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Comparing Riparian and Catchment Influences on Stream Habitat in a Forested, Montane Landscape

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Abstract.—Multiscale analysis of relationships with landscape characteristics can help identify areas and physical processes that affect stream habitats, and thus suggest where and how land management is likely to influence these habitats. Such analysis is rare for mountainous areas where forestry is the primary land use. Consequently, we examined relationships in a forested, montane basin between stream habitat features and landscape characteristics that were summarized at five spatial scales (three riparian and two catchment scales). Spatial scales varied in the area encompassed upstream and upslope of surveyed stream segments and, presumably, in physical processes. For many landscape characteristics, riparian spatial scales, approximated by fixed-width buffers, could be differentiated from catchment spatial scales using forest cover from 30-m satellite imagery and 30-m digital elevation data. In regression with landscape characteristics, more variation in the mean maximum depth and volume of pools was explained by catchment area than by any other landscape characteristic summarized at any spatial scale. In contrast, at each spatial scale except the catchment, variation in the mean density of large wood in pools was positively related to percent area in older forests and negatively related to percent area in sedimentary rock types. The regression model containing these two variables had the greatest explanatory power at an intermediate spatial scale. Finer spatial scales may have omitted important source areas and processes for wood delivery, but coarser spatial scales likely incorporated source areas and processes less tightly coupled to large wood dynamics in surveyed stream segments. Our findings indicate that multiscale assessments can identify areas and suggest processes most closely linked to stream habitat and, thus, can aid in designing land management to protect and restore stream ecosystems in forested landscapes.

INTRODUCTION

The condition of a stream ecosystem is largely a function of landscape characteristics in the surrounding catchment (Hynes 1975; Frissell et al. 1986; Naiman et al. 2000). A catchment contains a mosaic of patches and interconnected networks (Pickett and White 1985; Swanson et al. 1997; Jones et al. 2000) that control the routing of energy and materials to streams and that ultimately control stream ecosystems (Swanson et al. 1998; Jones et al. 2000; Puth and Wilson

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2001). These patches and networks have characteristics such as size, shape, type (e.g., forest or paved roads) and location (e.g., ridge top or riparian). Direct effects on streams of landscape characteristics in the local riparian area are well established (Osborne and Koviac 1993; Naiman et al. 2000; National Research Council 2002). However, relationships between streams and landscape characteristics are less well understood and agreed upon when landscape characteristics are considered upstream along a riparian network (Weller et al. 1998; Jones et al. 1999) or upslope throughout a catchment (Jones and Grant 1996, 2001; Thomas and Megahan 1998; Gergel 2005).

Influences of riparian and catchment characteristics on stream ecosystems have been examined predominantly in agricultural and urbanized areas. For example, the abundance of adult coho salmon *Oncorhynchus kisutch* in the Snohomish River, Washington was significantly related to land cover (expressed as percent urban, agriculture, or forest) summarized for the local riparian area and for the entire catchment (Pess et al. 2002). Riparian and catchment land cover may explain approximately equal proportions of physical (Richards et al. 1996) and biological (Van Sickle et al. 2004) variation in agricultural or urbanized stream systems.

Conclusions often differ, however, regarding the relative influence of riparian and catchment land cover on streams in agricultural and urban environments. Certain in-channel responses were best explained by land-cover characteristics summarized for the local riparian area (e.g., catch per 100 m of cool- and coldwater fish [Wang et al. 2003a]). Others were best explained by land-cover characteristics summarized for the entire catchment (e.g., total fish and macroinvertebrate species richness [Harding et al. 1998]). For water quality parameters, land-cover characteristics explained more variation when summarized for the riparian network in some studies (Osborne and Wiley 1988) but for the entire catchment in others (Omernik et al. 1981), or explained a variable degree of variation depending on data resolution, season or location of sampling, and modeling approach (Hunsaker and Levine 1995; Johnson et al. 1997). Even when the same response variable (index of biological integrity) was examined in the same river basin but at different spatial extents, judgments differed about the influences of riparian and catchment land cover (Roth et al. 1996; Lammert and Allan 1999). Given such variability, extrapolating understanding from multiscale studies in more developed landscapes to stream systems in forested landscapes may be ill advised.

Riparian and catchment land cover have seldom been compared for relationships to streams in mountainous areas where forest uses dominate. We are aware of few studies examining riparian and catchment influences on streams that drain forested regions or areas with minimal human development (Hawkins et al. 2000; Wang et al. 2003b; Weigel et al. 2003; Sandin and Johnson 2004). Understanding arising from such studies may contribute to conservation of Pacific salmon and trout, which are widely distributed in North America. Abundances of these fish and conditions of their freshwater habitat have been related to land-cover characteristics at different spatial scales, including the local riparian area (Bilby and Ward 1991), the riparian network (Botkin et al. 1995), and the catchment (e.g., Reeves et al. 1993; Dose and Roper 1994; Dunham and Rieman 1999; Thompson and Lee 2002). Although such studies offered valuable insights, none directly examined relationships between salmon, or their habitats, and land-cover characteristics summarized at more than one spatial scale.

Multiscale assessments may identify riparian and upslope areas that help create and maintain salmon habitats in forested, montane landscapes. Pools and large wood are essential components of salmon habitat in such landscapes, providing living space and cover from predators (Bilby and

Bisson 1998; McIntosh et al. 2000). Pools are areas of local scour caused by fluvial entrainment and transport of bed substrates that persist until sediment inputs to, and outputs from, a pool equilibrate. The creation and morphology (depth, volume, and surface area) of pools are driven by sediment supply, hydraulic discharge, and presence of flow obstructions (e.g., wood and boulders) (Buffington et al. 2002). All three factors are affected by channel-adjacent and hill-slope processes. For example, the amount of sediment and wood supplied to pools can increase with increases in the frequency of channel-adjacent processes, such as bank erosion, or of hill-slope processes, such as landsliding. The relative importance of channel-adjacent and hill-slope processes can vary with channel type (Montgomery and Buffington 1998; Buffington et al. 2002) and land cover (e.g., Bilby and Bisson 1998; Ziemer and Lisle 1998; Montgomery et al. 2000), and thus, the potential for land management to impact pools and large wood varies across the landscape. Consequently, studying relationships at multiple spatial scales can help identify which processes are, and where land management is, likely to alter salmon habitat.

Our goal was to understand relationships between salmon habitat and landscape characteristics, summarized at multiple spatial scales, in a montane basin where forestry is the dominant land use. Targeted habitat features were the mean maximum depth of pools, mean volume of pools, and mean density of large wood in pools. Three riparian scales (segment, subnetwork, and network) and two catchment scales (subcatchment and catchment) were considered for each stream segment where targeted habitat features were evaluated (Figure 1). Spatial scales differed in the area included upslope and upstream of surveyed stream segments, and presumably in vegetative, geomorphic, and fluvial processes that may affect targeted habitat features. Channel-adjacent processes (e.g., tree mortality in riparian stands and streamside landsliding) and in-channel process (e.g., debris flows and fluvial transport) were assumed to dominate at the riparian scales. Potential for nonchannelized hill slope processes (e.g., surface erosion and landsliding) were added at the two catchment scales. Specific study objectives were to (1) examine differences among spatial scales for landscape characteristics described with relatively coarse-resolution data, and (2) compare the proportion of variation in stream habitat features explained by landscape characteristics summarized within and among different spatial scales.

STUDY AREA

The study was conducted in tributaries of the upper Elk River, located in southwestern Oregon, USA (Figure 2). The main stem of the Elk River flows primarily east to west, entering the Pacific Ocean just south of Cape Blanco (42°5'N latitude and 124°3'W longitude). The Elk River basin (236 km^2) is in the Klamath Mountains physiographic province (Franklin and Dyrness 1988) and is similar to other Klamath Mountain coastal basins in climate, landform, vegetation, land use, and salmonid assemblage.

