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River profile controls on channel morphology, debris flow disturbance, and the spatial extent of salmonids in steep mountain streams

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[1] In the geologically and topographically diverse mountain ranges of the Pacific Northwest, a broad-scale means of prioritizing salmonid habitat conservation areas based on geomorphic process domains is examined. We propose that steepness and concavity indices derived from the relation between drainage area and channel slope provide a means of identifying basins that express different reach-scale morphologies, fish habitat capacity, and risk of episodic disturbance. Strongly concave river profiles that develop in mountainous terrain indicate that almost all of the relief in the drainage network occurs in headwater streams. In these basins a large proportion of the channel network has low-gradient morphologies, which provide favorable habitat for many salmonid species. The severity of pulse disturbances is also reduced because low-gradient main stem channels inhibit debris flow conveyance, and in these networks the distribution of fish can expand into tributaries, allowing for a spatial spreading of risk. In contrast, rivers with poorly concave or steeper profiles have a greater abundance of high gradient reaches that limit the distribution of fish to a small portion of the channel network and facilitate debris flow-passage. The combined influence of a limited spatial distribution of fish and an increased risk of debris flows may cause populations in these basins to be less resilient to pulse disturbances. A case example from the Klamath Mountains, an area with broad variation in the steepness and concavity of river profiles, was used to develop this approach and aid conservation planning for imperiled populations of anadromous salmonids.

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1. Introduction

[2] River systems in mountainous terrain vary greatly in their topography, disturbance regimes, and potential for forming productive habitat for salmonids. Because channel networks have a nested, hierarchical structure, this variation can be expressed over multiple spatial scales [*Frissell et al.*, 1986]. Previous studies have primarily focused on fish habitat relations at small spatial scales, such as individual pools and riffles (10^1 m) or stream reaches (10^2 m). However, a need for broader scale investigations at the network scale (10^5 m) motivated this study, primarily because variation at smaller scales is partially controlled by physical constraints imposed by larger scales [e.g., *Frissell et al.*, 1986; *Dunham and Rieman*, 1999; *Fausch et al.*, 2002], and because some patterns (e.g., dispersal and habitat connectivity) are only apparent at large spatial scales [e.g., *May*, 1994; *Lowe et al.*, 2006].

[3] At large spatial scales, channel network characteristics are primarily determined by the underlying geology, topography, and regional climate. Understanding the ecological implications of channel network characteristics, and the ability of organisms to disperse and access productive habitats, is critical for effective conservation, management, and restoration of salmonid fish populations [*Folt et al.*, 1998; *Dunham and Rieman*, 1999]. To complete their life cycle many salmonids undergo long dispersal and migration distances. Large-scale characteristics of the channel network can strongly influence the abundance and persistence of local populations because those that have the ability to interact with neighboring populations are more resilient to disturbance because of the increased potential for recolonization following severe disturbances [*Schtickzelle and Quinn*, 2007]. In contrast, populations that are spatially isolated have a greater risk of localized extirpation, and the effects of isolation are particularly severe for stream-dwelling organisms because of the branching nature of channel networks [*Fagan*, 2002]. Network-scale characteristics, as well as anthropogenic effects such as road construction [*Dunham and Rieman*, 1999], exotic species introductions [*Peterson*

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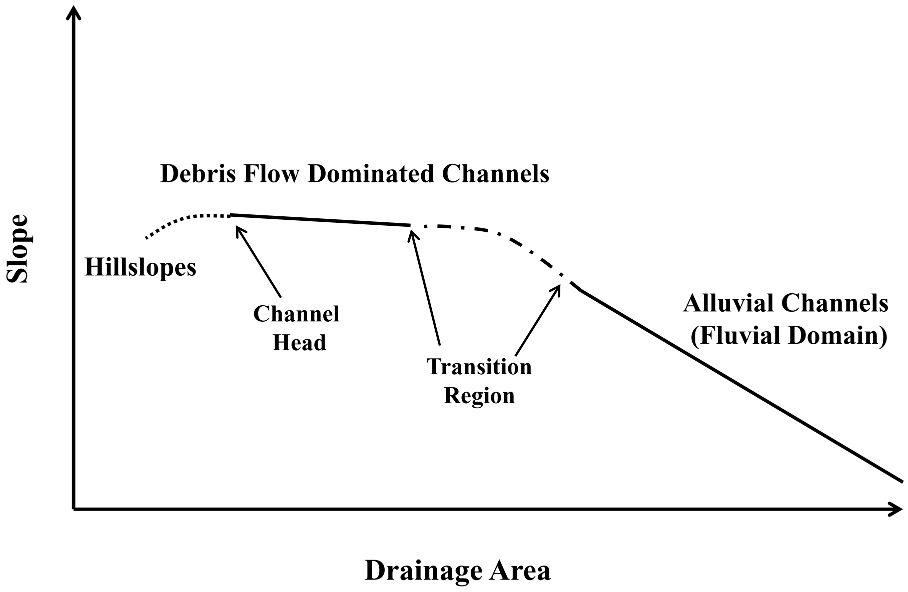

Figure 1. Schematic illustration of the topographic relation between drainage area, channel slope, and process domain (modified from *Montgomery and Foufoula-Georgiou* [1993]). Exact slope-area values for each transition will vary based on the steepness and concavity of the river profile.

et al., 2008; *Fausch et al.*, 2009], and migration barriers create important controls on the patterns of dispersal and migration for riverine fishes. Although the importance of large-scale dispersal and migration patterns of salmonids is well understood, data revealing the specific mechanisms that underlie large-scale effects of channel networks on the persistence of populations are very rare [*Lowe et al.*, 2006].

[4] We explored river profile analysis to determine whether it could be used as a tool to aid in understanding broad-scale patterns of fish distribution and debris flow disturbance. For many decades, geomorphologists have recognized the relation between drainage area (A) and channel slope (S) as an important predictor of river profile characteristics [*Hack*, 1957]; however, the ecological implications of this relation have not been explored. Empirical observations from river systems around the world reveal a consistent power law scaling of the slope-area relation, where the coefficient (K_S) represents the 'steepness index' and the exponent (Θ) represents the 'concavity index' [e.g., *Hack*, 1973; *Flint*, 1974; *Howard and Kerby*, 1983].

$$S = K_S A^{-\Theta}$$

The steepness index characterizes the overall relief of the river profile, and is essentially a measure of channel gradient expressed at a representative drainage area. The concavity index represents the shape of the river profile, and characterizes whether the transition from steep headwater streams to lowland valleys is abrupt or gradual over the length of the profile. High values of the concavity index are indicative of rivers that have strongly concave profiles, where steep channels abruptly grade to low-gradient river valleys. Low values represent river profiles that are poorly concave and have a gradual transition from steep to low-gradient valleys.

[5] The characteristic form of the slope-area relation displays a distinct curve in log-log space, with the slope gradient declining at small drainage areas [*Montgomery and Foufoula-Georgiou*, 1993; *Brummer and Montgomery*, 2003]. *Stock and Dietrich* [2003] interpreted this scaling-break as a shift from fluvial process dominance in larger channels to debris flow dominance in steep headwater channels (Figure 1). Using this topographic signature to identify process domains is desirable for ecological studies because it identifies areas characterized by distinct suites of geomorphic processes, and thus provides a way of systematically identifying structurally and functionally similar areas [*Montgomery*, 1999].

[6] The objective of this study is to explore how large-scale channel network characteristics exhibited in the slope-area relation control (1) the spatial distribution of reach-scale channel morphologies, (2) the severity of debris flow disturbance, and (3) the spatial extent of salmonid fishes. Through the conceptual framework developed here, we propose that the slope-area relation provides a useful context for identifying basins that have different capacities for developing productive fish habitat and risk of episodic disturbance. To illustrate this approach, the Klamath Mountains of northern California are used as a case example.

2. Study Area

[7] The Klamath basin extends from its headwaters in southern Oregon to where it meets the Pacific Ocean in northern California, draining a catchment area of approximately 34,000 km^2. Tributaries to the Klamath River that were investigated for this study drain the Klamath Mountain region, which is bounded on the upstream end by Iron Gate Dam and on the downstream end by the confluence with the Trinity River (drainage area ~7,600 km^2) (Figure 2). Major tributaries to the Klamath River in this area include the Salmon and Scott rivers. The area is densely forested and sparsely populated.

[8] The Klamath Mountains are composed of a complex mixture of strong metamorphic rocks, interspersed with weak sedimentary rocks and granitic plutons. The study area ranges

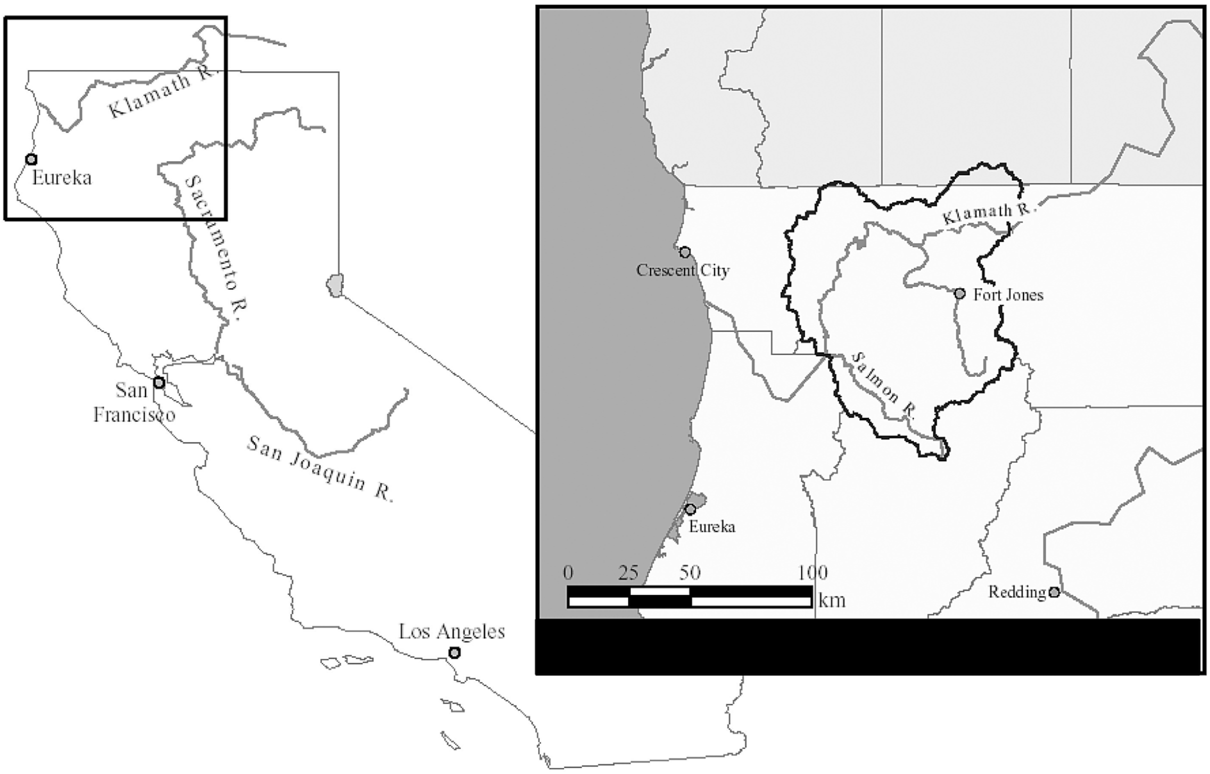

Figure 2. Map of the study area in the Klamath Mountains of northern California.

