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Explaining spatial variability in stream habitats using both natural and management-influenced landscape predictors

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ABSTRACT

1. The distribution and composition of in-stream habitats are reflections of landscape scale geomorphic and climatic controls. Correspondingly, Pacific salmon (*Oncorhynchus* spp.) are largely adapted to and constrained by the quality and complexity of those in-stream habitat conditions. The degree to which lands have been fragmented and managed can disrupt these patterns and affect overall habitat availability and quality.
2. Eleven in-stream habitat features were modelled as a function of landscape composition. In total, 121 stream reaches within coastal catchments of Oregon were modelled. For each habitat feature, three linear regression models were applied in sequence; final models were composed of the immutable and management-influenced landscape predictors that best described the variability in stream habitat.
3. Immutable landscape predictors considered proxies for stream power described the majority of the variability seen in stream habitat features. Management-influenced landscape predictors, describing the additional human impacts beyond that which was inherently entwined with the immutable predictors, explained a sizeable proportion of variability. The largest response was seen in wood volume and pool frequency.
4. By using a sequential linear regression analysis, management-influenced factors could be segregated from natural gradients to identify those stream habitat features that may be more sensitive to land-use pressures. These results contribute to the progressing notion that the conservation of freshwater resources is best accomplished by investigating and managing stream systems from a landscape perspective.

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KEY WORDS: landscape scale; fish habitat; conservation evaluation; habitat management; monitoring; stream; coastal

INTRODUCTION

Conceptual and empirical approaches to understand and conserve fluvial ecosystems increasingly integrate the principals of landscape ecology (Johnson and Gage, 1997; Poole, 2002; Johnson and Host, 2010). These approaches become more pertinent and timely in the face of climate change and widespread human disturbance. Regional topography, geology, and climate regulate the structure and function of stream environments and are frequently used to model in-stream habitats (Allan, 2004; Kaufmann and Hughes, 2006) and biological patterns influenced by in-stream conditions (Richards *et al*., 1996; Steel *et al*., 2010). Efforts to understand these patterns have significantly advanced knowledge of how stream systems vary along longitudinal and lateral gradients, in addition to revealing landscape patterns relating to Pacific salmonid distribution (Steel *et al*., 2004; Isaak and Thurow, 2006; Burnett *et al*., 2007), abundance (Thompson and Lee, 2000; Pess *et al*., 2002), and recruitment (Thompson and Lee, 2002). The widespread degradation and

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loss of freshwater habitats, contributing to the imperilment of aquatic species and decline of aquatic ecosystem integrity (Nehlsen *et al*., 1991; Master *et al*., 2000), in part motivates the recent proliferation of studies examining broad-scale associations among natural and modified landscapes, stream habitats, and salmonid populations.

Researchers continue to explore how relationships between the landscape and stream environment are generalized over large spatial domains and how these relationships can guide conservation efforts (Allan and Johnson, 1997; Spies *et al*., 2007) –for example, efforts to recover Pacific salmon target habitat rehabilitation over broad spatial scales. Given that the spatial extent of anadromous salmon life cycles span estuarine to headwater habitats, populations respond to regional processes and disturbances. Identifying relationships among in-stream conditions and landscape features can inform process-based restoration goals seeking to reestablish natural processes that form and modify in-stream habitats in response to human disturbance (Beechie *et al*., 2010). Owing to the co-varying nature of such landscape features and the extent of human disturbance, analytically flexible methods that account for and better manage inherent system variability are essential.

Quantifying the relationships among landscape patterns and in-stream habitat conditions is hindered by the spatial overlap among multiple landscape gradients. Scientists are challenged to understand how these confounding interactions affect stream habitats (Johnson and Host, 2010). The co-variation between landscape features makes it difficult to disassociate specific effects of modified or natural landscape features or to isolate pathways of influence over local habitat (Kaufmann and Hughes, 2006; Wang and Seelbach, 2006; Lucero *et al*., in press). The configuration and composition of these natural landscape features often influence the suitability and thereby the presence of particular land-use practices (Beschta *et al*., 1995; Allan, 2004).

Acknowledging that land use has been and continues to be inextricably linked to the landscape (Allan, 2004) will aid in developing analyses intending to differentiate between the myriad of landscape effects. The presence of multiple correlated predictors (multicollinearity) is analytically problematic as these tend to inflate the variance of coefficient estimates in regression analyses, reducing the reliability of explanatory models. Numerous techniques have been proposed to deal with this issue; residual regression, principal components regression, and hierarchical partitioning are a few alternatives (Mac Nally, 2002; Graham, 2003; King *et al*., 2005; Gromping, 2007). One of the proposed techniques partitions the relative importance of a set of collinear predictors on the response. This method assumes that some predictors are functionally more important and more mechanistically linked to the response (Graham, 2003), an assumption that also aligns with how in-stream habitats are formed and function. The nature of collinearity among natural and human factors can be incorporated in the development of explanatory models, which could improve the rigour and accuracy of modelling ecological relationships and aid in process-based restoration approaches.

The objectives in this study were (a) to evaluate how much in-stream habitat variation can be accounted for by landscape predictors, and (b) to determine whether a management-influenced signal, above and beyond that associated with immutable landscape predictors, can be detected. The approach in this study complements previous studies as it addresses the inherent correlation between the natural landscape and land use.