The climate is temperate maritime with restricted diurnal and seasonal temperature fluctuations (USFS 1998). Ninety percent of the annual precipitation occurs between September and May, principally as rainfall. Peak stream flows are flashy following 3–5-d winter rainstorms, and base flows occur between July and October. Elevation ranges from sea level to approximately 1,200 m at the easternmost drainage divide. Recent tectonic uplift produced a highly dissected terrain that is underlain by the complex geologic formations of the Klamath Mountains. Stream densities in these rock types range from 3 to 6 km/km^2 (FEMAT 1993).

Much of the study area is in mixed conifer and broadleaf forests that include tree species of Douglas fir *Pseudotsuga menziesii*, western hemlock *Tsuga heterophylla*, Port Orford cedar *Chamaecyparis lawsoniana*, tanoak *Lithocarpus*

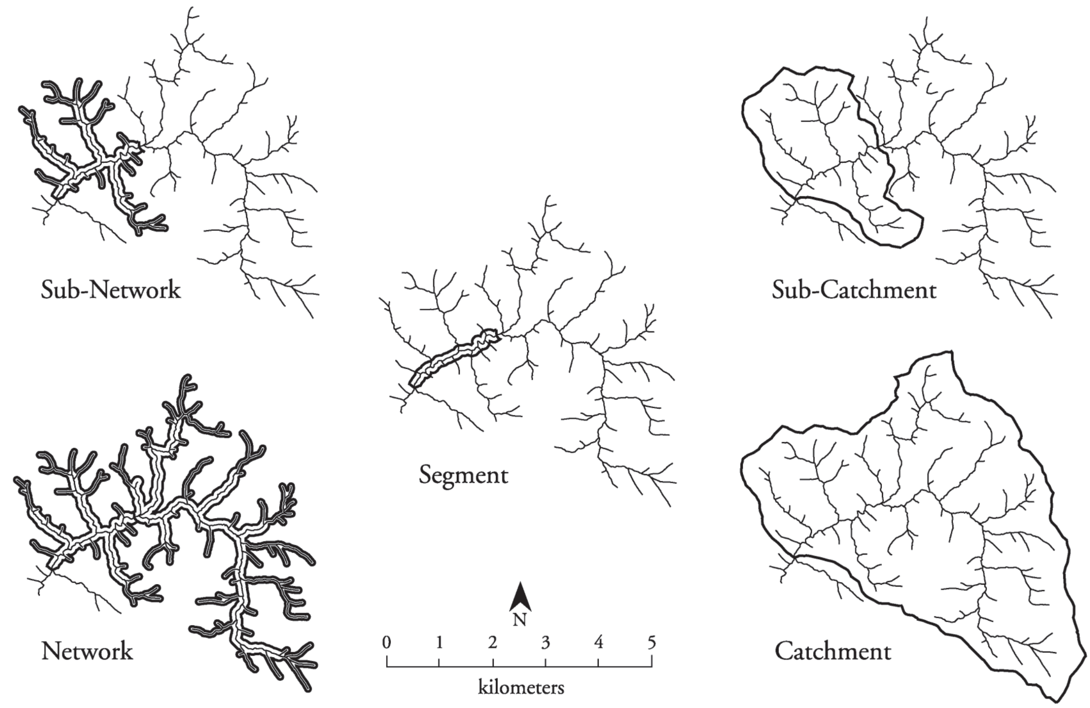

Figure 1. Analytical units used to summarize landscape characteristics at five spatial scales illustrated for a single surveyed stream segment. The segment scale analytical unit includes the area within a buffer extending 100 m on each side of the stream segment. The subnetwork scale analytical unit encompasses the segment-scale analytical unit scale plus the area within a buffer around channels orthogonal to the stream segment. The network scale analytical unit includes the subnetwork scale analytical unit plus the area within a buffer around all mapped channels upstream of the stream segment. Buffers at the subnetwork and network scales extend 100 m on each side of fish-bearing channels and 50 m on each side of nonfish-bearing channels. The subcatchment scale analytical unit contains catchments orthogonal to the stream segment and encompasses the entire area draining into the stream segment from adjacent hill slopes. The catchment scale analytical unit encompasses the subcatchment analytical unit and is the catchment of the stream segment.

densiflorus, Pacific madrone *Arbutus menziesii*, and California bay laurel *Umbellularia californica*. Typical additions in riparian areas are western red cedar *Thuja plicata*, big leaf maple *Acer macrophyllum*, and red alder *Alnus rubra*. Forests span early to late successional/old growth seral stages due to a disturbance regime driven by infrequent, intense wild fires and windstorms and by timber harvest (USFS 1998). The last major fire in the Elk River basin burned approximately 1.3 km^2 of the Butler Creek drainage in 1961. The next year a windstorm blew down approximately 2.8 km^2 of forest throughout the basin. Other than these events, timber harvest has been the dominant disturbance mechanism since fire suppression began in the 1930s (USFS 1998).

Ninety percent of the study area is federally owned with the majority of this managed by the U.S. Forest Service. The remainder is in private ownership. Much of the northern and eastern drainage is in the Grassy Knob Wilderness Area, Grassy Knob Roadless Area, and Copper Mountain Roadless Area.

The upper main stem of the Elk River and its tributaries provide spawning and rearing habitat for native ocean-type Chinook salmon *O. tshawytscha*, coho salmon, coastal cutthroat trout *O. clarkii*, and winter-run steelhead *O. mykiss*. The

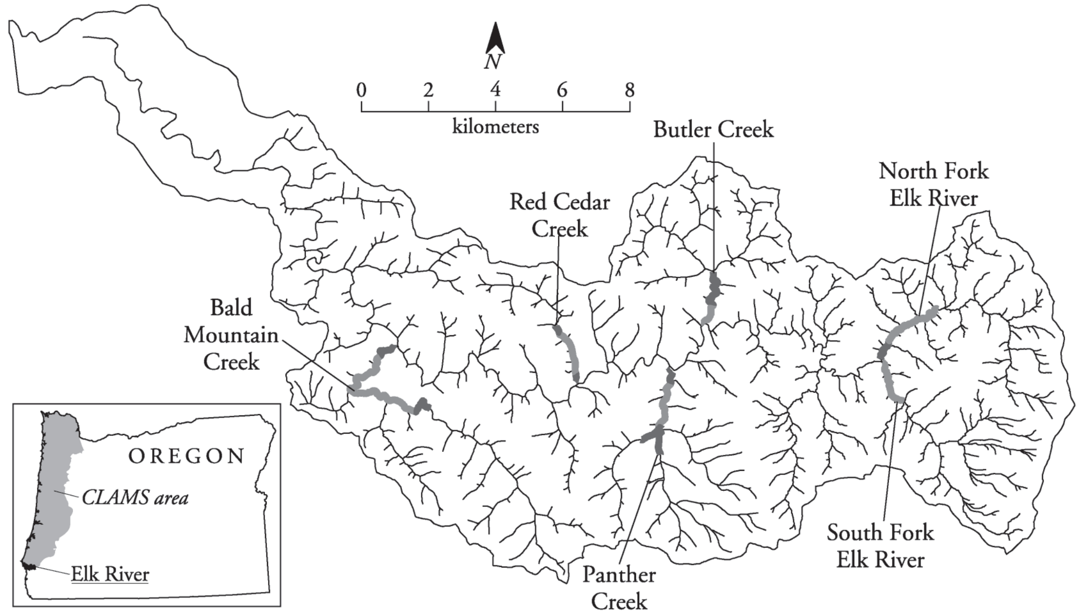

Figure 2. Location and map of the Elk River, Oregon. Stream segments surveyed in this study are shown.

basin is highlighted in both state and federal strategies for protecting and restoring salmonids (USFS and USBLM 1994; State of Oregon 1997).