in elevation from 140 m to 2715 m. The climate is characterized by cool, wet winters and warm, dry summers. Regional hydrographs are dominated by a distinct snowmelt period in the spring, punctuated by sporadic winter rain-on-snow events, and small-scale thunderstorms dispersed throughout the summer season. The west side of the study area receives higher annual precipitation than the east side. The region has a history of extensive gold mining, logging, and high severity forest fires. Anadromous salmonid species in the area include Coho salmon (*Oncorhynchus kisutch*), both spring and fall runs of Chinook salmon (*O. tshawytscha*), and steelhead trout (*O. mykiss*). Because of remote and rugged terrain, coupled with the broad spatial extent of the Klamath Mountains, no broad-scale data on fish distribution or abundance is available at the scale of our analysis.

3. Methods

3.1. Slope-Area Relation

[9] To calculate the slope-area relation for channel networks, two readily available data sources and one newly developed algorithm were used: (1) synthetic channel networks routed through 10 m-resolution digital elevation models (DEMs) following the protocol developed by *Miller* [2003] and *Clarke et al.* [2008], (2) watershed boundaries delineated for mid-sized watersheds using the national Hydrologic Unit Code (HUC) designation [*Seaber et al.*, 1987], and (3) an automated algorithm developed to define the stream reaches to be included in the regression of drainage area and channel slope (discussed further below), calculate the steepness and concavity indices, and plot these values at the topographic centerpoint of each HUC in a GIS framework.

[10] Because of the shift in process domains at the inflection point in the slope-area relation, calculating the steepness and concavity indices is only applicable to the fluvial process domain [*Stock and Dietrich*, 2003]. In our study area, stream reaches with $S > 20\%$ or $A < 1$ km^2 were assumed to reside solely in the debris flow process domain and were omitted from the automated algorithm used to identify the stream reaches to be included in the regression analysis that determined and mapped the spatial distribution of steepness and concavity. Our criteria are consistent with field observations in the study area and previous studies [*Sklar and Dietrich*, 1998; *Whipple*, 2004]; however, it may result in a conservative estimate of channels scoured by debris flow compared to the 3–10% range for the downstream extent documented by *Stock and Dietrich* [2003]. It should be noted that our general approach could be improved in future analysis by tailoring the inflection point to basin-specific values.

[11] Overlain on the channel network data were watershed boundaries delineated by 22 fifth field HUCs, which ranged in basin area from 190 to 750 km^2 (average = 345 km^2). Relatively large scale basins (10^2 km^2) were selected for analysis because smaller watersheds in steep portions of the study area resided largely in the debris flow domain. Because our analysis focused on tributaries to the Klamath River, the segment of the main stem that passes through the study area was not included in the data set because its headwaters lie outside the Klamath Mountain range (drainage area > 2,500 km^2 at the upstream extent of the study area).

[12] A single slope-area relation was fit to the ensemble of channel network data within each HUC. The center point of each HUC was assigned the corresponding K_S and Θ value, which was used to develop an interpolated map of how

Table 1. Network Characteristics of Three Example Basins in the Klamath Mountains

						Characteristic Slope for Drainage Area (m/m)	
	Basin Name	Drainage Area (km^2)	Steepness (Ks)	Concavity (θ)	Ratio (Ks/θ)	10 km^2	100 km^2
Basin 1	Wooley Creek	384	0.19	0.34	0.56	0.09	0.04
Basin 2	Dillon Creek	190	0.21	0.59	0.36	0.05	0.01
Basin 3	Moffett Creek	320	0.13	0.68	0.19	0.03	<0.01

steepness and concavity varied spatially between basins. We acknowledge that using a data set that combines primary and secondary tributary channels can accentuate the considerable scatter that is present in slope-area relations [*Sklar and Dietrich*, 1998]. Although this approach has less precision in calculating the index values than isolating and extracting individual main stem profiles, it allows for the use of readily available data to develop a rapid assessment of the spatial variation in steepness and concavity over a broad area. Data presented by *Sklar and Dietrich* [1998] indicate that channels <1 km^2 are the biggest source of error when using this type of aggregate data set, and these channels were omitted from our analysis because they reside solely in the debris flow process domain. Resolution of the topographic data that provide the basis for this analysis can also have a substantial effect on estimates of channel slope and to a lesser extent, drainage area [*Finlayson and Montgomery*, 2003], therefore 10 m DEMs were used because they provided the highest resolution available for the region.

[13] In addition to exploring the spatial variation in steepness and concavity across the study area, the correlation between index values was investigated. A correlation coefficient (r) was calculated at numerous spatial scales, using a regression of the index values calculated for the full data set of basins in the study area (n = 22) and solved for a broad range of drainage areas, in order to determine the pattern of scale-dependent correlation. This pattern of correlation provides insight into the relation between steepness and concavity at varying points in the channel network, and is necessary for determining covariance of the index values.

[14] To illustrate the differences in channel characteristics based on river profile analysis, three example basins were selected to represent a range of steepness and concavity values (Table 1). Terrain analysis and reconnaissance level field investigations of these basins were used to explore differences in the spatial distribution of reach-scale channel morphology, debris flow runout, and the extent of anadromous fish.

3.2. Reach-Scale Channel Morphology

[15] Morphologic reach types provide a basis for comparison of habitat capacity because they have characteristic slope, grain size, shear stress, and roughness ranges and thus express similar habitat characteristics. The process-based classification scheme by *Montgomery and Buffington* [1997] was used to identify five basic reach morphologies: colluvial, cascade, step-pool, plane-bed, and pool-riffle reaches. Each morphologic reach type occurs within a specific range of channel slopes [e.g., *Montgomery and Buffington*, 1997; *Buffington et al.*, 2004; *Wohl and Merritt*, 2005]. Although considerable overlap can occur between categories of channel slope, an extensive investigation by *Wohl and Merritt* [2005] found that channel slope was the most significant single explanatory variable for predicting channel type. Bedrock and wood-forced morphologies are an exception because they can occur on a wide range of channel slopes and thus cannot be predicted solely from DEMs [*Montgomery et al.*, 1996; *Massong and Montgomery*, 2000]. To determine the prevalence of bedrock and wood-forced morphologies, we conducted reconnaissance level field investigations by hiking numerous sections of each of the three example basins. Because much of the Klamath Mountain region is in roadless and/or wilderness areas, access to the stream network was very limited. We attempted to investigate a broad array of channel types, ranging from headwater streams to large main stem rivers, and hiked >20 km of channel. These field investigations indicated that the occurrence of wood-forced and bedrock reaches were very infrequent in the study area (<2% of channel reaches investigated) and were omitted from our analysis.

[16] Estimates of reach-scale channel slope were derived from 10 m resolution DEM-based channel networks developed by *Miller* [2003] and *Clarke et al.* [2008] for the entire study area. Slope categories used to distinguish channel types were based on published values [*Montgomery and Buffington*, 1997; *Buffington et al.*, 2004], which were found to be in good correspondence with field investigations in our study area. Specific slope categories were >10% (colluvial channels), 7–10% (cascade), 4–7% (step-pool), 1.5–4% (plane-bed), and <1.5% (pool-riffle).

3.3. Debris Flow Disturbance

[17] Within the study area, reconnaissance level field investigations and sequential aerial photographs were used to identify the disturbance pattern of debris flows and hyperconcentrated flows. *Mondry* [2004] provided detailed descriptions of the morphologic signature of such flows in three tributaries to the Klamath River following a severe flood in 1997. Debris flows that ended in log jams or fans at tributary junctions were identified as having discrete deposits. In contrast, debris flows that combined with flood flows in steep alluvial channels (S = 3–7%) produced ‘hyperconcentrated’ or ‘debris floods’ [*Costa*, 1984; *Benda*, 1985; *Hungr et al.*, 2001]. These hyperconcentrated flows frequently traveled for long distances downstream (10^4 m), and were identified by toppled riparian vegetation, lobate deposits on the valley floor, and boulder-laden terrace deposits [*Mondry*, 2004]. Hyperconcentrated flows were distinguished from flood deposits by extensive deposits of coarse, poorly sorted sediment and radically altered or obliterated pre-existing channel morphology and forest vegetation. In contrast, coarse sediment deposits from flood flows were typically confined within the channel and less radically modified pre-existing channel morphology and

forest vegetation. We used these field indicators to confirm the direct impact of debris flows on channels with $S \geq 3\%$.