MATERIALS AND METHODS

Study area

The study area encompassed 121 coastal catchments in the Oregon Coastal Range (Figure 1) that are generally characterized by sedimentary or volcanic bedrock and elevations ranging from sea level to 380 m. The area has a temperate maritime climate with mild, wet winters and dry summers. Coniferous forests, spanning early successional and old growth seral stages, dominate the study area, although broadleaf species such as big leaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*) are common. Inland species that predominate are Douglas fir (*Psuedotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), while Sitka spruce (*Picea sitchensis*) prevails along the coast. Most of the province is privately owned by the forest industry and non-industrial forest owners; however, one third of the province is publicly managed by state or federal agencies (Spies *et al*., 2007). Disturbance regimes in this region include infrequent but intense wildfire, annual windstorms, landslides, timber harvest, and agriculture at the lower elevations (Burnett *et al*., 2007).

In general, stream flow in the Oregon Coast Range varies intra-annually but the pattern is relatively consistent across years. The majority of precipitation occurs as rainfall, with peak stream flows following winter rain storms and base flows occurring between July and October (Harr, 1976). The channel hydraulic characteristics vary with stream size and upslope catchment processes. Management activities affect catchment and channel hydraulics influencing peak flows, overland flows, and sedimentation rates (Harr, 1976). Five species of anadromous salmon reside in the study area: coastal cutthroat trout (*Oncorhynchus clarki*), Chinook salmon (*Oncorhynchus tschawytscha*), chum salmon (*Oncorhynchus keta*), steelhead (*Oncorhynchus mykiss*) and coho salmon (*Oncorhynchus kisutch*), which belong to the Oregon Coastal Coho Evolutionarily Significant Unit (ESU) (Weitkamp *et al*., 1995) listed as threatened under the US Endangered Species Act (1973).

In-stream habitat data

In-stream data for this study are from a coast-wide, integrated programme in Oregon to monitor adult coho salmon abundance, juvenile coho salmon abundance, and freshwater habitat (Firman and Jacobs, 2001). Potential sample reaches were selected using a generalized random tessellation stratified design to obtain a spatially balanced random sample (Stevens and Olsen, 2004). A rotating panel design, with rotations of 1, 3, and 9 years to correspond with the 3-year life cycle of coho salmon, was imposed to optimize status estimates and enable trend detection (Stevens and Olsen, 2004). In this analysis, only reaches surveyed annually and every 3 years were used.

Stream habitats were surveyed from mid-June to late September each year. Surveyed lengths for stream reaches were 500 m outside the current distribution of coho salmon and 1000 m for those inside the current distribution. Data