METHODS

All GIS manipulations of digital coverages were conducted with ARC/INFO (Version 7.1, ESRI, Inc., Redlands, California). All statistical analyses were performed with SAS statistical software (Version 8.2, 2001, SAS Institute Inc., Cary, North Carolina).

Digital Stream Layer and Stream Segment Identification

The UTM projection, Zone 10, Datum NAD 27 was used for digital coverages. A 1:24,000, center-lined, routed, vector-based, digital stream coverage representing all perennially flowing streams within the Elk River basin was obtained from the Siskiyou National Forest. The coverage identified each stream as either fish-bearing or nonfish-bearing. Surveyed tributaries were either third- or fourth-order channels (Strahler 1957) on this stream coverage.

Fifteen stream segments were delineated that encompassed the entire extent accessible by anadromous salmonids in each surveyed tributary (Table 1; Figure 2). Accessibility was determined in the field based on the absence of barriers to adult fish migrating upstream. In the spatially nested, hierarchical stream classification system of Frissell et al. (1986), stream segments are lengths of stream (10^2–10^3 m) that are bounded by abrupt changes in drainage area or gradient and are relatively homogeneous in bedrock geology, valley gradient, and channel constraint over long time frames (10^3–10^4 years). Stream segments subsume reaches, habitats, and microhabitats, which are lower levels in the hierarchy. Boundaries of stream segments used in this study were originally mapped by Frissell (1992) and then adjusted through additional field reconnaissance (Burnett 2001).

Table 1. Characteristics of tributary stream segments in the Elk River, Oregon. Numbers identifying stream segments increase in the upstream direction.

Stream segment	Surveyed Length (m)	Mean Wetted Width (m)	Drainage area (ha)	Mean (SD) % gradient	Mean (SD) maximum depth of pools (m)	Mean (SD) volume of pools (m^3)	Mean (SD) density of wood in pools (no./100m)
Bald Mountain 1	826	7.7	2,715	3.1 (3.8)	1.32 (0.58)	97.3 (97.2)	6(10)
Bald Mountain 2	4,251	7.0	2,679	2.4 (2.7)	0.89 (0.32)	54.5 (50.9)	8(16)
Bald Mountain 3	965	5.6	1,511	2.3 (2.6)	0.94 (0.35)	44.8 (36.7)	9(22)
Butler 1	763	4.8	1,752	3.3 (4.3)	0.78 (0.41)	56.3 (72.8)	4 (8)
Butler 2	1,588	5.1	1,724	1.2 (1.8)	0.83 (0.29)	61.6 (46.9)	1 (2)
North Fork Elk 1	648	9.4	2,456	3.3 (4.9)	1.35 (0.38)	73.0 (36.1)	7(11)
North Fork Elk 2	2,511	7.1	2,303	1.6 (2.9)	1.08 (0.32)	81.6 (70.3)	13(16)
Panther 1	727	7.7	2,347	0.6 (0.8)	0.89 (0.47)	85.5 (73.1)	5(15)
Panther 2	1,697	8.0	2,275	2.3 (2.0)	0.90 (0.34)	71.8 (51.3)	1 (5)
Panther 3	1,165	6.2	929	1.9 (1.9)	0.69 (0.32)	34.2 (30.2)	9(17)
W. Fork Panther	806	4.3	575	2.8 (2.7)	0.51 (0.16)	8.7 (4.0)	12(23)
Red Cedar 1	344	3.2	743	4.7 (3.3)	0.63 (0.13)	13.1 (12.8)	11(19)
Red Cedar 2	1,418	4.4	737	2.1 (1.9)	0.81 (0.55)	19.7 (10.5)	13(20)
Red Cedar 3	419	3.8	565	3.3 (3.4)	0.80 (0.20)	13.1 (6.0)	17(26)
South Fork Elk	1,544	7.6	1,988	5.6 (6.2)	1.17 (0.44)	63.4 (35.2)	9(14)

Landscape Characterization

The three steps in landscape characterization were to (1) delineate analytical units at five spatial scales for each stream segment; (2) overlay analytical units onto digital coverages of lithology, land form, and land cover, then calculate the percent area of each analytical unit occupied by each landscape characteristic; and (3) compare landscape characteristics among the five spatial scales.

Analytical units.—Five analytical units, one for each spatial scale, were delineated for each stream segment. Spatial scales considered ranged from the local riparian area to the entire catchment draining into surveyed stream segments (Figure 1). Analytical units were developed for three riparian scales (segment, subnetwork, and network) and two catchment scales (subcatchment and catchment). Buffers for riparian scales were based on the Riparian Reserve widths in the report of the Forest Ecosystem Management and Assessment Team (FEMAT 1993). Consequently, buffers extended 100 m on either side of fish-bearing channels and 50 m on either side of nonfish-bearing channels. Subcatchment and catchment boundaries were screen digitized from contour lines generated using U.S. Geological Survey (USGS) 30-m digital elevation models (DEMs).

Segment scale analytical units included the area within a buffer on each side of stream segments (22 ± 19 ha, mean ± SD; Figure 1). Channel-adjacent processes (e.g., tree mortality in riparian stands and bank erosion) were assumed to dominate at the segment scale. Subnetwork scale analytical units encompassed segment-scale analytical units plus the area within a buffer around mapped channels orthogonal to stream segments (53 ± 82 ha; Figure 1). Channelized processes (e.g., debris flows and fluvial transport of wood and sediment) were assumed to be added to channel-adjacent processes at the subnetwork scale. Network scale analytical units included subnetwork scale analytical units plus the area within a buffer around all mapped channels upstream of stream segments (367 ± 211 ha; Figure 1). This increased the length over which channelized processes could affect stream segments. Subcatchment scale analytical units contained catchments orthogonal to stream segments and encompassed the entire area draining into stream segments from adjacent hill slopes (190 ± 299 ha; Figure 1). This added unmapped channels capable of transporting debris flows and nonchannelized hill slope processes (e.g., surface erosion and landsliding). Catchment scale analytical units encompassed subcatchment scale analytical units and were the catchments of stream segments (1,562 ± 820 ha; Figure 1), increasing the area over which nonchannelized and channelized hill slope processes could affect a stream segment.

Digital coverages of landscape characteristics.— Lithology, landform, and land-cover data layers were classified as described in Table 2. The lithology coverage was generalized by the FEMAT (1993) from the 1:500,000-scale Quaternary geologic map of Oregon (Walker and MacLeod 1991). The landform layer of percent slope was generated for the basin from USGS 30-m DEMs. Slope classes were similar to those in Lunetta et al. (1997). Road density (km/km^2) was calculated from a vector coverage of roads on all ownerships within the Elk River basin. The Siskiyou National Forest developed this coverage by augmenting the 1:24,000, 7.5-min USGS quadrangle Digital Line Graph (DLG) data with roads interpreted from Resource Orthophoto Quadrangles.

The forest-cover layer was clipped from a coverage for western Oregon. It was developed by a regression modeling approach with spectral data from 1988 Landsat Thematic Mapper (TM) Satellite imagery and elevation data from USGS 30-m DEMs (Cohen et al. 2001). In areas such as the Elk River basin where forestry-related activities are the primary disturbance mechanism, age and stem diameter of forest cover reflects time since timber harvest. More older, larger trees generally mean less logging. Most researchers relating stream and landscape characteristics in forested areas of the Pacific Northwest used harvest intensity or percent area logged (Reeves et al. 1993; Dose and Roper 1994; Ralph et al. 1994); however, a few researchers (Botkin et al. 1995; Wing and Skaugset 2002; Van Sickle et al. 2004) used forest-cover data similar to that available for the Elk River basin.

Table 2. Description of landscape characteristics for the Elk River, Oregon. All variables except road density were expressed as percent area of analytical units at each spatial scale.