3.4. Spatial Extent of Salmonids

[18] Broad scale studies of limits to the distribution of anadromous salmonids that are based on channel slope are frequently used in conservation planning (e.g., designating potential habitat in endangered species recovery plans developed by state and federal agencies [*Agrawal et al.*, 2005]). Based on the available data [*Reeves et al.*, 1989; *NOAA*, 2005; *Burnett et al.* 2007; Klamath National Forest, unpublished data, 2005], the upper extent for the distribution of anadromous salmonids is commonly defined as ending when a consistent reach-scale (10^2 m) slope of 7% is exceeded. We used this criteria to define the upstream limit to anadromous fish habitat ($S < 7\%$), and we defined the portion of habitat that is at risk from direct flow impacts ($S = 3$–7%). These criteria only address the upper limit of habitat and those areas at risk of direct disturbance; however, the highest quality habitat for many species, such as coho salmon, occurs at $S < 3\%$ [*Reeves et al.*, 1989; *NOAA*, 2005; *Burnett et al.*, 2007]. In contrast, resident trout populations can occur in steeper channels that approach $S = 12\%$ [*Reeves et al.*, 1989; *Adams et al.*, 2000; *NOAA*, 2005], but this study focused on anadromous fish habitat and did not address resident fish populations higher in the network.

4. Results and Discussion

4.1. Slope-Area Relations

[19] Broad-scale mapping of the slope-area relation allows for quantitative comparisons of steepness and concavity of river profiles across an entire region. In the Klamath Mountains, this mapping revealed that river profiles tend to be exceptionally steep and poorly concave, although there was considerable spatial variation. Values for the steepness index (K_S) varied by an order of magnitude in the basins we investigated, from a low of 0.024 to a high of 0.250 (0.158 average) (Figure 3). Values of the concavity index (Θ) were also highly variable and ranged from a low of 0.222 to a high of 0.680 (0.407 average) (Figure 4).

[20] Spatial variation in channel steepness has been attributed to differential uplift rates [*Snyder et al.*, 2000; *Kirby and Whipple*, 2001; *Kirby et al.*, 2003; *Kobor and Roering*, 2004; *Wobus et al.*, 2006], precipitation gradients [*Roe et al.*, 2002], rock type [*VanLaningham et al.*, 2006], and variation in rock strength and sediment supply [*Sklar and Dietrich*, 1998; *Sklar and Dietrich*, 2001]. Previous studies have also documented that the concavity index can vary widely from 0.3–1.2, and have provided insights into the underlying mechanisms for spatial variation in concavity of river profiles (see review by *Whipple* [2004]). Low values (<0.4) are associated with steep drainages importantly influenced by debris flows, or with downstream increases in either incision rate or rock strength, commonly associated with knickpoints. Moderate values (0.4–0.7) are associated with actively uplifting channels in homogenous substrates experiencing close to uniform tectonic uplift rates. High concavities (>0.7) are associated with downstream decreases in rock uplift or rock strength, downstream transitions to fully alluvial conditions and/or disequilibrium conditions resulting from a temporal decline in rock uplift rate. Rivers with high concavity (>0.7) are noticeably absent in the Klamath Mountains but are common in the nearby Coast Range of Oregon [*Kobor and Roering*, 2004; *VanLaningham et al.*, 2006].

[21] Previous studies have expressed differing views on the correlation between steepness and concavity [*Sklar and Dietrich*, 1998; *VanLaningham et al.*, 2006]. Some perceive an inverse relation between steepness and concavity, while others perceive a positive relation. To resolve this controversy and explore the appropriateness of using a ratio of K_S to Θ, scale-dependent correlations between steepness and concavity values were explored with data from the Klamath Mountains (Figure 5). Here, we expand our analysis to consider a broad range of drainage areas encompassing both the debris flow and fluvial domains. Although <1 km^2 catchments were omitted from other aspects of the analysis, it was necessary to calculate values for small catchments in this assessment for a determination how the relation varies with scale. For very small catchments (<0.1 km^2) that reside solely in the debris flow process domain (Figure 1), there is an inverse correlation between steepness and concavity. For basins between 0.1 and 10 km^2, K_S and Θ are not correlated. Basins of this size are located in the vicinity of the scaling break recognized by *Stock and Dietrich* [2003], and this break corresponds with a transition from an inverse relation between steepness and concavity in the debris-flow domain and a positive relation in the fluvial process domain.

4.2. Reach-Scale Channel Morphology

[22] Variation in salmonid abundance, spawning activity, community composition, and habitat productivity are often attributed to differences in channel gradient and reach-scale morphology [e.g., *Reeves et al.*, 1989; *Hicks and Hall*, 2003; *Buffington et al.*, 2004; *Moir et al.*, 2004; *Burnett et al.*, 2007; *Hall et al.*, 2007; *Buffington and Tonina*, 2009]. Because morphologic reach types are predictable features that can be mapped from DEMs, these slope-based maps can serve as a surrogate for habitat availability mapping [*Lunetta et al.*, 1997; *Wohl and Merritt*, 2005]. River profiles were constructed from the K_S and Θ values for three example basins that represent a broad range of steepness and concavity (Table 1). These idealized profiles were developed to illustrate the coarse-scale effect of the slope-area relation on the expression of different reach morphologies. Basins with steep and poorly concave profiles (Basin 1) are dominated by high gradient morphologies such as cascade and step-pool sequences (Figure 6a). Alternatively, basins that are equally steep but more concave (Basin 2) show a contraction in the domain of steep morphologies and a greater expression of low-gradient reach types such as plane-bed and pool-riffle sequences. In basins that are both less steep and strongly concave (Basin 3), the domain of steep morphologies is greatly restricted and the majority of the fluvial channel network is composed of low-gradient morphologies.

[23] Idealized river profiles, such as illustrated in Figure 6a, typically show a sequential transition from colluvial, cascade, step-pool, plane bed, to pool-riffle reaches [*Montgomery and Buffington*, 1997]. However, discontinuities in the longitudinal expression of reach morphologies are common. Such discontinuities in the sequence of reach morphologies typically result from accumulations of wood that act as dams and force the accumulation of sediment [*Montgomery et al.*, 1996;

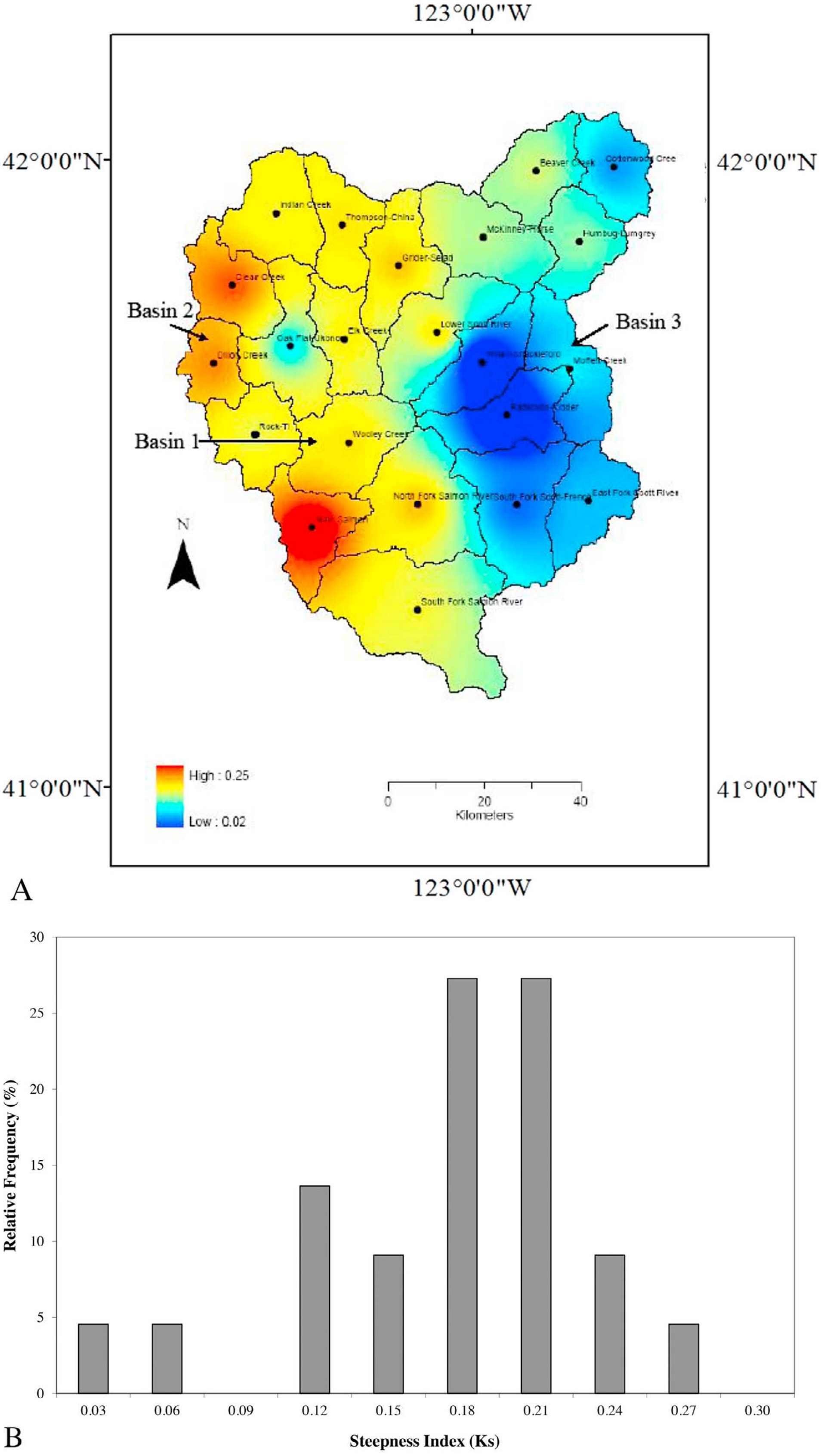

Figure 3. (a) Map of the spatial distribution of the steepness index (*Ks*), and (b) corresponding histogram of values. Solid lines represent watershed boundaries; large dots represent the center point of each basin and were used to develop a interpolated map of how steepness and concavity vary across the landscape.