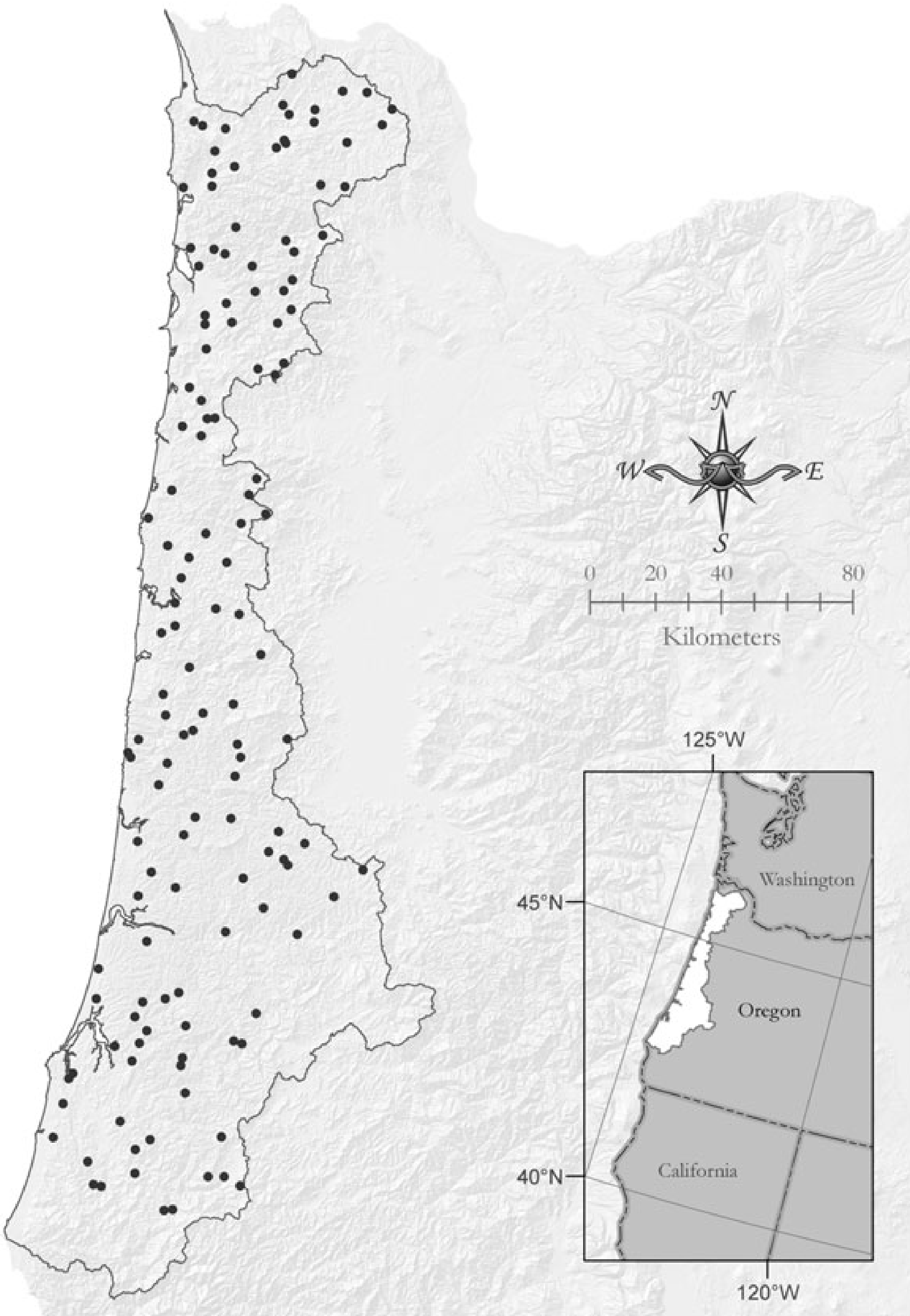

Figure 1. Distribution of in-stream habitat survey sites within the Oregon Coast Range.

were collected on specific features of the stream channel and the physical structure of the valley and riparian areas using methods described by Moore *et al.* (2007). Eleven in-stream habitat features were selected as response variables for analysis (Table 1). These are important habitat features in summer and reflect conditions limiting for coho salmon in winter.

A reach-level complexity feature is included to reflect potential interrelationships among in-stream habitat features and is consistent with other freshwater habitat complexity and diversity indices developed for similar reasons (Gorman and Karr, 1978; Nickelson and Lawson, 1998; Horan *et al.*, 2000). Five stream habitat features comprise the reach complexity feature: percentage secondary channel area, percentage pool habitat, number of pools, variance of residual pool depth, and pool diversity. Pool diversity was calculated as:

$$|(50-|(50\text{–per cent of pool habitat in a reach})|)|$$

which allows values to decrease on either side of 50, demonstrating an optimal balance between slow- (pool) and fast-water habitats. To standardize values for each of the five component habitat features, the mean and standard deviation were calculated across all reaches within a particular year,

Table 1. All in-stream habitat features (response) used in the analyses. Values were summarized for a reach (500 m or 1000 m) and averaged across years. Data were collected in the field using methods described in Moore *et al*. (2007)

In-stream Habitat Feature	Description	Data Transformation
Active Channel Width	Distance across the channel at bankfull flow (attained on average every 1.5 years) (m).	$\ln(x+1)$
Percentage Secondary Channel Area	Percentage of total reach area that is classified as secondary channel.	$\ln(x+1)$
Pools/100 m	Pools per 100 m of reach length.	$\ln(x+1)$
Residual Pool Depth	The difference of max depth and pool tail crest (meters).	$\ln(x+1)$
Valley Width Index (VWI)	Average Valley Width Index for the reach; VWI equates to the total number of active channel widths that will fit between each hillslope.	$\ln(x+1)$
Percentage Undercut Banks	Percentage of the perimeter of the habitat unit composed of undercut banks.	$\ln(x+1)$
Percentage Shade	Percentage of the stream channel that is shaded.	Logit(x)
Percentage Fine Sediments	Proportion of the stream-bed area that is classified as silt, sand, and organics (<2 mm).	$\ln(x+1)$
Percentage Gravel	Proportion of the stream-bed area that is classified as gravel (2–64 mm).	N/A
Wood Volume	Volume of in-stream wood per 100 m of reach length (m^3 per 100 m).	$\ln(x+1)$
Reach Level Complexity	The sum of secondary channel area, number of pools, the variance of residual pool depths, and a pool diversity metric. The diversity metric is calculated by subtracting 50 from the percentage of pools in a reach. Standardized across all years and all sites.	N/A

and then for each reach the mean was subtracted from the reach value and divided by the standard deviation. The five standardized values for each reach were summed to create the reach-level complexity feature.

Landscape predictors

Geospatial data layers, reflecting landform and human influences on local in-stream habitats, provided the landscape predictors (Table 2). Each predictor was summarized for the catchment flowing into each study reach, which encompassed the entire drainage area upstream. Immutable landscape predictors are relatively unaffected by human influence (gradient, precipitation, drainage area, elevation, flow, temperature, geology) and management-influenced landscape predictors are affected by or are a direct result of human influence (forest cover, land ownership, disturbance, and land use) (Table 2).