Landscape characteristic	Description
Lithology:	
Sedimentary rock types	Cretaceous - Rocky Point Formation sandstones/siltstones; Humbug Mountain Formation conglomerates
Meta-sedimentary rock types	Jurassic - Galice Formation shales; Colebrook Formation schists
Igneous intrusive rock types	Granite and diorite
Landform:	
Catchment drainage area	
Slope class ≤ 30%	
Slope class 31–60%	
Slope class > 60%	
Land cover:	
Road density	(km/km^2)
Open and semi-closed canopy	<70% tree cover
Broadleaf	>70% deciduous tree and shrub cover
Mixed broadleaf–conifer forests:	>70% of deciduous and conifer tree cover
small diameter	≤25 cm diameter at breast height (dbh)
medium diameter	26–50 cm dbh
large diameter	51–75 cm dbh
very large diameter	>75 cm dbh
medium - very large diameter[a]	>25 cm dbh

[a] Encompasses all tree diameters capable of contributing large wood (diameter ≥ 30 cm) to streams.

Differences among spatial scales in landscape characteristics.—To investigate whether or not the five spatial scales differed, we assessed among-scale differences in variances and medians for each landscape characteristic. Among-scale differences in variances were analyzed using Levene's test of homogeneity of variance (Snedecor and Cochran 1980) on the absolute value of residuals from one-way analysis of variance (ANOVA), with scale as the independent variable. Among-scale differences in medians were evaluated with one-way ANOVA (SAS version 8.2; PROC GLM) on the ranked data because parametric assumptions could not be met. Data were blocked by stream segment to address potential correlations among spatial scales for each stream segment. Whenever an ANOVA F-test was significant ($\alpha = 0.05$), posthoc pair-wise comparisons of differences between spatial scales were conducted maintaining the overall type I error rate at $\alpha = 0.05$ (SAS version 8.2; option LSMEANS, TUKEY). Although extreme values were observed when landscape characteristics were screened for outliers, all data points were considered valid and were included in analyses.

We recognize that analytical units were not independent; analytical units at coarser scales subsumed those at finer scales. For example, the subcatchment scale completely encompassed the subnetwork scale. Spatial dependence inherent in the design of analytical units could reduce the actual degrees of freedom below the nominal value and inflate the probability of a type I error (Hurlbert 1984; Legendre 1993). All significance values should be evaluated with this in mind, but are presented to indicate the relative strength of differences in ANOVA and posthoc comparisons and of relationships in regressing stream habitat features with landscape characteristics, even though multiple models were considered.

Regression of Stream Habitat Features with Landscape Characteristics

Stream habitat features.—Between July 25 and August 5, 1988, habitat data were collected for every channel unit in the 20 km of stream comprising the 15 delineated stream segments, which taken together are the extent of anadromy in the surveyed tributaries. The length of each stream segment was at least 70 times its wetted channel width. Channel-unit habitat data were collected to derive salmonid habitat features (mean maximum depth of pools [m], mean volume of pools [m^3], and mean density of large wood in pools [no. pieces/100 m]) for each stream segment. These habitat features were chosen in part because each helped discriminate between level of use of stream segments by juvenile ocean-type Chinook salmon in Elk River tributaries (Burnett 2001).

Each channel unit was classified by type (pool, fastwater [Hawkins et al. 1993], or side channel [<10% flow]). The length, mean wetted width, and mean depth of each channel unit were estimated using the method of Hankin and Reeves (1988). Channel units were at least as long as the estimated mean active channel width (1–10 m). The number of wood pieces ($\geq$3 m long and $\geq$0.3 m diameter) was counted in each channel unit. Maximum depth of pools was measured to the nearest centimeter using a meter stick for pools $\leq$ 1 m deep (70% of pools) and was estimated to the best ability of each surveyor for pools deeper than this. Channel unit data were georeferenced to the digital stream network through Dynamic Segmentation in ARC/INFO, then were summarized for each stream segment to obtain stream habitat features for subsequent regression analyses.

Developing regression models.—Three sets of regression models were developed to explain variation in stream habitat features: (1) we regressed each stream habitat feature with catchment area only; (2) we attempted to develop five "best" within-scale linear regression models for each stream habitat feature by selecting from landscape characteristics summarized at each of five spatial scales; and (3) we attempted to develop a single "best" among-scale linear regression model for each stream habitat feature by selecting from among catchment area and landscape characteristics at all spatial scales.

We considered models with no more than two explanatory variables to avoid overfitting because relatively few stream segments (n = 15) were available for analyses. This is a more conservative criterion than the 5:1 cases to explanatory variables ratio of Johnston et al. (1990) but still somewhat below ratios identified elsewhere (Flack and Chang 1987). The proportion of variation explained in linear regression was reported as R^2 and calculated as the coefficient of determination for one-variable models and as R^2_{adj} and calculated as the adjusted coefficient of determination for two-variable models. Three landscape characteristics were not considered in any regression procedure. The percent area in metasedimentary rock types was excluded due to significant ($r > 0.7$; $n = 15$; $P \leq 0.005$) negative pair-wise correlations with percent area in sedimentary rock types at each spatial scale. Percent area in igneous intrusive rock types and percent area in forests of small diameter trees were excluded because variation among valley segments was generally low at each spatial scale (Figure 3).

For each within- and among-scale regression procedure, the 10 models with the largest R^2_{adj} were identified using best-subsets procedures (SAS version 8.2, Proc REG, option ADJRSQ, AIC). We further considered models from this set that included, or were within, two Akaike's information criteria (AIC) units of the model with the lowest AIC value. Of this subset, we reported models only if slope estimates for explanatory variables and the overall model were significant (α = 0.05) and if variance inflation factors (VIF) were less than four. Larger values of VIF indicate that multivariate multicollinearity has doubled the standard error of regression slopes (Fox 1991). The pair-wise correlation between explanatory variables was not significant ($P > 0.05$) for any of the reported two-variable models, providing further evidence that multicollinearty was of little concern. The reported ΔAIC is the difference in AIC values between the regression model with catchment area alone and the particular regression model for a given stream habitat feature. Small values of ΔAIC suggest a model is as good as, or better than, the one containing only catchment area. Reported models met parametric assumptions based on evaluation of regression residuals: (1) for normality using the Shapiro-Wilk test and box and normal probability plots (SAS version 8.2, Proc UNIVARIATE), and (2) for constant variance using residual-versus-predicted plots.

We recognize that variable selection procedures cannot guarantee the best-fitting or most relevant model. Thus, the "best" regression model for a stream habitat feature from each within-scale selection process had a larger F-value and generally explained more of the variation than other models at that scale but was reported only if it had a ΔAIC $\leq$ 5. The "best" among-scale regression model for a stream habitat feature had a larger F-value and generally explained more of the variation than other models, including the one containing only catchment area.

The AIC from Proc REG (SAS version 8.2) is calculated by an earlier method (Akaike 1969) than the method (Akaike 1974) recommended in Burnham and Anderson (1998) and is not corrected for small sample size (AIC_C). Thus, we evaluated the potential for these differences to affect our results. Values of AIC_C were obtained (SAS version 8.2, Proc MIXED, option IC) for the 10 among-scale regression models originally identified for each stream habitat feature. For the mean maximum depth and volume of pools, the models that met our reporting and best-model criteria using AIC_C were identical to those using AIC. For the mean density of large wood in pools, three more models would have been reported using AIC_C than AIC; however, these models had larger AIC_C values and smaller F-values than the models we originally reported. The among-scale regression model for the mean density of large wood in pools that met our best-model criterion would have been the same using either metric. Based on these considerations, we are confident that results from within-scale regressions were also negligibly influenced by the use of AIC (Akaike 1969) instead of AIC_C.