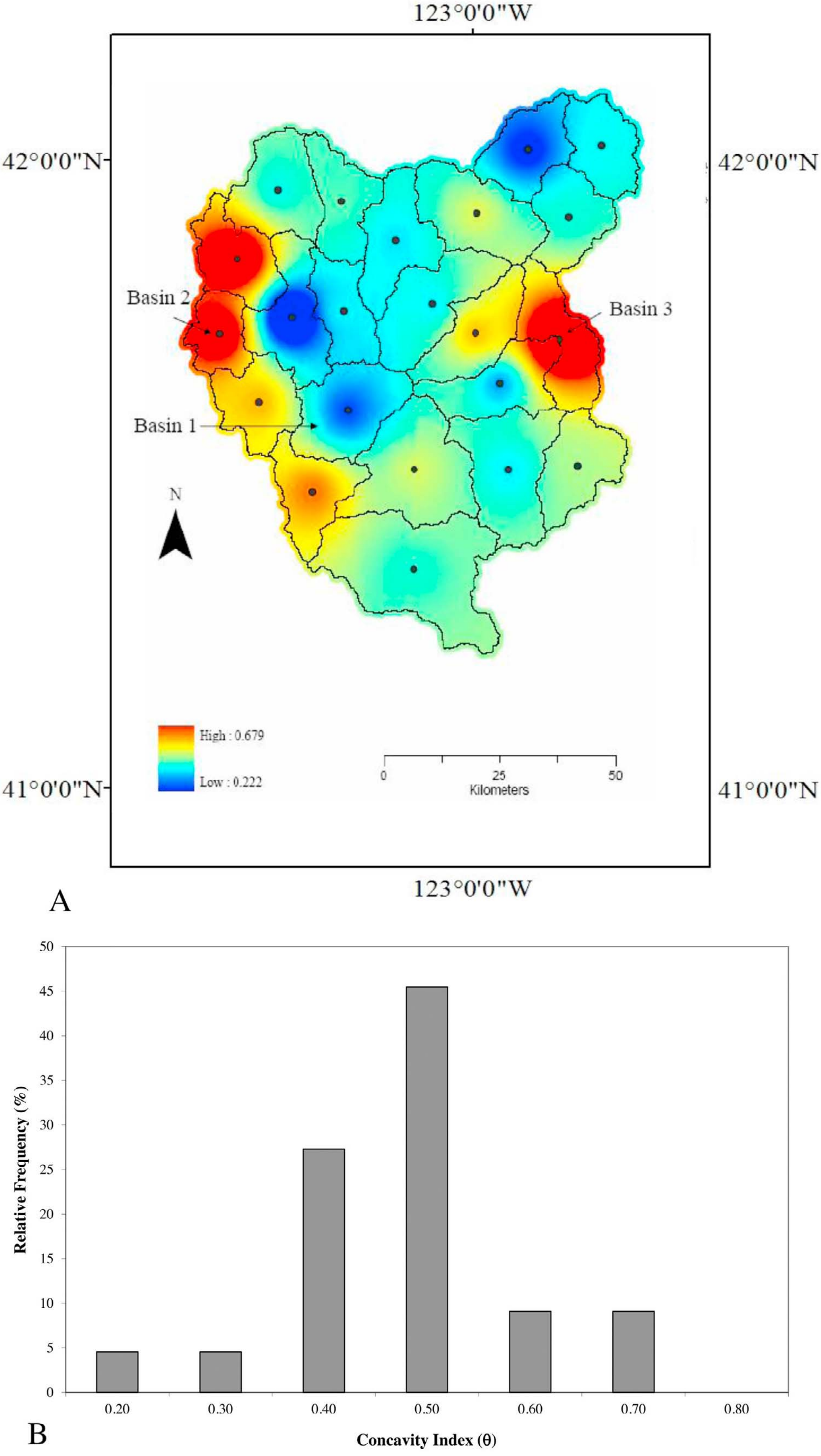

Figure 4. (a) Map of the spatial distribution of the concavity index (⊖), and (b) corresponding histogram of values.

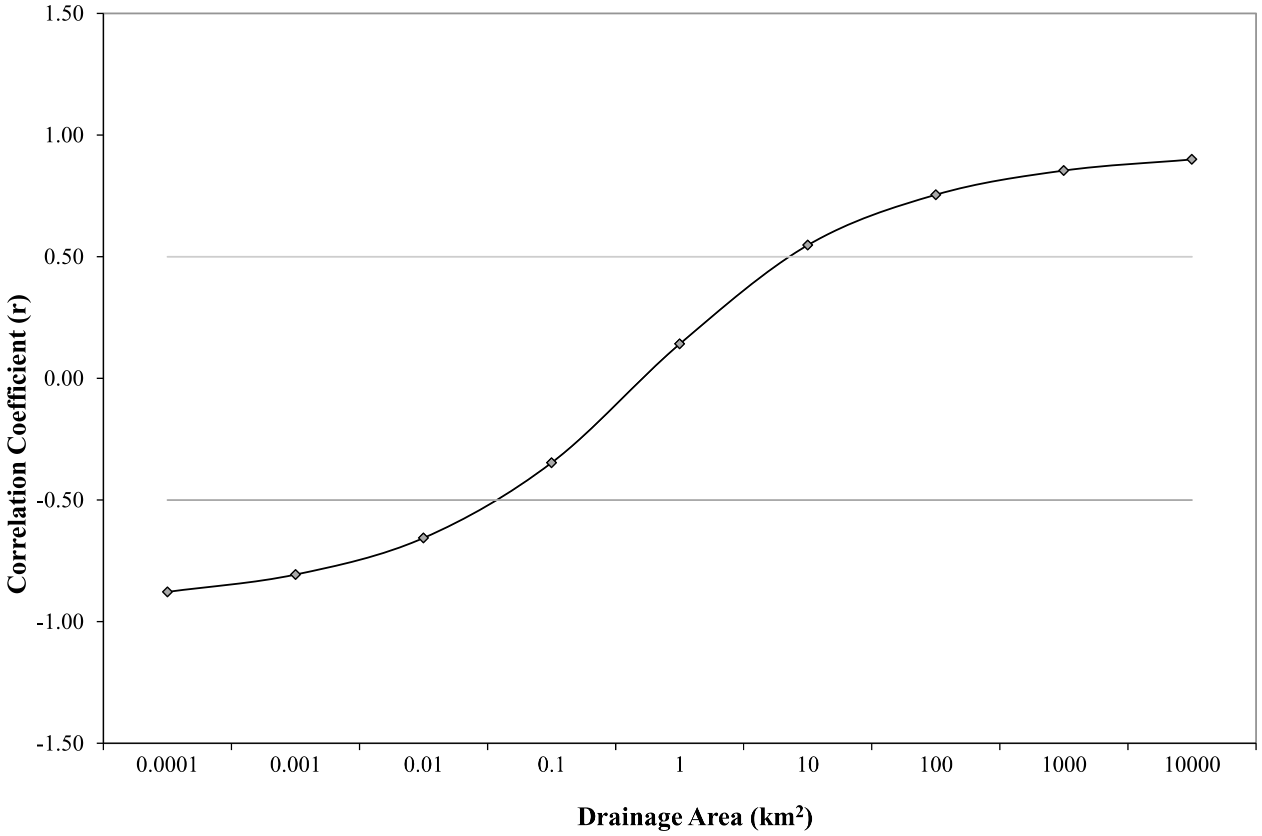

Figure 5. Scale-dependent correlation in steepness (*Ks*) and concavity (ϴ) developed from the correlation coefficient (r), using index values for the full data set of basins in the study area (n = 22) and solved for a broad range of drainage areas. Dark black line represents interpolation between data points. Grey lines highlight where correlations change from being less than or greater than 50.

Massong and Montgomery, 2000], and other features that affect channel slope, such as earth flows [*Kelsey*, 1978; *Korup*, 2005]. Geologic structures such as faults and dikes, geomorphic history such as glaciation and volcanism, and changes in rock type or strength can also cause discontinuities in longitudinal profile development [*Brardinoni and Hassan*, 2006]. Identifying the large-scale potential for different reach morphologies using the slope-area approach cannot distinguish many important smaller-scale controls on channel morphology and longitudinal profile development, so caution must be taken when interpreting these results. For example, wood can greatly affect channel form in forested basins but this effect is not manifest in this broad scale analysis.

[24] In addition to identifying habitat potential from the idealized profiles, the network-scale abundance of each morphologic reach type was characterized for the example basins using the actual reach-scale slope values in the synthetic stream layers for the entire network (Figure 6b). These data support the conceptual framework illustrated above, where the proportion of the channel network in the fluvial process domain, especially pool-riffle channels, increases substantially as the ratio of steepness to concavity decreases. Because many salmonid species prefer low gradient pool-riffle habitats [*Burnett et al.*, 2007], with associated side-channel sloughs [*Beechie et al.*, 1994] and complex hyporheic exchange [*Buffington and Tonina*, 2009], the steepness and concavity values provide a means of distinguishing basins that have inherent differences in their ability to develop high quality habitat.

4.3. Debris Flow Disturbance

[25] The inflection point in the drainage area – channel slope relation reflects the shift from debris flow process dominance in headwater streams to fluvial process dominance lower in the network [*Montgomery and Foufoula-Georgiou*, 1993; *Stock and Dietrich*, 2003]; however, this inflection point does not occur at a uniform position in the slope-area relation. To explore how differences in steepness and concavity affect the proportion of the channel network scoured by debris flows, data from *Stock and Dietrich* [2003] was analyzed. This international data set was used because *Stock and Dietrich* [2003] conducted detailed statistical analysis on individual profiles to determine the precise location of the inflection point in the slope-area relation, marking the transition from debris flow to fluvial processes. Our analysis of the data presented by *Stock and Dietrich* [2003] reveals that basins that are steeper and/or less concave can transport debris flows further down in the drainage network, indicated by a shifting in the inflection point toward larger drainage areas with greater steepness and lesser concavity (Figure 7). In contrast, the inflection point for less steep or more concave channels occurs at a smaller drainage area.