Model development and statistical analysis

Each of the 11 in-stream habitat features was regressed against multiple immutable and management-influenced landscape predictors using Proc GLM in SAS. Because temporal variability was low (Anlauf *et al*., 2011), in-stream habitat data were averaged across the 10 years for which data were available and mean values were used as regression responses. To improve model fit, a habitat feature was transformed if its distribution departed sufficiently from normal. A sequential regression approach was used (Graham, 2003; Kaufmann and Hughes, 2006). In the first step, in-stream habitat features were regressed against immutable landscape predictors indicative of stream power (gradient, drainage area, precipitation, and their natural log counter-part) (Table 2), which are first-order controls that determine the amount and size of material that flowing water can transport. These three predictors are related to many in-stream habitat variables (Kaufmann and Hughes, 2006; Johnson and Host, 2010). In the next step, additional immutable landscape predictors (Table 2) were added to the best stream power indicators for each in-stream habitat feature. In the final step, management-influenced landscape predictors (Table 2) were added to the best immutable landscape predictors identified in the two preceding steps.

At each step in the regression sequence for each in-stream habitat response, one and two landscape predictor combinations were evaluated (see below) before the third and final landscape predictor was added to a model. Akaike Information Criterion (AIC) was used to select the final model from a set of competing models at each step. Models with ΔAIC (AIC_{model} – $AIC_{null\ model}$) less than 4 as competing models were considered (Burnham and Anderson 2002). Only models with a condition index (Belsley *et al*., 1982) less than 25 were included in the original candidate pool to avoid serious collinearity problems that can inflate variance estimates and affect model reliability (Ott and Longnecker, 2001). Only models with a Cook's D (Cook, 1977) less than 1 were included in the original candidate pool to eliminate instability due to data points with high leverage. When the best model identified by AIC did not meet these additional criteria, the next model in ascending AIC that met the criteria was chosen. The final 11 models were cumulative, composed of the immutable and management-influenced landscape predictors that met the above criteria.

The ΔAdjusted R^2 was used to calculate the difference in the coefficient of determination with the addition of (1) the immutable predictors, and (2) the management-influenced predictors. To determine the specific contribution of management-influenced landscape predictors, while all other immutable predictors were held constant, the coefficient of partial determination (partial R^2) was calculated.

Model diagnostics and collinearity

To evaluate model predictions, correlations were examined between predicted and observed values for each habitat feature. Variance inflation factors (VIFs) were calculated to detect multi-collinearity among immutable and management-influenced landscape predictors in the final model for each in-stream habitat feature. A VIF value greater than 5 indicates a serious collinearity problem (Ott and Longnecker, 2001).

Table 2. Description of geospatial landscape predictors used in the regression analysis

Landscape predictor	Description	Data layer	Reference	Map scale/ gridcell size
Stream Power Indicators				
DA (drainage area)	Catchment area upstream of study reach	Generated from a USGS 10 m DEM	USGS	1:24,000
Gradient	DEM-derived stream gradient	Stream Layer	Clarke *et al*., 2008	10 m
Precipitation	Mean annual precipitation (mm)	Cumulative mean annual precipitation (1961–1990) from the Precipitation Elevation Regressions on Independent Slopes Model (PRISM)	Daly *et al*., 1997; WCCNRCS, 1998	4000 m
Additional Immutable				
Elevation	Mean elevation	DEM	USGS	1:24,000
Flow	Stream flow ($m^3 s^{-1}$)	CLAMS	Clarke *et al*., 2008	10 m
Temperature	Max, Min, Annual, Summer, Winter	PRISM Climate	Daly *et al*., 1997	4,000 m
Resistant	% Resistant sedimentary			
Sedimentary	% Intermediate sedimentary	Geomorphology	Forest Ecosystem Management Assessment	1: 500,000
Weak	% Pyroclastic, schists		Team (FEMAT), 1993	
Mafic	% Intrusive, pyroclastic, volcanic flows	Lithology	Walker *et al*., 2003	
Management Influenced				
BigTrees	% Large conifers (>50 cm)			
MedTrees	% Medium trees			
SmallTrees	% Small trees	Forest cover	Ohmann and Gregory, 2002	25 m
Hardwoods	% Hardwoods			
BLM	% US Bureau of Land Management	Land ownership	Oregon Department of Forestry, 2004	1: 126,720
USFS	% US Forest Service			
PrivateInd	% Private Industrial (Industrial Forests			
Cut	% Burned or harvested before 1998	Disturbance	Lennartz, 2005	25 m
NoDisturb	% Not burned or harvests before 2004			
NonForest	Non forest cover			
CowDen	Cow density	Land Use	Burnett *et al*., 2007	30 m
RoadDen	Road density		BLM Ground Transportation Roads Publication, 2011	1: 24,000

RESULTS

Variation explained by landscape predictors

Immutable predictors

The variation in habitat features explained by gradient, precipitation, and/or drainage area ranged from 0.05 to 0.72 (Table 3; Figure 2). Active channel width (Adjusted $R^2 = 0.72$) and percentage of fine sediments (Adjusted $R^2 = 0.48$), which are expected to be largely influenced by the stream power indicators, had the highest adjusted R^2 values. Those least correlated with these landscape predictors were percentage gravel (Adjusted $R^2 = 0.05$), pools per 100 m (Adjusted $R^2 = 0.11$), and percentage secondary channel area (Adjusted $R^2 = 0.12$). The additional variation in habitat features explained by immutable landscape predictors representing elevation, flow, temperature, and geology ranged from 0.001 to 0.08, with the largest increase for wood volume (Table 3; Figure 2). Landscape habitat predictors characterizing geology explained most of the additional variation associated with this suite of immutable predictors. Of the final models for the 11 in-channel habitat features, fewer than half included elevation or flow but none included temperature predictors.