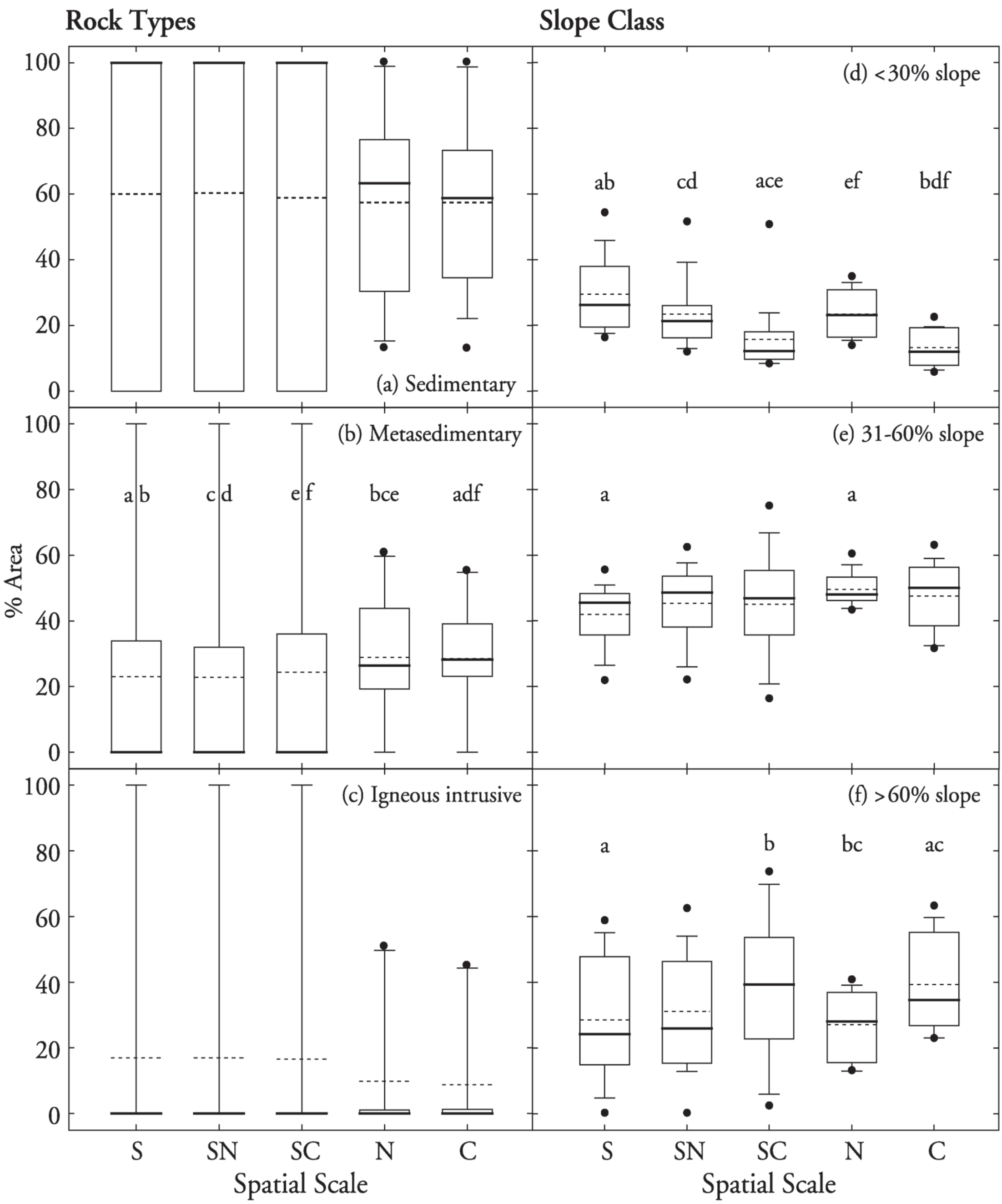

Figure 3. Distribution of landscape characteristics among analytical units at each of the five spatial scales in tributaries of the Elk River, Oregon. Spatial scales were the segment (S), subnetwork (SN), subcatchment (SC), network (N), and catchment (C). Boxes designate the 25th and 75th percentiles, the solid line indicates the median and the dotted line the mean, whiskers denote the nearest data point within 1.5 times the interquartile range, and 5th and 95th percentiles are shown by disconnected points. For a given landscape characteristic, two scales with the same letter label above their box plots have a significant pair-wise difference between medians when the overall type I error rate is controlled at $\alpha = 0.05$.

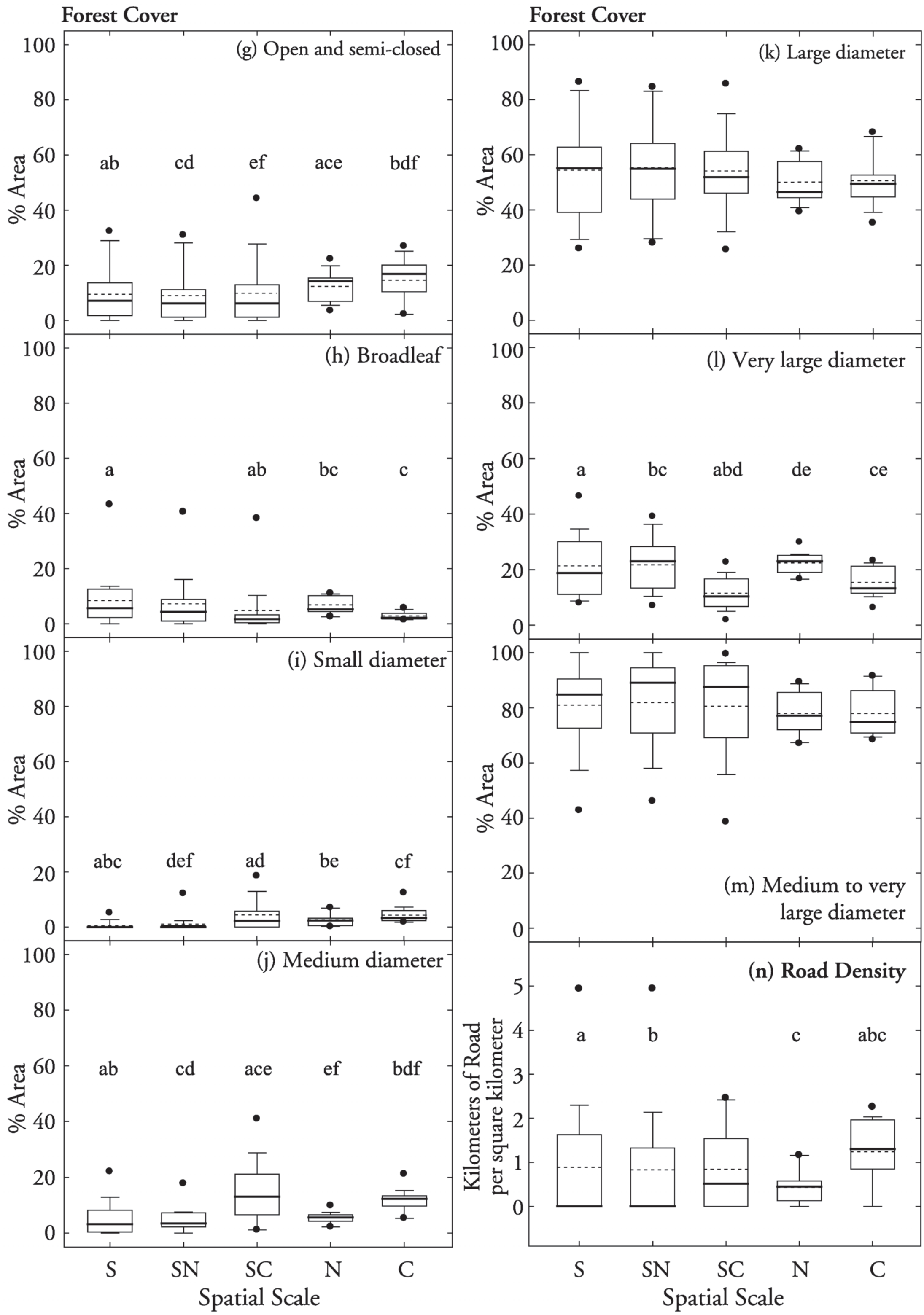

Figure 3. continued

Because stream segments were not selected with a probability sampling design, we assessed regression residuals from each best among-scale model for nonrandom errors that might reflect spatial autocorrelation. For all possible pairs of stream segments, stream distance and the absolute difference between regression residuals were calculated. These two sets of values were regressed to determine the proportion of the variation in the absolute difference between regression residuals explained by the stream distance between stream segments.