[26] Debris flows can affect channels in a variety of ways, ranging from channels that are directly impacted by debris

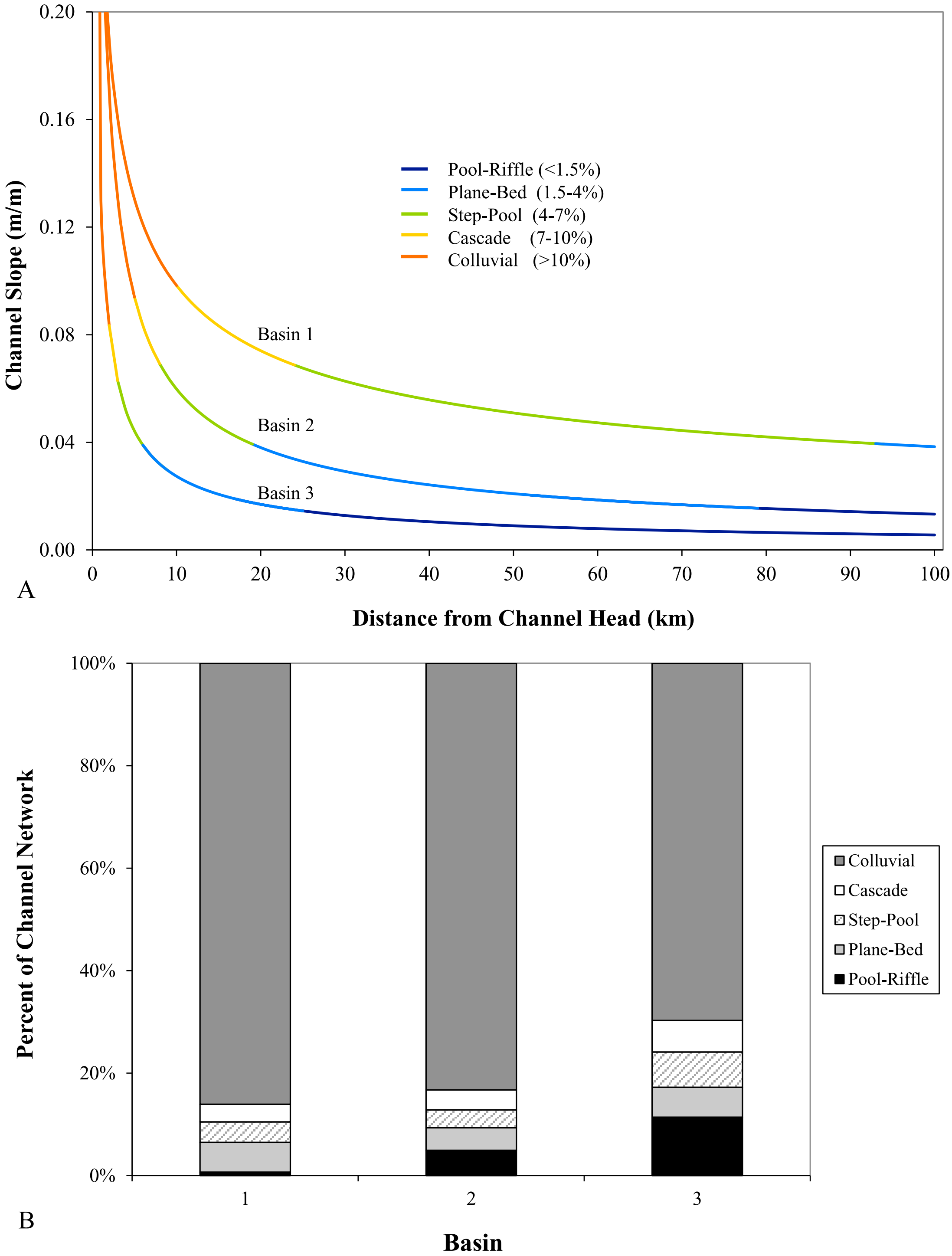

Figure 6. (a) Idealized river profiles constructed from steepness and concavity values and used to illustrate the potential for different reach-scale channel morphologies to develop along the main stem of the three example basins; (b) actual network-scale abundance of various reach morphologies in the example basins, which was inferred from reach-scale estimates of channel slope from channel networks routed through 10 m DEMs.

flows scour, deposition, or transition into hyperconcentrated flows. Direct scour occurs when channel slope exceeds 10% slope [*May*, 2002]. Downstream of channels that are scoured by debris flows, large influxes of sediment and wood can alter habitat in alluvial channels for long distances downstream. Mass flows rarely travel down channels that are <3 to 10% slope [*Stock and Dietrich*, 2003]; however, debris flows can combine with flood flows in main stem river channels to produce hyperconcentrated flows [*Costa*, 1984; *Benda*, 1985; *Hungr et al.*, 2001]. Evidence of

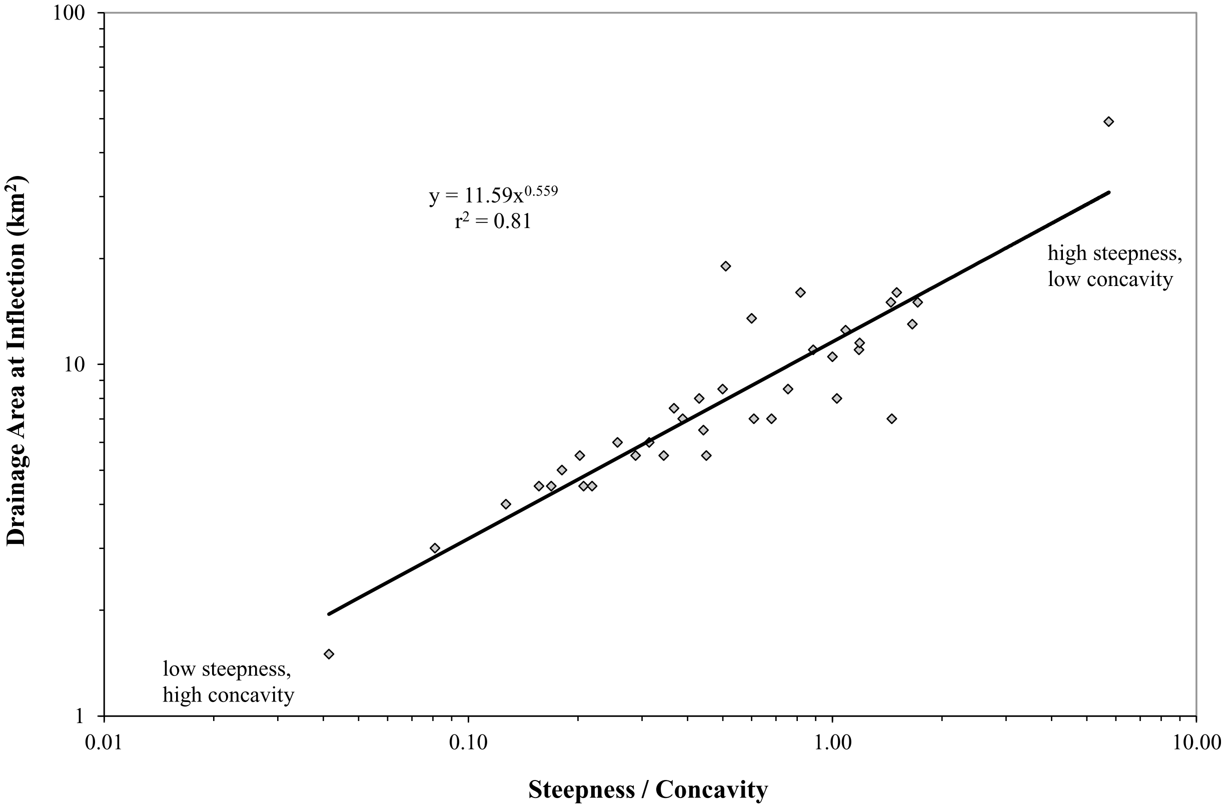

Figure 7. Variation in drainage area at the transition from debris flow to fluvial process domains (inflection of the slope-area curve), expressed as a function of the ratio of steepness (*Ks*) to concavity (ϴ) using data presented in Stock and Dietrich (2003).

hyperconcentrated flows was observed in the Klamath region in channels with slopes as low as 3%. In steep basins with poorly concave profiles, the transformation from debris flows to hyperconcentrated flows is more likely because main stem river channels are often steep enough to continue transporting a mass flow, especially in tightly confined river canyons.

[27] Debris flows and hyperconcentrated flows can reorganize channels [*Cenderelli and Kite*, 1998; *Mondry*, 2004], topple riparian vegetation across the valley floor [*Johnson et al.*, 2000; *Mondry*, 2004], and mantle the streambed with coarse particles that may be difficult to mobilize by fluvial transport [*Wohl and Pearthree*, 1991; *Miller and Benda*, 2000]. Scour of the unsorted debris flow and hyperconcentrated flow deposits would be inhibited by the wide range in particle size that allows a resistant armor layer to form as the smaller particles are selectively transported from the bed surface [*Lisle and Church*, 2002]. Field observations in the study area indicate that large cobbles and boulders that are periodically mobilized by debris floods form the basis for most cascade, step-pool and plane-bed reaches in the Klamath region. Results from re-surveyed cross-sections indicate that long-term channel morphology is largely structured by these infrequent, high magnitude events (T. Lisle, unpublished data, 2006). Boulder deposition in this portion of the channel network may inhibit channel incision into the underlying bedrock and thereby maintain the relatively steep channel slopes, similar to inferences drawn by *Seidl et al.* [1994] in Hawaiian streams. For tributaries to the Klamath River, field observations suggest that knickpoint propagation is the primary mechanism for channel incision. All of the tributaries investigated had large bare-rock knickpoints that propagated upstream through incised gorges from the main stem Klamath River. Base-level fall of the Klamath River is evident by fans and terraces perched high above the modern-day channel.

[28] In addition to the effects of mass flows on channel morphology, these events can also have severe ecological consequences. Debris flows and hyperconcentrated flows can impact long distances of channel in rivers with steep profiles, and can cause widespread disturbance with limited refuge for aquatic organisms. Localized extirpations of salmonids have been observed following debris flows that travel through fish bearing streams [*Lamberti et al.*, 1991; *Roghair et al.*, 2002; B.C. Harvey, personal communication, 2005]. Rivers that are steep (high *Ks*) or less concave (low ϴ) are especially prone to this type of disturbance because channels are steep enough to convey mass flows. In channels that are less steep or have strongly concave profiles, slope abruptly decreases at tributary junctions where channels that are scoured by debris flows enter low gradient main stem rivers. In these channel networks, debris flows typically end in discrete deposits that form massive log jams in channels or fans on valley floors, particularly at confluences [*Benda and Cundy*, 1990; *Benda et al.*, 2004; *May and Gresswell*, 2004]. The resulting pattern of disturbance is patchy, and undisturbed areas can act as refuges [*Benda et al.*, 2004].