Management-influenced predictors

Management-influenced predictors explained up to 16% additional variation in habitat features (Table 3; Figure 2). After accounting for immutable predictors, partial R^2 values were highest for pools per 100 m (partial $R^2 = 0.21$) and wood volume (partial $R^2 = 0.28$). Wood volume was associated with several landscape predictors reflecting wood availability (% non-forest, % small trees, and % remnant forests), whereas pools per 100-m was associated with disturbances affecting pool retention (cow density, road density) and pool formation (% small trees).

Model diagnostics and collinearity

Predicted versus observed responses were correlated, with r-values ranging from 0.419–0.866 (Table 4) and predicted values varying spatially (Figure 3). Variance inflation factors (VIF) indicated low collinearity among landscape predictors in the final models; 100% of the predictors had

Table 3. Final model equations for each in-stream habitat feature response once immutable and management-influenced landscape predictors were added to models fitted with stream power indicators. $AdjR^2$ = Adjusted R^2

Response	Model	$AdjR_1^2$	partial R_2^2	partial R_3^2	$AdjR_4^2$
Active Channel Width	1.122 + (0.00019*Precip + 0.384*lnDA) – (0.0025*Sedimentary) – (0.0091*Hardwoods - 0.061*RoadDen + 0.0033*Cut)	0.716	0.035	0.072	0.737
Percentage Secondary Channel Area	0.569 + (0.112 *lnGradient + 0.00021*Precip + 0.074*lnDA) – (0.0027*Sedimentary) – (0.019*NonForest)	0.124	0.013	0.021	0.139
Pools/100 m	1.255 – (0.0269*Gradient – 0.0284*lnDA) + (0.00050*Elev – 0.0017*Flow – 0.0023*Weak) + (0.107*RoadDen – 0.0094*SmallTrees – 0.0054*CowDensity)	0.112	0.124	0.210	0.336
Residual Pool Depth	−0.824 – (0.0343*Gradient + 0.00011*Precip + 0.060*lnDA) – (0.0008*Sedimentary) – (0.0048*Remnant + 0.049*RoadDen – 0.0097*NonForest)	0.266	0.009	0.090	0.316
VWI Reach	2.171 – (0.441*lnGradient – 0.210*lnDA) – (0.0015*Resistant + 0.0041*BLM +0.023*NonForest – 0.0084*SmallTrees)	0.268	0.011	0.082	0.313
Percentage Undercut Banks	2.561 – (0.102*Gradient + 8.957*10^{-5}*Precip – 0.219*lnDA) – (0.0030*Flow – 0.0039*Resistant – 0.0043*Weak) – (0.0163*CowDensity – 0.0111*SmallTrees +0.138*RoadDen)	0.335	0.091	0.122	0.422
Percentage Shade	−1.257 + (0.523*lnGradient + 5.875*10^{-5}*Precip) + (0.0087*Sedimentary −0.0066*Weak) + (0.0150*NoDisturb + 0.0095*PrivateInd + 0.225*RoadDen)	0.233	0.074	0.129	0.355
Percentage Fine Sediments	5.255 – (0.568*lnGradient – 0.0002*Precip – 0.444*lnDA) – 0.003*Resistant – 0.021*NonForest - 0.0063*SmallTrees	0.479	0.052	0.064	0.526
Percentage Gravel	23.023 – (1.267*Gradient – 3.908 *lnDA) + (0.0488*Flow + 0.0632*Resistant) + (0.105*BLM – 0.136*NoDisturb + 0.135*BigTrees)	0.047	0.042	0.096	0.134
Wood Volume	2.024 + (0.382*lnGradient) + (0.0016*Elev + 0.0028*Resistant + 0.0024*Flow) – (0.085*NonForest – 0.0091*SmallTrees + 0.009*Remnant)	0.301	0.164	0.279	0.544
Reach Level Complexity	−3.514 – (0.221*Gradient + 0.00077*Precip + 0.342*lnDA) – (0.00074*Elev) + (0.0186*NoDisturb + 0.288*RoadDen + 0.010*BLM)	0.346	0.029	0.106	0.410

[1]Adjusted R-square for stream power immutable landscape predictors representing indicators of stream power.
[2]Coefficient of partial determination for additional immutable predictors after accounting for gradient, precipitation and drainage area.
[3]Coefficient of partial determination for management-influenced predictors after accounting for all immutable predictors.
[4]Final Adjusted R-square value.