RESULTS

Landscape Characterization

Variance across stream segments differed significantly (df = 4,70; $P \leq 0.05$) among spatial scales for all but four landscape characteristics, the percent area in (1) igneous intrusive rock types, (2) slopes ≤ 30%, (3) slopes > 60%, and (4) open and semiclosed canopy forest. The smallest variance was observed at either the network or catchment scale for all landscape characteristics except the percent area in forests of small diameter trees.

In one-way ANOVA, the blocking factor, stream segment, was significant ($F_{(4,14)}$; $P \leq 0.0001$) for all landscape characteristics, and medians differed significantly ($F_{(4,14)}$; $P \leq 0.03$) among spatial scales for 10 of 14 landscape characteristics (Figure 3). Pair-wise differences in medians were not significantly ($P > 0.05$) different between the segment and subnetwork scales for any landscape characteristic. For most landscape characteristics, pair-wise differences between medians were significant ($P \leq 0.05$) between a catchment scale (subcatchment or catchment) and one or more of the riparian scales (segment, subnetwork, or network) (Figure 3). To illustrate, for the percent area in slopes ≤ 30% (Figure 3D), the medians of the subcatchment (12.2%) and the catchment (11.9%) scales, although not significantly different from each other, were significantly different from those of the segment (26.2%), subnetwork (21.3%), and network (23.1%) scales. Pair-wise differences between the riparian scales were not significant for this landscape characteristic.

Regression of Stream Habitat Features with Landscape Characteristics

Mean maximum depth and mean volume of pools.—Both of these stream habitat features were positively related to catchment area (Table 3). In one or more of the within-scale regressions, landscape characteristics explained a significant proportion of the variation in the mean maximum depth of pools ($R^2 \leq 0.29$; df = 14; $P \geq 0.04$; $\Delta AIC \geq 7.3$) and in the mean volume of pools ($R^2 \leq 0.48$; 14 < df <13; $P \geq 0.008$; $\Delta AIC \geq 20.2$). However, no within-scale model met the reporting criterion of $\Delta AIC \leq 5$ and each explained about half or less of the variation explained by catchment area alone. Therefore, a best within-scale regression model was not identified for either the mean maximum depth or volume of pools.

The best among-scale regression model for the mean maximum depth of pools contained only catchment area (Table 3). This was the only one of seven models for the mean maximum depth of pools, which included or were within two AIC units of the smallest AIC value, to meet the reporting criteria. In among-scale regression for the mean volume of pools, only one model met the reporting criteria (Table 3). However, the *F*-value of this model was substantially lower than that of the model containing catchment area alone, which was therefore considered the best among-scale regression model for the mean volume of pools (Table 3). Stream distance between each pair of stream segments explained only a small proportion of the variation in the absolute differences between residuals from the best among-scale regression model for the mean maximum depth of pools ($R^2 = 0.04$; df = 104; $P = 0.06$) or for the mean volume of pools ($R^2 = 0.01$; df = 104; $P = 0.36$).

Mean density of large wood in pools.—Although the mean density of large wood in pools

Table 3. Results from among-scale linear regression to explain variation in stream habitat features among 15 stream segments for tributaries of the Elk River, Oregon. Explanatory variables were catchment area alone and catchment area plus landscape characteristics summarized at the segment (S), subnetwork (SN), subcatchment (SC), network (N), and catchment (C) scales. For among-scale regressions, the number of models that included, or were within two AIC units of the smallest AIC value, is given after the stream habitat feature. Reported models had explanatory variables with significant slope estimates ($\alpha = 0.05$) and little multicollinearity (VIF < 4). Methods are fully described in the text for identifying the set of reported models and best among-scale models indicated by *. Direction of relationships with explanatory variables is indicated by +/–. The ΔAIC is relative to the model with catchment area alone for that stream habitat feature.

Stream habitat feature Explanatory variable in model	+/– $P > \|t\|$	VIF	Model F	$P > F$	R^2 (R^2_{adj})	ΔAIC
Mean maximum depth of pools						
Catchment area			17.1	+0.001*	0.57	
Mean volume of pools						
Catchment area			84.7	+<0.0001*	0.87	
Mean density of large wood in pools						
Catchment area			6.99	–0.02	0.35	
Mean volume of pools (4)						
Catchment area	+<0.0001	1.00	57.9	<0.0001	0.89	–3.2
% very large trees (N)	+0.05					
Mean density of large wood in pools (3)						
% sedimentary rock types (SC)	–0.004	1.07	10.48	0.002*	0.58	–6.8
% medium–very large trees (SC)	+0.003					
% sedimentary rock types (SN)	–0.004	1.08	9.89	0.003	0.56	–6.2
% medium–very large trees (SC)	+0.004					
% sedimentary rock types (S)	–0.005	1.08	9.84	0.003	0.56	–6.2
% medium–very large trees (SC)	+0.004					

was negatively related to catchment area (Table 3), an equal or greater proportion of the variation was explained by other landscape characteristics summarized at each of the five spatial scales (Table 4). The best within-scale regression model at the segment, subnetwork, subcatchment, and network scales contained the percent area in sedimentary rock types and the percent area in forests of medium to very large diameter trees (Table 4). The best catchment-scale model for the mean density of large wood in pools consisted simply of the percent area in open area and semiclosed canopy forests (Table 4).

Two other models for the mean density of large wood in pools met the reporting criteria at the network scale (Table 4). These models contained the percent area in sedimentary rock types along with a land-cover characteristic (road density or percent area in open and semiclosed canopy forests). The three significant land-cover characteristics for the mean density of large wood in pools were correlated with one another at the network scale. This was true also at each of the other spatial scales. For example, as the density of roads increased, the percent area in forests of medium to very large diameter trees decreased at the network scale ($R^2 = 0.69$; df = 14; $F = 28.2$; $P = 0.0001$) (Figure 4) and at each of the other four spatial scales ($R^2 = 0.35$ [segment scale], $R^2 = 0.46$ [subnetwork scale], $R^2 = 0.37$ [subcatchment scale], and $R^2 = 0.85$ [catchment scale]; df = 14; $F \leq 72.7$; $P \leq 0.02$).

The best among-scale regression model contained two landscape characteristics, each summarized at the subcatchment scale: the mean density of large wood in pools was negatively related to the percent area of sedimentary rock types and positively related to the percent area

Table 4. Results from within-scale linear regression to explain variation in the mean density of large wood in pools among 15 stream segments in tributaries of the Elk River, Oregon. Explanatory variables are landscape characteristics summarized at five spatial scales. The number of models that included, or were within two AIC units of, the smallest AIC value is listed after the spatial scale. Reported models had explanatory variables with significant slope estimates ($\alpha = 0.05$) and little multicollinearity (VIF < 4). Methods are fully described in the text for identifying the set of reported models and the best model for each spatial scale, indicated by *. Direction of relationships with explanatory variables is indicated by +/–. The ΔAIC is relative to the model with catchment area alone for the stream habitat feature.