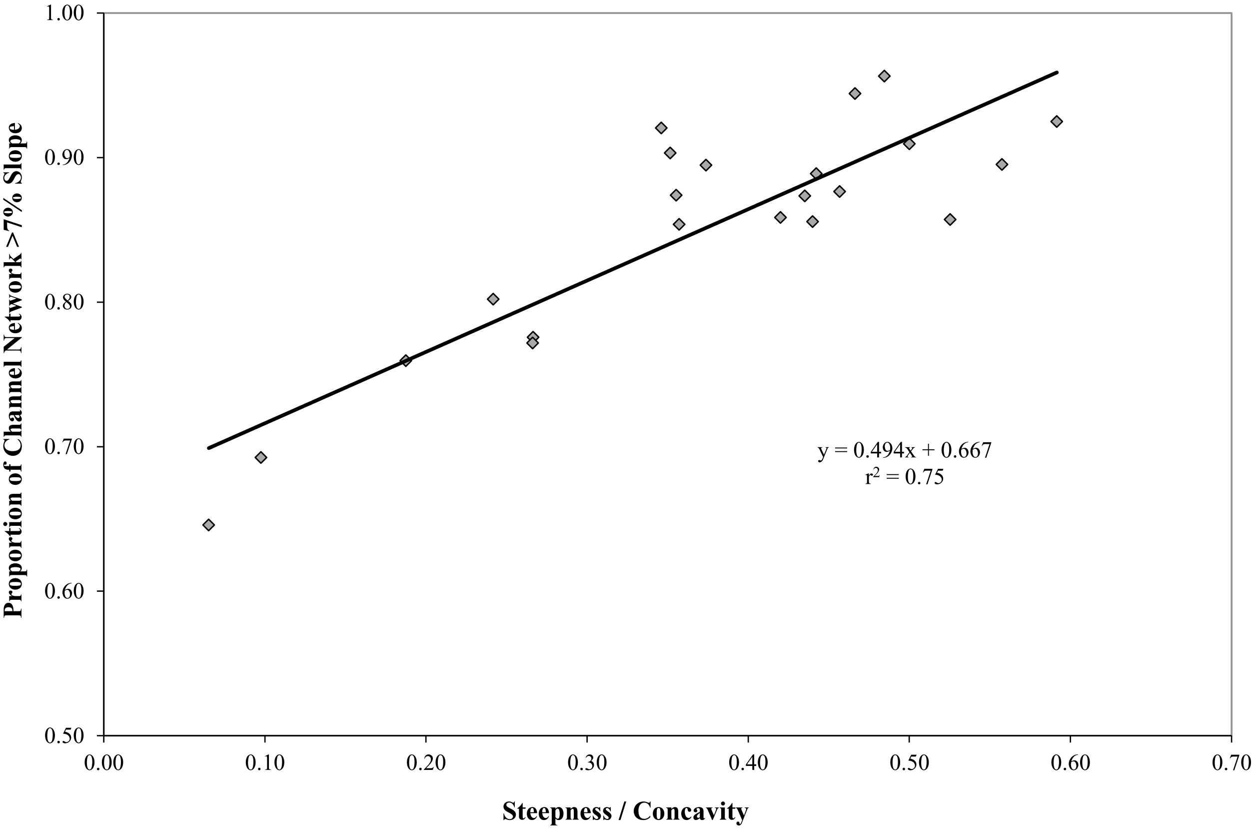

Figure 8. Proportion of the channel network in the debris flow process domain and not utilized by anadromous fish, inferred as reach-scale slopes >7%.

4.4. Spatial Extent of Salmonids

[29] In our analysis, the ratio of steepness to concavity is highly correlated with the portion of the channel network that is not accessible to anadromous fish $S > 7\%$ (correlation coefficient r = 0.87) (Figure 8). Our results further demonstrate that on average 55% of the channel length within the anadromous fish bearing portion of the network ($S < 7\%$) is at risk of direct debris flow impact ($S = 3–7\%$). Similar to the relation in Figure 8, the portion of the network with $S = 3–7\%$ is highly variable (range from 35 to 81%) and is correlated with the ratio of steepness to concavity (correlation coefficient, r = 0.71). Basins that are more steep or less concave have a greater proportion of the channel network at risk of debris flow disturbance within the range of anadromous fish habitat.

[30] To illustrate the effect of the slope-area relation on the potential extent of salmonid habitat and the risk of debris flow disturbance, the planform network structure (i.e., overhead map view) of Basin 1 (Figure 9a) was maintained while the slope-area relation was used to infer the slope-induced limit on the distribution of fish for Basin 2 (Table 1 and Figure 9b) and Basin 3 (Table 1 and Figure 9c). The characteristic drainage area for a channel with a slope of 7% was 19 km^2, 6.5 km^2, and 2.5 km^2 for Basins 1 through 3 (respectively). This simulation was conducted so that a common planform view could be maintained, which illustrates the effect of slope-area relationships more effectively.

[31] In channel networks that have steep and poorly concave profiles, fish distribution is confined to the main stem channel because most tributaries are too steep to provide habitat and the extent of habitat at direct risk of debris flows is greatly increased (Figure 9a). When the steepness of the channel is maintained but the concavity increases, fish distribution ($S < 7\%$) can expand into some of the major tributaries (Figure 9b). When the steepness is reduced and the concavity is increased, there is a dramatic increase in the proportion of the network that contains potential habitat for salmonid fishes (Figure 9c). In addition to expanding the distribution of fish, the area of overlap between debris flows and fish habitat ($S = 3–7\%$) is also greatly reduced.

[32] Identifying the ability of fish populations to expand into tributary channels is important, not only for increasing the total abundance of habitat, but also because it allows for a spatial spreading of risk [*Boer*, 1968] that can stabilize fish abundance in dynamic river systems prone to episodic disturbance. However, caution should be used when delineating slope-dependent limits on preferred habitat because in some river systems patterns of stream temperature, discharge, water chemistry or migration barriers can also play a critical role in determining the extent of anadromous fish [e.g., *Dunham et al.*, 2002]. Wood can also play an important role in creating more favorable channel types in steep reaches [*Montgomery and Buffington*, 1997; *Montgomery et al.*, 1996; *Buffington et al.*, 2004], an effect which is not evident in our analysis.

[33] Although it was not possible to obtain field data on the distribution of fish throughout our study area, we used broadly accepted published values on the effect of channel

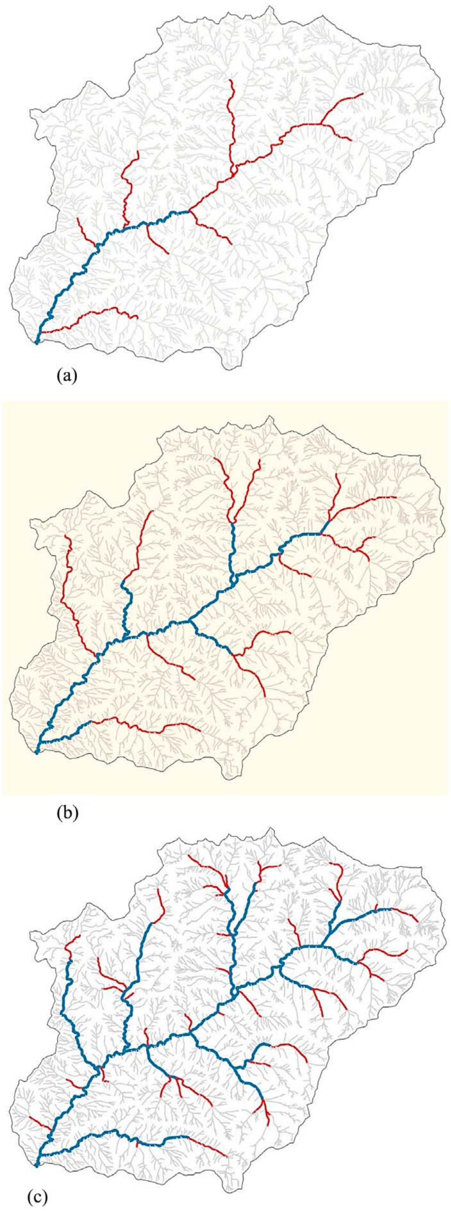

Figure 9. (a) The spatial extent of anadromous fish based on a slope-induced limit of 7% in Basin 1. Simulated profiles for (b) Basin 2 and (c) Basin 3 based on steepness and concavity values overlain on the planform network of Basin 1 (see text for details). Thin gray lines represent the full extent of the channel network, red lines represent the portion of the network in the overlap region between debris flows and anadromous fish habitat (S = 3–7%), blue lines represent reaches beyond the direct risk of debris flows and that provide low-gradient fish habitat (S < 3%).

slope on limiting, and therefore predicting, the maximum spatial extent of fish in the channel network. The logistical constraints of collecting localized field data on the scale of our study area, which encompasses an entire mountain range and focuses on contiguous large catchments (>100 km^2), is one of the primary reasons that the vast majority of previous studies have focused on fish habitat relations at small spatial scales, such as individual pools and riffles (10^1 m) or stream reaches (10^2 m). However, there is a need for broad scale investigations at the river network scale (10^5 m) to reveal patterns of fish distribution and habitat conditions that facilitate or impeded dispersal and connectivity, which are inherent in the network structure and manifested at large scales.

4.5. Management Implications

[34] Insights gained from identifying the steepness and concavity of river profiles, and their influence of fish habitat, can provide a useful framework for broad-scale conservation planning. However, this approach is not meant to replace full ecological assessment of a particular river. Basins with low steepness and high concavity have the greatest potential for producing high quality habitat, resulting in abundant and stable populations. If the goal of conservation efforts is to protect or restore the 'best-of-the-best' habitat, basins with low steepness and high concavity can be targeted. In contrast, if the conservation goal is to protect the most imperiled populations, basins with high steepness and low concavity could be targeted. These basins have less available habitat, fish are confined to a small portion of the channel network, and the risk of debris flows are more severe. This approach is more useful than simply calculating the proportion of the channel network accessible to fish (<7% slope) because it provides a mechanism for understanding (1) the variation in channel morphology across a broad area, (2) the extent and severity of debris flows, and (3) the potential for dispersal and migration of fish throughout the network.