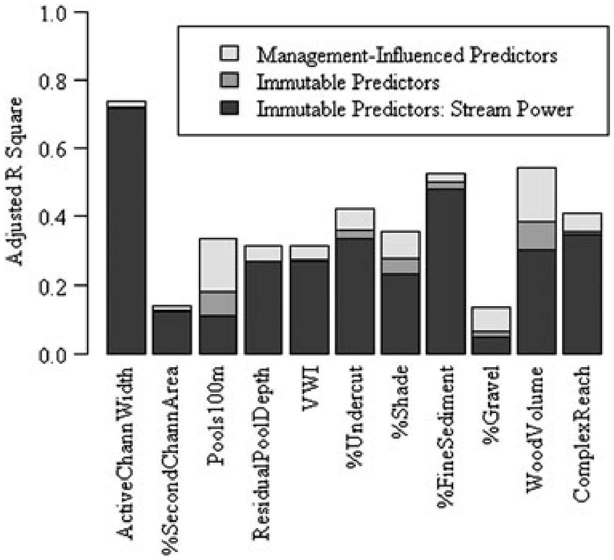

Figure 2. Proportion of variability attributed to management-influenced predictors, immutable predictors (climate, geology, topography), and stream power indicators (gradient, precipitation, drainage area) for the 11 in-stream habitat response features evaluated.

VIF values less than 5 and 80% were less than 2. However, the co-occurrence of certain landscape predictors (e.g. drainage area with gradient or flow) repeatedly produced VIF values greater than 2.5.

DISCUSSION

One of the central goals in this study was to account for natural gradients, enabling a better understanding of the management-influenced effects on stream habitats as a basis for conserving freshwater ecosystems. After accounting for landscape predictors representing stream power, results of this study indicate that other immutable landscape predictors explained little in-stream habitat variation, and adding management-influenced predictors explained up to 28% (partial R^2) more variation. This result shows the substantial influence recent and historical land management can have on stream habitat beyond that of natural gradients. This study summarizes habitat conditions that are predominantly constrained by topographic and climatic gradients but have variable sensitivity to land-use pressures. Our approach to landscape partitioning in this study can help determine the degree of human influence among in-stream habitat metrics, providing a foundation for managers to understand stream condition in the context of the landscape, and prescribe the appropriate restoration. The focus of this discussion will be on those habitat metrics that were best modelled using these methods and most relevant in terms of ecological process and biological significance.

Influence of land management on in-stream habitat

For some in-stream habitat features, longitudinal controls expressed by topographic and geomorphic landscape features may be more important than predictors reflecting current

Table 4. Predicted mean value with associated root mean square error (RMSE) for in-stream habitat response features and corresponding 95% confidence intervals (±2 (RMSE)). Correlations between observed and predicted in-stream habitat response features also calculated

Response	Observed mean	Predicted mean	Correlation	RMSE	95% Confidence interval	
					Lower	Upper
Active Channel Width (log)	1.822	1.436	0.866	0.342	1.138	2.506
Percentage Secondary Channel Area (log)	1.048	0.734	0.419	0.632	−0.216	2.312
Pools/100 m (log)	1.100	1.345	0.617	0.286	0.528	1.672
Residual Pool Depth (log)	−0.607	−0.764	0.596	0.295	−1.197	−0.017
VWI Reach (log)	1.300	1.537	0.589	0.630	0.040	2.560
Percentage Undercut Banks (log)	1.443	2.339	0.683	0.570	0.303	2.583
Percentage Shade (logit)	1.863	−0.314	0.626	0.977	−0.091	3.817
Percentage Fine Sediments (log)	3.163	4.210	0.741	0.517	2.129	4.197
Percentage Gravel	28.617	33.219	0.430	13.598	1.421	55.813
Wood Volume (log)	2.690	2.328	0.755	0.690	1.310	4.070
Reach Level Complexity	−0.082	−3.074	0.667	1.526	−3.134	2.9699

