2003. The rural West: diversity and dilemma. Canada West Foundation, Calgary, Alberta, Canada.

Brown, D. G., K. M. Johnson, T. R. Loveland, and D. M. Theobald. 2005. Rural land-use trends in the conterminous United States, 1950–2000. Ecological Applications 15:1851–1863.

Byrne, M. 1996. California salmonid inventory: a dynamic segmentation application. ESRI User's Conference, Redlands, California, USA.

Carpenter, S. R. 2003. Regime shifts in lake ecosystems: pattern and variation. International Ecology Institute, Oldendorf/Luhe, Germany.

Chan, K. M. A., M. R. Shaw, D. R. Cameron, E. C. Underwood, and G. C. Daily. 2006. Conservation planning for ecosystem services. PLoS Biology 4:e379.

Clark, J. S., et al. 2001. Ecological forecasts: an emerging imperative. Science 293:657–660.

Dietrich, W. E., D. Bellugi, and R. R. de Asua. 2001. Validation of the shallow landslide model, SHALSTAB, for forest management. Pages 195–227 *in* M. S. Wigmosta and S. J. Burges, editors. Land use and watersheds. American Geological Union, Washington, D.C., USA.

Donohoe, I., M. L. McGarrigle, and P. Mills. 2006. Linking catchment characteristics and water chemistry with the ecological status of Irish rivers. Water Research 40:91–98.

Dubost, F. 1998. De la maison de campagne à la résidence secondaire. Pages 10–37 *in* F. Dubost, editor. L'autre maison: la 'résidence secondaire', refuge des générations. Autrement, Paris, France.

ESRI. 2002. ArcView extension FlowZones. Version 1.2. ESRI, Redlands, California, USA.

Everest, F. L., R. L. Beschta, J. C. Scrivener, K. V. Koski, J. R. Sedell, and C. J. Cederholm. 1987. Fine sediment and salmonid production—a paradox. Pages 98–142 *in* E. O. Salo and T. W. Cundy, editors. Streamside management: forestry and fishery interactions. University of Washington, Seattle, Washington, USA.

Foley, J. A., et al. 2005. Global consequences of land use. Science 309:570–574.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution, and Systematics 35:557–581.

Forman, R. T. T., et al. 2003. Road ecology: science and solutions. Island Press, Washington, D.C., USA.

Greig, S. M., D. A. Sear, and P. A. Carling. 2005. The impact of fine sediment accumulation on the survival of incubating salmon progeny: implications for sediment management. Science of the Total Environment 344:241–258.

Groot, C., and L. Margolis. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver, British Columbia, USA.

Gunderson, L. H., and C. S. Holling. 2002. Panarchy: understanding transformations in human and natural systems. Island Press, Washington, D.C., USA.

Hansen, A. J., R. L. Knight, J. M. Marzluff, S. Powell, K. Brown, P. H. Gude, and A. Jones. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecological Applications 15:1893–1905.

Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. I. Jones. 1998. Stream biodiversity: the ghost of land use past. Proceedings of the National Academy of Sciences (USA) 95:14843–14847.

Harte, J. 2001. Land use, biodiversity, and ecosystem integrity: the challenge of preserving earth's life support system. Ecology Law Quarterly 27:929–965.

Havlick, D. G. 2002. No place distant: roads and motorized recreation on America's public lands. Island Press, Washington, D.C., USA.

Heimlich, R. E., and W. D. Anderson. 2001. Development at the urban fringe and beyond: impacts on agriculture and rural land. Department of Agriculture, Economic Research Service, Washington, D.C., USA.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. Second edition. John Wiley and Sons, New York, New York, USA.

Johnston, R. A., and M. E. Madison. 1997. From landmarks to landscapes. Journal of the American Planning Association 63:365–379.

Kondolf, G. M. 2000. Assessing salmonid spawning gravel quality. Transactions of the American Fisheries Society 129: 262–281.

McIntosh, B. A., J. R. Sedell, R. F. Thurow, S. E. Clarke, and G. L. Chandler. 2000. Historical changes in pool habitats in the Columbia River Basin. Ecological Applications 10:1478–1496.

Merenlender, A. M., K. L. Heise, and C. Brooks. 1998. Effects of subdividing private property on biodiversity in California's north coast oak woodlands. Transactions of the Western Section of the Wildlife Society 34:9–20.

Merenlender, A. M., L. Huntsinger, G. G. Guthey, and S. K. Fairfax. 2004. Land trusts and conservation easements: Who is conserving what for whom? Conservation Biology 18:65–75.

Morse, C. C., A. D. Huryn, and C. Cronan. 2003. Impervious surface area as a predictor of the effects of urbanization on stream insect communities in Maine, USA. Environmental Monitoring and Assessment 89:95–127.

National Research Council. 2001. Grand challenges in environmental sciences. Oversight Commission for the Committee on Grand Challenges in Environmental Sciences. National Academy Press, Washington, D.C., USA.

Neter, J., M. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models. Fourth edition. Irwin, Chicago, Illinois, USA.

Newburn, D. A., and P. Berck. 2006. Modeling suburban and rural residential development beyond the urban fringe. Land Economics 82:481–499.