5. Conclusions

[35] Steepness and concavity indices derived from the power function relation between drainage area and channel slope provide a process-based characterization of river profiles. Although this relation has long been recognized by geomorphologists, it has not been used by ecologists to explore the implications for aquatic habitat or riverine fish populations. The conceptual framework proposed by this study illustrates that the geomorphic indices of steepness and concavity provide a useful context for identifying basins that express different reach morphologies, fish habitat capacity, and risk of episodic disturbance. This approach provides a means of mapping and analyzing habitat conditions over a large area, and thus prioritizing conservation areas for anadromous salmonids in the context of evolutionarily significant spatial and temporal scales. However, it must be recognized that important smaller-scale habitat features can be masked at larger scales and that all scales of analysis are important.

[36] Within the nested, hierarchical structure of channel networks [*Frissell et al.*, 1986] the slope-area analysis can be used as a first-order assessment at a broad spatial scale that provides important context for higher resolution assessments. For example, finer-scale assessments of stream temperature may be of critical importance for determining the distribution of coldwater species in areas that reach or exceed lethal temperatures. Although the slope-area analysis cannot provide a direct predictor for other physical limitations, it can provide context. For example, fish residing in streams with poorly concave profiles may not have access to headwater

streams with inherently colder temperatures because they are too steep or are at greater risk of disturbance by debris flows, so identifying downstream site-specific limits to coldwater and the availability of thermal refugia are of vital importance. Similarly, stream discharge may limit the upper distribution of fish in areas that experience a prolonged dry season or have extremely low base flows. Limits imposed by discharge may be especially important in basins with strongly concave profiles because fish have the potential for extending higher up into the drainage network. In contrast, limits of fish distribution imposed by discharge in intermittent streams may be more important in low concavity basins because habitat is already spatially limiting. Other important habitat characteristics for salmonids, including barriers to migration, wood-facilitated habitats, and the availability of floodplain habitats, are also examples of finer-scale assessment that warrant attention as areas are prioritized for conservation. It must be recognized that the slope-area analysis is merely one simple tool that should be used in conjunction with other ecological assessments of habitat.

[37] The primary insight drawn from the slope-area analysis is a conceptual framework of how river profiles exert a broad-scale control on fish habitat. Strongly concave profiles that develop in steep terrain indicate that almost all of the relief in the drainage network occurs in small headwater streams. In these basins a large proportion of the drainage network has low-gradient morphologies, such as pool-riffle sequences, which provide favorable spawning and rearing habitat for many salmonid species. The severity of pulse disturbances is also reduced because debris flows typically form discrete deposits where steep tributaries abruptly encounter low-gradient main stem channels at tributary junctions. In contrast, less concave profiles in steep terrain indicate that the spatial extent of high-gradient morphologies, such as step-pool and cascade sequences, is more extensive. Furthermore, the change in slope at tributary junctions is less pronounced and debris flows rarely form discrete deposits, but continue to travel down steep main stem channels as debris floods and alter aquatic and riparian habitats for long distances.

[38] In steep mountainous terrain debris flows and hyperconcentrated flows are one of the most prevalent large-scale disturbances to aquatic ecosystems [e.g., *Reeves et al.*, 1995]. Insights from our study also suggest that the physical habitat template and the severity of pulsed disturbances that are characterized by the steepness and concavity indices can have a strong effect on population resiliency. Specifically, we hypothesize that populations residing in basins with high steepness and/or low concavity will have more severe fluctuations in population abundance and may be at greatest risk of localized extirpation because most tributaries are too steep to provide habitat, confining fish to main stem channels. In contrast, fish distribution in basins with low steepness and/or high concavity can expand into the tributaries, allowing for a spatial spreading of risk that may enhance a population's ability to persist during adverse conditions for survival and growth. Maintaining population connectivity across the channel network enhances population persistence by increasing the likelihood of dispersal and recolonization after severe disturbances [e.g., *Anderson and Quinn*, 2007; *Schtickzelle and Quinn*, 2007]. The combined influence of a broader spatial distribution of salmonid habitat, and the decreased extent and severity of debris flows, may result in less extreme fluctuations in fish abundance because populations are more resilient to pulse disturbances. Unfortunately no long-term data on fish abundance or distribution is available to test this hypothesis, and further research is needed verify the predictions set forth in this analysis.

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References

Adams, S. B., C. A. Frissell, and B. E. Rieman (2000), Movements of nonnative brook trout in relation to stream channel slope, *Trans. Am. Fish. Soc.*, *129*, 623–638, doi:10.1577/1548-8659(2000)129<0623:MONBTI>2.3.CO;2.

Agrawal, A., R. S. Schick, E. P. Bjorkstedt, R. G. Szerlong, M. N. Goslin, B. C. Spence, T. H. Williams, and K. M. Burnett (2005), Predicting the potential for historical coho, Chinook and steelhead habitat in Northern California, *NOAA Tech. Rep. NMFS*, *379*, 25 pp.

Anderson, J. H., and T. P. Quinn (2007), Movements of adult coho salmon (Oncorhynchus kisutch) during colonization of newly accessible habitat, *Can. J. Fish. Aquat. Sci.*, *64*(8), 1143–1154, doi:10.1139/f07-087.

Beechie, T., E. Beamer, and L. Wasserman (1994), Estimating coho salmon rearing habitat and smolt production losses in a large river basin, and implications for habitat restoration, *N. Am. J. Fish. Manage.*, *14*, 797–811, doi:10.1577/1548-8675(1994)014<0797:ECSRHA>2.3.CO;2.

Benda, L. E. (1985), Delineation of channels susceptible to debris flows and debris floods, in *Proceedings of International Symposium on Erosion, Debris Flow and Disaster Prevention*, pp. 195–201, Erosion Control Eng. Soc., Tsukuba, Japan.

Benda, L. E., and T. W. Cundy (1990), Predicting deposition of debris flows in mountain channels, *Can. Geotech. J.*, *27*, 409–417, doi:10.1139/t90-057.

Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock (2004), The network dynamics hypothesis: How channel networks structure riverine habitats, *BioScience*, *54*(5), 413–427, doi:10.1641/0006-3568(2004)054[0413:TNDHHC]2.0.CO;2.

Boer, P. J. (1968), Spreading of risk and stabilization of animal numbers, *Acta Biotheor.*, *18*, 165–194.

Brardinoni, F., and M. A. Hassan (2006), Glacial erosion, evolution of river long profiles, and the organization of process domains in mountain drainage basins of coastal British Columbia, *J. Geophys. Res.*, *111*, F01013, doi:10.1029/2005JF000358.

Brummer, C. J., and D. R. Montgomery (2003), Downstream coarsening in headwater channels, *Water Resour. Res.*, *39*(10), 1294, doi:10.1029/2003WR001981.

Buffington, J. M., and D. Tonina (2009), Hyporheic exchange in mountain rivers II: Effects of channel morphology on mechanics, scales, and rates of exchange, *Geogr. Compass*, *3*(3), 1038–1062, doi:10.1111/j.1749-8198.2009.00225.x.

Buffington, J. M., D. R. Montgomery, and H. M. Greenberg (2004), Basin-scale availability of salmonid spawning gravel as influenced by channel type and hydraulic roughness in mountain catchments, *Can. J. Fish. Aquat. Sci.*, *61*, 2085–2096, doi:10.1139/f04-141.

Burnett, K. M., G. H. Reeves, D. J. Miller, S. Clarke, K. Vance-Borland, and K. Christiansen (2007), Distribution of salmon-habitat potential relative to landscape characteristics and implications for conservation, *Ecol. Appl.*, *17*, 66–80, doi:10.1890/1051-0761(2007)017[0066:DOSPRT]2.0.CO;2.

Cenderelli, D. A., and J. S. Kite (1998), Geomorphic effects of large debris flows on channel morphology at North Fork Mountain, Eastern West Virginia, USA, *Earth Surf. Processes Landforms*, *23*, 1–19, doi:10.1002/(SICI)1096-9837(199801)23:1<1::AID-ESP814>3.0.CO;2-3.

Clarke, S. E., K. M. Burnett, and D. J. Miller (2008), Modeling streams and hydrogeomorphic attributes in Oregon from digital and field data, *J. Am. Water Resour. Assoc.*, *44*, 459–477, doi:10.1111/j.1752-1688.2008.00175.x.

Costa, J. E. (1984), Physical geomorphology of debris flows, in *Developments and Applications of Geomorphology*, edited by J. E. Costa and

P. J. Fleisher, pp. 268–317, Springer, New York, doi:10.1007/978-3-642-69759-3_9.

Dunham, J. B., and B. E. Rieman (1999), Metapopulation structure of bull trout: Influences of physical, biotic, and geometrical landscape characteristics, *Ecol. Appl.*, *9*, 642–655, doi:10.1890/1051-0761(1999)009[0642:MSOBTI]2.0.CO;2.

Dunham, J. B., B. E. Rieman, and J. T. Peterson (2002), Patch-based models of species occurrence: Lessons from salmonid fishes in streams, in *Predicting Species Occurrences: Issues of Scale and Accuracy*, edited by J. V. Scott et al., pp. 327–334, Island Press, Covelo, Calif.

Fagan, W. F. (2002), Connectivity, fragmentation, and extinction risk in dendritic metapopulations, *Ecology*, *83*, 3243–3249, doi:10.1890/0012-9658(2002)083[3243:CFAERI]2.0.CO;2.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li (2002), Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes, *BioScience*, *52*, 483–498, doi:10.1641/0006-3568(2002)052[0483:LTRBTG]2.0.CO;2.

Fausch, K. D., B. E. Rieman, J. B. Dunham, M. K. Young, and D. P. Peterson (2009), Invasion versus isolation: Trade-offs in managing native salmonids with barriers to upstream movement, *Conserv. Biol.*, *23*, 859–870, doi:10.1111/j.1523-1739.2008.01159.x.