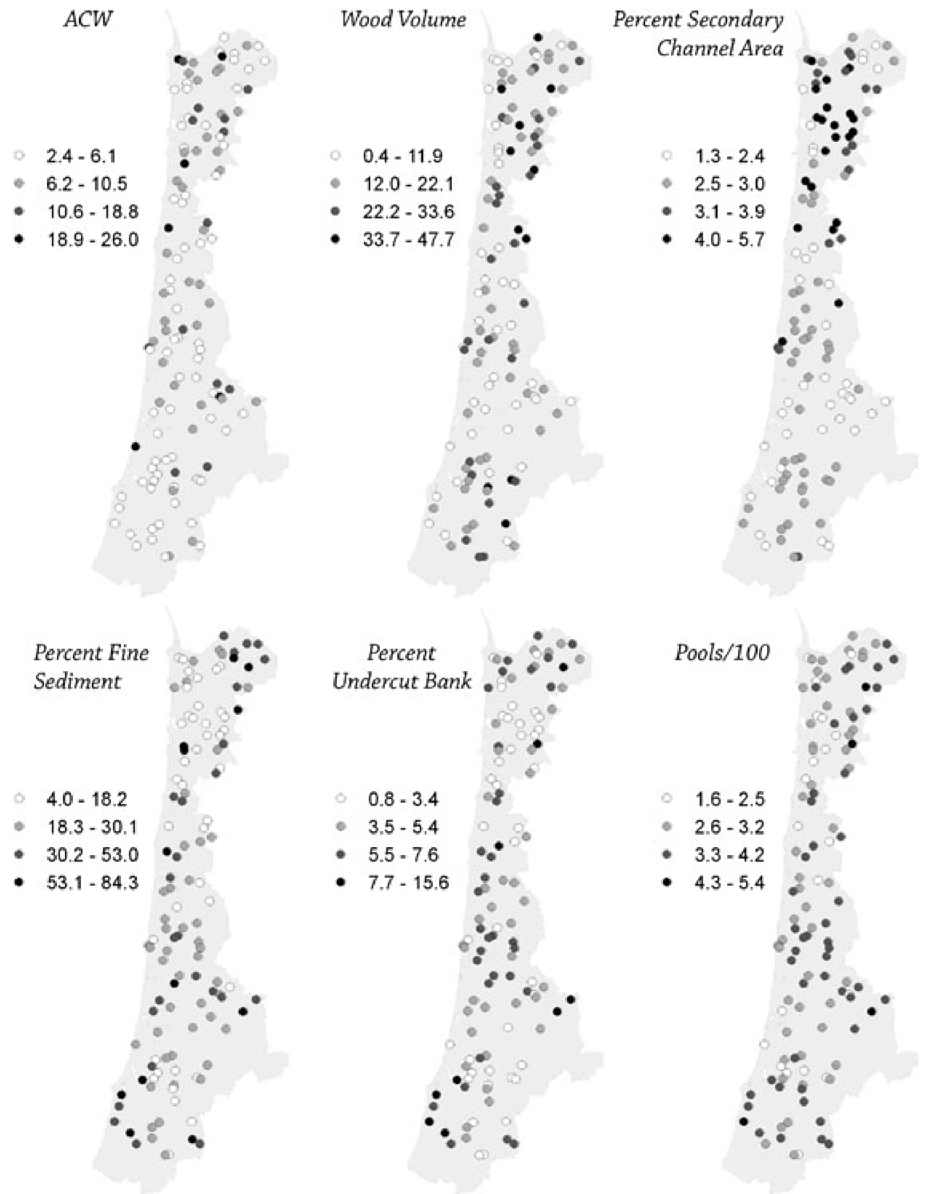

Figure 3. Spatial representation of predicted values for six of the in-stream habitat response features.

human influence. Consistent with this, management-influenced predictors explained little variation in active channel width or percentage fine sediment beyond that of natural gradients already incorporated in the sequentially fitted models. Several studies have identified similar immutable predictors as primary drivers of sediments or geomorphic conditions describing stream size (e.g. pool volume or depth) Burnett *et al.*, 2006; Jorgensen *et al.*, 2009). Much of the current research has shown that sediment dynamics in streams is sensitive to land use and management (Wood and Armitage, 1997; Kaufmann *et al.*, 2008; Larsen *et al.*, 2008). While the human activities that widen stream channels and exacerbate in-stream sedimentation do occur in the study area, the effects of these activities may co-vary with the stronger signals of stream power and other immutable landscape predictors (Lucero *et al.*, in press). These two features are commonly monitored in habitat monitoring programmes (Roper *et al.*, 2010) and are useful and pertinent for monitoring goals that often vary across agencies and regions.

Although immutable landscape predictors explained a large percentage of the variation in wood volume, management-influenced predictors accounted for over a quarter of the total. The positive relationships between immutable landscape features and in-stream wood have been noted before (Burnett *et al.*, 2007; Lucero *et al.*, in press) and are probably a result of the spatial scale at which the landscape data were summarized, and the location of the study reaches relative to that extent. While the results are the inverse of what is expected in relation to stream power, the use of a sequential regression approach partitioned landscape features making the results comprehensible in the context of land management in the Oregon Coast Range. As Lucero *et al.* (in press) noted, larger spatial scales will tend to include higher elevations and gradients, and more mature forest. The predictors related to forest composition, representing upslope conditions influencing wood recruitment in streams, emerged as the strongest correlates. Wood volumes varied as catchments became less forested and were harvested and replanted. Other studies have noted in-stream reductions in both the condition of large wood and the resulting habitats it fosters (Al-Chokhachy *et al.*, 2010), and wood recruitment as a result of forest practices (Wing and Skaugset, 2002; Czarnomski *et al.*, 2008). Given that in-stream wood is sensitive to management and is a catalyst for direct and indirect influences on sediment transport and storage, stream stability, and complexity for salmonids (Montgomery and Piegay, 2003), it is a particularly useful indicator of human disturbance. However, to contribute more fully to recovery goals in the Oregon Coast Range and elsewhere, one should consider both the complexity of the coastal geomorphology and the landscape mosaic of forest management affecting fluvial processes that drive in-stream wood dynamics. Considering the role of in-stream wood relative to disturbances upstream may make this frequently measured feature within monitoring programmes (Roper *et al.*, 2010) more pertinent and effective in implementing restoration and monitoring.