Spatial scale Explanatory variable in model	+/– $P > \|t\|$	VIF	Model F	$P > F$	R^2 (R^2_{adj})	ΔAIC
Segment (7)						
% sedimentary rock types	–0.04	1.00	4.55	0.03*	0.34	0.0
% medium–very large trees	+0.05					
Subnetwork (2)						
% sedimentary rock types	–0.01	1.03	7.47	0.008*	0.48	–3.7
% medium–very large trees	+0.01					
Subcatchment (1)						
% sedimentary rock types	–0.004	1.07	10.48	0.002*	0.58	–6.8
% medium–very large trees	+0.003					
Network (4)						
% sedimentary rock types	–0.04	1.09	5.94	0.02*	0.41	–1.9
% medium–very large trees	+0.01					
% sedimentary rock types	–0.04	1.08	5.92	0.02	0.41	–1.9
% open and semi-closed	–0.01					
% sedimentary rock types	–0.02	1.29	5.63	0.02	0.40	–1.5
% road density (km/km^2)	–0.01					
Catchment (10)						
% open and semi-closed			7.31	–0.02*	0.36	–0.2

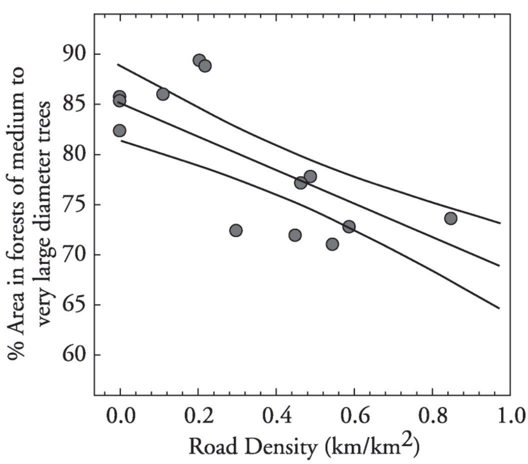

Figure 4. Results of linear regression between the percent area in forests of medium to very large diameter trees and road density at the network scale to explain variation among stream segments for tributaries of the Elk River, Oregon. The linear regression line and 95% mean confidence curves are shown ($y = 85.7–16.7x$; $R^2 = 0.69$; $P = 0.0001$).

in forests of medium to very large diameter trees (Table 3). Stream distance between each pair of stream segments explained little of the variation in the absolute difference between residuals from this among-scale regression ($R^2 = 0.01$; df = 104; $P = 0.26$).

DISCUSSION

This study illustrated the value of multiscale analysis in relating stream habitat to riparian and catchment characteristics in a landscape dominated by forest uses. Although ecologists acknowledge the importance of matching the scale of inquiry to the questions posed (Wiens 1989, 2002), often the "right scale" is not known at the outset of an investigation. Analysis at multiple scales may be necessary to elucidate linkages among stream organisms, their habitats, and the surrounding landscape. Indeed, we found that relationships between stream-habitat features and specific landscape characteristics differed depending on spatial scale, enabling us to suggest processes responsible for observed variation. Fausch et al. (2002) emphasized that information most germane to land management decisions will likely stem from research in stream ecology at intermediate temporal and spatial scales. Our finding that the mean density of large wood in pools of mid-order channels was best explained with landscape characteristics summarized at an intermediate spatial scale seems to bolster their case. We recognize that the scale at which stream habitat and landscape characteristics are most tightly coupled is undoubtedly influenced by where examination is focused in the drainage network. Had we targeted low-order, headwater channels instead of mid-order channels, stream habitat features may have been more directly affected by landscape conditions throughout these smaller catchments, increasing the likelihood of more variation being explained at the catchment scale.

Differences among Spatial Scales in Landscape Characteristics

The smallest variance among analytical units for landscape characteristics was generally observed at one of the coarser spatial scales (network or catchment scale). Because the spatial resolution of landscape coverages was typically finer than the area of analytical units, variance declined as the area of analytical units increased. Our results agree with predictions from landscape ecology that variability in landscape characteristics decreases as grain or patch size increases (Forman and Godron 1986; Syms and Jones 1999).

Given that significant pair-wise differences in medians for landscape characteristics were generally between catchment and riparian scales, riparian areas were distinguished when delineated with a fixed width buffer and described by 30-m digital elevation data and 30-m Landsat Thematic Mapper Satellite imagery. This method detected expected geomorphic and ecological differences between riparian and upslope areas and so appears to be useful for characterizing riparian areas over broad spatial extents in forested systems. For example, our buffer characterization distinguished low-gradient valley bottoms in that segment, subnetwork, and network scales contained greater percentages of the lowest slope class than either of the catchment scales. Futhermore, among-scale differences in percentage area of broadleaf forest apparently reflect the greater likelihood of red alder occurrence in the wetter and more frequently disturbed areas near streams (Pabst and Spies 1999).

Previous studies characterizing riparian areas over a broad region generally used a fixed-width buffer rather than attempting to delineate the actual riparian area. Some of these studies found similarities between riparian and upslope areas in landscape characteristics (e.g., Richards and Host 1994; Wang et al. 1997; Van Sickle et al. 2004), but others did not (e.g., Lammert and Allan 1999). Alternative, and potentially more accurate, methods for delineating and characterizing riparian areas include mapping valley bottoms from finer-resolution digital topographic data (e.g., Hemstrom et al. 2002), classifying digital imagery of higher spectral or spatial resolution, interpreting standard aerial photography, and field mapping. The latter two methods are time and labor intensive, however, and thus may limit the spatial extent reasonably addressed.

Spatial Autocorrelation in Regression of Stream Habitat Features with Landscape Characteristics

Residuals from among-scale regression of the three stream habitat features (mean maximum depth of pools, mean volume of pools, and mean density of large wood in pools) suggested little evidence of spatial autocorrelation, and so we did not attempt to remove or account for it in regression models (Cliff and Ord 1973; Legendre 1993). However, relatively small sample size may have limited our ability to detect spatial autocorrelation.

We are aware of no ideal technique to assess spatial dependence for stream networks when using relatively coarse-grained analytical units that differ in size and spacing. Consequently, we adapted an approach that assesses the degree of relationship for geographic distances between all pairs of locations and corresponding differences between values of variables at those locations (Legendre and Fortin 1989). Geographic distances are usually calculated with *x*-*y* coordinates (e.g., Hinch et al. 1994), but we chose stream distance to better reflect potential connectivity between stream segments.

Stream Habitat Features and Catchment Area

Catchment area explained more among-stream segment variation in the mean maximum depth of pools and the mean volume of pools than other landscape characteristics at any of the five spatial scales we examined. Land-cover variables also had less explanatory power for channel morphology than catchment area in agricultural systems (Richards et al. 1996) and in a relatively undegraded forest ecoregion (Wang et al. 2003b). Catchment area is related to stream power through its direct influence on stream discharge. Streams with higher discharge generally have greater stream power, an index of the ability to transport materials, and tend to be deeper and wider than those with lower discharge (Gordon et al. 1992). Accordingly, the mean maximum depth and volume of pools in Elk River tributaries increased as catchment area increased, paralleling results of Buffington et al. (2002).

Although we determined that land cover explained little of the variation in maximum depth or volume of pools, previous studies have demonstrated relationships between channel morphology and land use/cover. Based on correlative studies, stream morphology is thought to be affected by land uses (Roth et al. 1996; Snyder et al. 2003; Wang et al. 2003a, 2003b), including timber harvest (Bilby and Ward 1991; Reeves et al. 1993; Dose and Roper 1994; Wood-Smith and Buffington 1996). Our ability to discern relationships between land cover and the mean maximum depth of pools may have been hampered because the maximum depths of the deepest pools were estimated and not measured. Given the apparent influence of catchment area, a sample size larger than ours may be necessary to account for catchment area and thus to distinguish relationships between timber harvest and pool morphology. Scaling by catchment area did improve the ability to detect anthropogenic effects on IBI metrics in Pacific Northwest coastal streams (Hughes et al. 2004; Kaufmann and Hughes 2006, this volume).