Newburn, D. A., P. Berck, and A. M. Merenlender. 2006. Habitat and open space at risk of land-use conversion: targeting strategies for land conservation. American Journal of Agricultural Economics 88:28–42.

Newburn, D. A., S. E. Reed, P. Berck, and A. M. Merenlender. 2005. Economics and land-use change in prioritizing private land conservation. Conservation Biology 19:1411–1420.

Nilsson, C., J. E. Pizzuto, G. E. Moglen, M. A. Palmer, E. H. Stanley, N. E. Bockstael, and L. C. Thompson. 2003. Ecological forecasting and the urbanization of stream ecosystems: challenges for economists, hydrologists, geomorphologists, and ecologists. Ecosystems 6:659–674.

O'Connor, W. C. K., and T. E. Andrew. 1998. The effects of siltation on Atlantic salmon, *Salmo salar* L., embryos in the River Bush. Fisheries Management and Ecology 5:393–401.

Odell, E. A., and R. L. Knight. 2001. Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. Conservation Biology 15:1143–1150.

Odell, E. A., D. M. Theobald, and R. L. Knight. 2003. Incorporating ecology into land use planning: the songbirds' case for clustered development. American Planning Association Journal 69:72–81.

Opperman, J. J., K. A. Lohse, C. Brooks, N. M. Kelly, and A. M. Merenlender. 2005. Influence of land use on fine sediment in salmonid spawning gravels within the Russian River Basin, California. Canadian Journal of Fisheries and Aquatic Sciences 62:2740–2751.

Osmundson, D. B., R. J. Ryel, V. L. Lamarra, and J. Pitlick. 2002. Flow-sediment-biota relations: implications for river regulation effects on native fish abundance. Ecological Applications 12:1719–1739.

Parsons, H., K. French, and R. E. Major. 2003. The influence of remnant bushland on the composition of suburban bird assemblages in Australia. Landscape and Urban Planning 66: 43–56.

Pess, G. R., D. R. Montgomery, E. A. Steel, R. E. Bilby, B. E. Feist, and H. M. Greenberg. 2002. Landscape characteristics, land use, and coho salmon (*Oncorhynchus kisutch*) abundance, Snohomish River, Wash., U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 59:613–623.

Phillips, R. W., R. L. Lantz, E. W. Claire, and J. R. Moring. 1975. Some effects of gravel mixtures on emergence of coho salmon and steelhead trout fry. Transactions of the American Fisheries Society 104:461–466.

Radko, M. A. 1997. Spatially linking basinwide stream inventories to arcs representing streams in a Geographic Information System. INT-GTR-345, USDA Forest Service, Washington, D.C., USA.

Reiser, D. W., and R. G. White. 1988. Effects of two sediment size-classes on survival of steelhead and chinook salmon eggs. North American Journal of Fisheries Management 8:432–437.

Ricciardi, A., and J. B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. Conservation Biology 13: 1220–1222.

Richter, B. D., D. P. Braun, M. A. Mendelson, and L. L. Master. 1997. Threats to imperiled freshwater fauna. Conservation Biology 11:1081–1093.

Rindfuss, R. R., S. J. Walsh, B. L. Turner, J. Fox, and V. Mishra. 2004. Developing a science of land change: challenges and methodological issues. Proceedings of the National Academy of Sciences (USA) 101:13976–13981.

Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11:141–156.

Scheffer, M., S. Carpenter, J. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591–596.

Soulsby, C., A. F. Youngson, H. J. Moir, and I. A. Malcolm. 2001. Fine sediment influence on salmonid spawning habitat in a lowland agricultural stream: a preliminary assessment. Science of the Total Environment 265:295–307.

Strayer, D. L., R. E. Beighley, L. C. Thompson, S. Brooks, C. Nilsson, G. Pinay, and R. J. Naiman. 2003. Effects of land cover on stream ecosystems: roles of empirical models and scaling issues. Ecosystems 6:407–423.

Suttle, K. B., M. E. Power, J. M. Levine, and C. McNeely. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. Ecological Applications 14:969–974.

Sutton, P. C., T. J. Cova, and C. Elvidge. 2006. Mapping exurbia in the conterminous United States using nighttime satellite imagery. Geocarto International 21:39–45.

Theobald, D. M. 2001. Land use dynamics beyond the American urban fringe. Geographical Review 91:544–564.

Theobald, D. M. 2003. Targeting conservation action through assessment of protection and exurban threats. Conservation Biology 17:1624–1637.

Theobald, D. M., T. Spies, J. Kline, B. Maxwell, N. T. Hobbs, and V. H. Dale. 2005. Ecological support for rural land-use planning. Ecological Applications 15:1906–1914.

Van Sickle, J., J. Baker, A. Herlihy, P. Bayley, S. Gregory, P. Haggerty, L. Ashkenas, and J. Li. 2004. Projecting the biological condition of streams under alternative scenarios of human land use. Ecological Applications 14:368–380.

Wang, L., J. Lyons, P. Kanehl, and R. Bannerman. 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. Environmental Management 28:255–266.

Yuan, L. L., and S. B. Norton. 2004. Assessing the relative severity of stressors at a watershed scale. Environmental Monitoring and Assessment 98:323–349.

APPENDIX

A figure showing the change in probability distribution of spawning site quality with forecasted land-use change in the study watersheds (*Ecological Archives* A018-013-A1).