Habitat features insensitive to either immutable or management variables

Several in-stream habitat features (e.g. pool frequency, residual pool depth, percentage gravel, secondary channel area) were poorly explained by landscape predictors in this study. Reasons for this include mismatches in the scale of analysis with some relationships possibly perceivable at finer or coarser scales than those examined (Lucero *et al.*, in press), need for a multi-scale approach (Feist *et al.*, 2003; Lowe *et al.*, 2006), and differing patterns of disturbance across catchments. Regarding the last of these, Roper *et al.*, (2007) also had difficulties relating stream habitat features to vegetative disturbance, a result they attribute in part to the differences between patterns of natural and human disturbance. The frequency and intensity of natural disturbances (e.g. fires and landslides), can be exacerbated by past and present land use (e.g. timber harvest and persistence of non-forest) (Stanley *et al.*, 2010). Several studies have successfully evaluated these broad-scale relationships to in-stream habitat when managed and un-managed (reference) catchments can be distinguished (Kershner *et al.*, 2004; Al-Chokhachy *et al.*, 2010). In the Oregon Coast Range, however, few reference catchments are available given extensive contemporary or historical human disturbances. The degree to which historical land-use has affected stream habitat features is neither well documented nor understood and could hamper abilities to detect relationships with variables reflecting current management. Historical land-use can influence stream conditions long after the disturbance has ceased, modifying stream habitat and biotic community structure and diversity (Harding *et al.*, 1998; Maloney *et al.*, 2008; Zhang *et al.*, 2009). The legacy of splash dams (Miller, 2010) and mill dams (Walter and Merritts, 2008) in the Oregon Coast Range and elsewhere illustrate how historical disturbance has homogenized stream channels, altered floodplain sedimentation, and modified the perception of natural channel geometry. Further research on legacy effects and disturbance thresholds on stream habitats and fish species would provide insight into future studies seeking to appreciate these landscape linkages.

Many of the in-stream habitat metrics evaluated here relate directly to the quality of fish habitat (McMahon and Hartman, 1989) and so are commonly measured in monitoring programmes (Roper *et al.*, 2010), and are often the target of restoration measures (e.g. wood placement to accumulate gravels, form pools, and increase area in secondary channels). When evaluating habitat metrics to include or retain in a monitoring programme, important considerations include the pertinence of the metric to fish, its spatial and temporal variability across the landscape, as well as its sensitivity to management. For example, only a small proportion of the variation in pool habitat was explained by landscape features ($AdjR^2 = 0.34$), but management-influenced predictors did account for the majority (60% of the total). Alternatively, the percentage of gravel substrates and secondary channel area, which are regularly monitored, could not be usefully explained by landscape features. This could be due to the common but patchy nature of gravel-bed substrates and the increasingly rare presence of secondary channels and off-channel habitats. Given these results, perhaps these two metrics are ill suited for understanding associations across the landscape or may be better incorporated into an integrated metric with other local habitat attributes.

Measure of stream complexity

Integrating multiple stream habitat features into a single metric or index has proved valuable when trying to understand and describe occupancy (Gorman and Karr,

1978) and abundance (Horan *et al.*, 2000; Hasegawa and Maekawa, 2008). Although habitat complexity ensures the diversity of fish communities (Smokorowski and Pratt, 2007) and can thwart the persistence of non-native species (Rich *et al.*, 2003), few studies have evaluated the landscape effects on in-stream habitat complexity. One exception is a recent study by Al-Chokhachy *et al.* (2010) who used a multimetric index approach when evaluating the effects of management activities on habitat condition. They found that habitat index values were significantly related to land management predictors of road density and grazing. In the current study, immutable landscape predictors describing stream power explained most of the variation in the pool complexity habitat feature with relatively little variance accounted for by adding management-influenced predictors to the model. This result was somewhat unexpected given that the reduction of complex habitat structure and the simplification of channel habitats are a result of land management, and has been noted as one of the bottlenecks to the recovery of Oregon coast coho salmon (NOAA, 1997; OCSRI, 1997). Perhaps a more comprehensive complexity metric, versus one limited to pool habitats alone, would be more informative in the context of these data.

Study implications and conclusions

One of the primary purposes of correlative studies is to further understanding on how in-stream habitats are influenced by landscape controls at broad spatial extents, which is often impractical using controlled experiments. Relationships identified in these studies may generate testable hypotheses about landscape controls on habitat but have immediate value in suggesting landscape features important for conserving critical salmon habitats. This is important to more effectively meet recovery and conservation goals. In addition, these relationships can help inform monitoring strategies for adult and juvenile salmon whose occupancy may be driven directly by in-stream conditions. Results of this study can guide restoration efforts in times of tight budget by suggesting activities and areas that have the greatest likelihood to yield improvements. Similarly, targeting those in-stream habitat metrics that seem to be more sensitive to management may also be those that are sensitive to restoration measures. Restoration efforts are often focused on improving habitat conditions in general, and specifically for juvenile salmonid species. However, identifying areas that benefit multiple salmonid life stages may ensure long-term population viability. Habitat colonization and expansion of geographic distributions is important to the evolutionary sustainability of a population (Anderson and Quinn, 2007). Describing how variability in stream habitats can be partitioned among landscape predictors is particularly applicable when assessing the population status of coho salmon whose most suitable habitats, characterized by low stream gradients in low valley slopes, are also where human influences tend to be concentrated (Giannico, 2000; Sharma and Hilborn, 2001; Burnett *et al.*, 2007). Understanding the relationships that currently exist among in-stream habitat and management-influenced landscapes will aid in understanding how current and natural processes differ. Ultimately, these results can be used to set goals in stream restoration that enhance ecosystem processes with a focus on sustaining fish populations under changing climate and ocean regimes.

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