The mean density of large wood in pools was also related to catchment area. The inverse relationship between these two variables likely arises from an increased ability of larger streams to transport wood. An inverse relationship was found with stream size in other forestry-dominated systems of the Pacific Northwestern United States (Bilby and Ward 1991; Montgomery et al. 1995; Wing and Skaugset 2002) but not in Midwestern agricultural systems (Richards et al. 1996; Johnson et al. 2006, this volume) or when data from mixed-use and silvicultural systems were combined (Wing and Skaugset 2002). A direct relationship was found in midwestern agricultural systems (Richards et al. 1996; Johnson et al. 2006) and in mixed-use silvicultural systems (Wing and Skaugset 2002). As the intensity and duration of human-caused disturbance increases, the presence of large wood in a stream may be determined more by sources of new recruitment than by transport capacity of the stream.

Wood density and an indicator of stream discharge, bank-full stream width, were related in old-growth forests with few human impacts (Bilby and Ward 1989). Bilby and Ward (1989) noted the value of this relationship for determining if wood density at another site was similar to that expected for a "natural" stream of the same size. Regression parameters or proportion of variation explained by such a relationship may be useful benchmarks for assessing whether wood dynamics at broader spatial scales are operating naturally (within the range of natural variability [Landres et al. 1999]). Deviations from such benchmarks may indicate that anthropogenic disturbances have disrupted wood dynamics and constrained variability of in-channel wood across a landscape.

Density of Large Wood in Pools and Landscape Characteristics

We found that landscape characteristics at each spatial scale generally explained as much or more of the variation in the mean density of large wood in pools as catchment area. The mean density of large wood in pools was negatively related to the percent area of sedimentary rock types summarized at one or more spatial scales when considered in combination with land cover. The importance of mass-wasting processes, such as debris flows, to large wood delivery has been established in the Oregon Coast Range (Reeves et al. 2003) and the Olympic Peninsula, Washington (Benda et al. 2003). Although possibly more prevalent in other systems, debris flows occur in the Elk River basin on all lithologies and deliver to higher order channels (Ryan and Grant 1991). However, less mass-wasting debris reaches streams of the Elk River basin in sedimentary rock types than in other rock types (McHugh 1986), which is consistent with interpretations of results from elsewhere in western Oregon (Scott 2002; Kaufmann and Hughes 2006), and may help explain the negative relationship we found between sedimentary rock types and the mean density of large wood in pools.

The mean density of large wood in pools was positively related to stand age. Age or stem diameter of forest cover reflects time since timber harvest in areas such as the Elk River basin, where logging dominates the disturbance regime. Thus, the positive associations we found between large wood and the percent area in forests of medium to very large diameter trees, for example, corroborate negative associations with percent area logged or harvest intensity in other forested systems (Bilby and Ward 1991; Reeves et al. 1993; Montgomery et al. 1995; Wood-Smith and Buffington 1996; Lee et al. 1997). Large wood was also positively related to the amount of forested land in systems with more agricultural and urbanized area (Richards et al. 1996; Wang et al. 1997; Snyder et al. 2003). The large wood in the stream and indicators of timber harvest may not always be related (Lisle 1986; Frissell 1992; Ralph et al. 1994), particularly considering time lags in tree mortality as forests age, decay of in-channel wood from the previous stand, and wood delivery following episodic disturbances (fires, storms). Because land cover variables had more explanatory power for the mean density of large wood in pools than for pool morphology, large wood metrics may be the more sensitive indicators of land management effects, especially where logging has been moderate as in the Elk River basin.

Importance of Spatial Scale in Understanding Variation in Large Wood Density

Our use of multiscale analysis suggests areas and processes that are most closely linked to large wood in pools. The relatively low proportion of variation explained with lithology and forest cover summarized at the segment scale implies that wood is delivered from sources in addition to those immediately adjacent to surveyed stream segments. Explanatory power was greater at the subnetwork than at the segment scale, possibly because the subnetwork scale included many of the lower-order tributaries capable of delivering large wood via debris flows to surveyed stream segments. The most variation was explained at the subcatchment scale. This scale incorporates unmapped lower-order tributaries and upslope areas capable of delivering wood from unchannelized hill slope processes. The proportion of variation explained by landscape characteristics decreased at spatial scales beyond the subcatchment, indicating that regression relationships may be less reflective of processes and source areas influencing wood dynamics in surveyed stream segments.

We did not determine the distance upstream from surveyed segments that explanatory power began to decline. Identification of any such upstream threshold may help in comparing the importance of fluvial transport and other wood delivery processes in these higher-order channels and, therefore, in designing riparian protection and timber harvest. To more thoroughly mitigate negative of effects of logging on wood in streams, our findings indicate that it may be necessary to modify management practices along low-order tributaries and on hill slopes susceptible to mass wasting, as well as along fish-bearing channels. This is consistent with the conclusion drawn from other multiscale studies that riparian buffers alone may not fully protect streams from land use impacts (Roth et al. 1996; Wang et al. 1997; Snyder et al. 2003).

With landscape characteristics summarized at the network scale, an approximately equal proportion of variation in the mean density of large wood in pools was explained by substituting road density (km/km^2) for forest cover in regression with percent area of sedimentary rock types. Dose and Roper (1994) found similar results in the South Umpqua River basin of Oregon where the percent area harvested and road density were highly correlated with each other and were almost equally correlated with change in stream width. Road density and forest cover variables (the percent area in forests of medium to very large diameter trees, the percent area in open and semiclosed canopy forests, and the percent area in large diameter forests) were correlated at all five spatial scales. The degree of correlation, however, generally increased with increasing spatial scale, suggesting that roads and forest disturbances were not always sited together.

Although road density and forest cover can be highly correlated, one variable or the other may have more explanatory power for a particular response (Bradford and Irvine 2000) or at a particular spatial scale, as we found. Roads and timber removal share effects on some processes that shape stream ecosystems (e.g., increasing landsliding and surface runoff rates) but not all (e.g., increasing direct insolation to streams) (Hicks et al. 1991) and may differ in the quality, timing, or magnitude of those effects shared (e.g., Jones and Grant 1996; Jones 2000). Roads can intercept debris flows that would have otherwise delivered wood to streams (Jones et al. 2000). However, the amount of wood available for delivery in our study was probably influenced more by timber harvest. Two findings suggest this: (1) more variation in large wood density was explained by a model containing forest cover at each scale than by the model containing road density; and (2) the only significant relationship to road density was at the network scale, one of the two spatial scales that road density and forest cover were most strongly related. Before one concludes that conditions of aquatic habitat or biota are unrelated to silvicultural activities, it may be prudent to examine relationships with both forest cover and road density, particularly when these are summarized at finer spatial scales. Additionally, primary influences may be indicated by determining if a response variable is related to road density or forest cover or both and at what scales.

In conclusion, the spatial scales explored can influence interpretations about the importance of particular landscape characteristics, physical processes, or terrestrial areas to stream ecosystems. For example, our finding that variation in the mean density of large wood in pools was best explained with landscape characteristics summarized at an intermediate spatial scale suggested that source areas for important processes were probably not fully encompassed at finer scales, but at coarser scales, source areas were included that were less connected to large wood dynamics in surveyed stream segments. Additionally, had only the catchment scale been examined, we might have incorrectly concluded that the amount of large wood in pools is unrelated to lithology and forest cover. Although multiscale analysis has contributed to exploring land-use effects on stream ecosystems in urbanized and agricultural settings, this study demonstrated its benefits for understanding relationships between landscape characteristics and stream habitat in a mountainous area where forestry is the primary land use. Among-scale similarities and differences in relationships suggested key processes responsible for those relationships. Consequently, analysis at multiple scales may provide critical knowledge about system function and inform land management decisions to better protect and restore stream ecosystems.

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