Finlayson, D. P., and D. R. Montgomery (2003), Modeling large-scale fluvial erosion in geographic information systems, *Geomorphology*, *53*, 147–164, doi:10.1016/S0169-555X(02)00351-3.

Flint, J. J. (1974), Stream gradient as a function of order, magnitude, and discharge, *Water Resour. Res.*, *10*(5), 969–973, doi:10.1029/WR010i005p00969.

Folt, C. L., K. H. Nislow, and M. E. Power (1998), Implications of temporal and spatial scale for Atlantic salmon (*Salmo salar*) research, *Can. J. Fish. Aquat. Sci.*, *55*, 9–21, doi:10.1139/d98-017.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley (1986), A hierarchical framework for stream habitat classification: Viewing streams in a watershed context, *Environ. Manage. N. Y.*, *10*, 199–214, doi:10.1007/BF01867358.

Hack, J. T. (1957), Studies of longitudinal stream profiles in Virginia and Maryland, *U.S. Geol. Surv. Prof. Pap.*, *294-B*, 94pp.

Hack, J. T. (1973), Stream profile analysis and stream-gradient index, *U.S. Geol. Surv. J. Res.*, *1*(4), 421–429.

Hall, J. E., D. M. Holzer, and T. J. Beechie (2007), Predicting river floodplain and lateral channel migration for salmon habitat conservation, *J. Am. Water Resour. Assoc.*, *43*, 786–797, doi:10.1111/j.1752-1688.2007.00063.x.

Hicks, B. J., and J. D. Hall (2003), Rock type and channel gradient structure salmonid populations in the Oregon Coast Range, *Trans. Am. Fish. Soc.*, *132*, 468–482, doi:10.1577/1548-8659(2003)132<0468:RTACGS>2.0.CO;2.

Howard, A. D., and G. Kerby (1983), Channel changes in badlands, *Geol. Soc. Am. Bull.*, *94*, 739–752, doi:10.1130/0016-7606(1983)94<739:CCIB>2.0.CO;2.

Hungr, O., S. G. Evans, M. J. Bovis, and J. N. Hutchinson (2001), A review of the classification of landslides of the flow type, *Environ. Eng. Geosci.*, *3*(3), 221–238.

Johnson, S. L., F. J. Swanson, G. E. Grant, and S. M. Wondzell (2000), Riparian forest disturbances by a mountain flood: The influence of floated wood, *Hydrol. Processes*, *14*, 3031–3050, doi:10.1002/1099-1085(200011/12)14:16/17<3031::AID-HYP133>3.0.CO;2-6.

Kelsey, H. M. (1978), Earthflows in Franciscian mélange, Van Duzen River basin, *Calif. Geol.*, *6*, 361–364.

Kirby, E., and K. Whipple (2001), Quantifying differential rock-uplift rates via stream profile analysis, *Geology*, *29*, 415–418, doi:10.1130/0091-7613(2001)029<0415:QDRURV>2.0.CO;2.

Kirby, E., K. X. Whipple, W. Tang, and Z. Chen (2003), Distribution of active rock uplift along the eastern margin of the Tibetan Plateau: Inferences from bedrock channel longitudinal profiles, *J. Geophys. Res.*, *108*(B5), 2217, doi:10.1029/2001JB000861.

Kobor, J. S., and J. Roering (2004), Systematic variation of bedrock channel gradients in the central Oregon Coast Range: Implications for rock uplift and shallow landsliding, *Geomorphology*, *62*, 239–256, doi:10.1016/j.geomorph.2004.02.013.

Korup, O. (2005), Large landslides and their effect on sediment flux in South Westland, New Zealand, *Earth Surf. Processes Landforms*, *30*, 305–323, doi:10.1002/esp.1143.

Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, R. C. Wildman, and K. Moore (1991), Stream ecosystem recovery following a catastrophic debris flow, *Can. J. Fish. Aquat. Sci.*, *48*, 196–208, doi:10.1139/f91-027.

Lisle, T. E., and M. Church (2002), Sediment transport-storage relations for degrading, gravel bed channels, *Water Resour. Res.*, *38*(11), 1219, doi:10.1029/2001WR001086.

Lowe, W. H., G. E. Likens, and M. E. Power (2006), Linking scales in stream ecology, *BioScience*, *56*, 591–597, doi:10.1641/0006-3568(2006)56[591:LSISE]2.0.CO;2.

Lunetta, R. S., B. L. Cosentino, D. R. Montgomery, E. M. Beamer, and T. J. Beechie (1997), GIS-based evaluation of salmon habitat in the Pacific Northwest, *Photogramm. Eng. Remote Sens.*, *63*, 1219–1229.

Massong, T. M., and D. R. Montgomery (2000), Influence of sediment supply, lithology, and wood debris on the distribution of bedrock and alluvial channels, *Geol. Soc. Am. Bull.*, *112*(4), 591–599, doi:10.1130/0016-7606(2000)112<591:IOSSLA>2.0.CO;2.

May, C. L. (2002), Debris flows through different forest age classes in the central Oregon Coast Range, *J. Am. Water Resour. Assoc.*, *38*(4), 1097–1113, doi:10.1111/j.1752-1688.2002.tb05549.x.

May, C. L., and R. E. Gresswell (2004), Spatial and temporal patterns of debris flow deposition in the Oregon Coast Range, U.S.A, *Geomorphology*, *57*, 135–149, doi:10.1016/S0169-555X(03)00086-2.

May, R. M. (1994), The effects of spatial scale on ecological questions and answers, in *Large-Scale Ecology and Conservation Biology*, edited by P. J. Edwards, R. M. May, and N. R. Webb, pp. 1–17, Blackwell Sci., Oxford, UK.

Miller, D. (2003), Programs for DEM analysis, report, Earth Syst. Inst., Seattle, Wash.

Miller, D. J., and L. E. Benda (2000), Effects of punctuated sediment supply on valley-floor landforms and sediment transport, *Geol. Soc. Am. Bull.*, *112*(12), 1814–1824, doi:10.1130/0016-7606(2000)112<1814:EOPSSO>2.0.CO;2.

Moir, H. J., C. N. Gibbons, C. Soulsby, and J. Webb (2004), Linking channels geomorphic characteristics to spatial patterns of spawning activity and discharge use by Atlantic salmon (*Salmo salar* L.), *Geomorphology*, *60*, 21–35, doi:10.1016/j.geomorph.2003.07.014.

Mondry, Z. (2004), 1997 flooding in three northern California Klamath Mountain streams: Geomorphic effectiveness and sediment and large wood budgets, MS thesis, Dep. of Geol., Humboldt State Univ., Arcata, Calif.

Montgomery, D. R. (1999), Process domains and the river continuum, *J. Am. Water Resour. Assoc.*, *35*(2), 397–410, doi:10.1111/j.1752-1688.1999.tb03598.x.

Montgomery, D. R., and J. M. Buffington (1997), Channel-reach morphology in mountain drainage basins, *Geol. Soc. Am. Bull.*, *109*(5), 596–611, doi:10.1130/0016-7606(1997)109<0596:CRMIMD>2.3.CO;2.

Montgomery, D. R., and E. Foufoula-Georgiou (1993), Channel network source representation using digital elevation models, *Water Resour. Res.*, *29*, 3925–3934, doi:10.1029/93WR02463.

Montgomery, D. R., T. B. Abbe, N. P. Peterson, J. M. Buffington, K. M. Schmidt, and J. D. Stock (1996), Distribution of bedrock and alluvial channels in forested mountain drainage basins, *Nature*, *381*, 587–589, doi:10.1038/381587a0.

National Oceanic and Atmospheric Administration (2005), Predicting the potential for historical coho, Chinook, and steelhead habitat in northern California, *NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-379*, Santa Cruz, California.

Peterson, D. P., B. E. Rieman, J. B. Dunham, K. D. Fausch, and K. D. Young (2008), Analysis of trade-offs between threats of invasion by nonnative brook trout (Salvenilus fontinalis) and intentional isolation for native westslope cutthroat trout (Oncorhynchus clarkia lewisi), *Can. J. Fish. Aquat. Sci.*, *65*, 557–573, doi:10.1139/f07-184.

Reeves, G. H., F. H. Everest, and T. E. Nickelson (1989), Identification of physical habitats limiting the production of coho salmon in western Oregon and Washington, *Gen. Tech. Rep. PNW-GTR-245*, U.S. For. Serv., Pac. Southwest Res. Stn., Portland, Oreg.

Reeves, G. H., L. E. Benda, K. M. Burnett, P. A. Bisson, and J. R. Sedell (1995), A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionary significant units of anadromous salmonids in the Pacific Northwest, *Am. Fish. Soc. Symp.*, *17*, 334–349.

Roe, G. H., D. R. Montgomery, and B. Hallet (2002), Effects of orographic precipitation variations on the concavity of steady-state river profiles, *Geology*, *30*, 143–146, doi:10.1130/0091-7613(2002)030<0143:EOOPVO>2.0.CO;2.

Roghair, C. N., C. A. Dollof, and M. K. Underwood (2002), Response of a brook trout population and instream habitat to a catastrophic flood and debris flow, *Trans. Am. Fish. Soc.*, *131*, 718–730, doi:10.1577/1548-8659(2002)131<0718:ROABTP>2.0.CO;2.

Schtickzelle, N., and T. P. Quinn (2007), A metapopulation perspective for salmon and other anadromous fish, *Fish Fish.*, *8*(4), 297–314, doi:10.1111/j.1467-2979.2007.00256.x.

Seaber, P. R., F. P. Kapinos, and G. L. Knapp (1987), Hydrologic unit maps, *U.S. Geol. Surv. Water. Supply Pap.*, *2294*, 63 pp.

Seidl, M. A., W. E. Dietrich, and J. W. Kirchner (1994), Longitudinal profile development into bedrock: An analysis of Hawaiian channels, *J. Geol.*, *102*, 457–474, doi:10.1086/629686.

Sklar, L., and W. E. Dietrich (1998), River longitudinal profiles and bedrock incision models: Stream power and the influence of sediment supply, in *Rivers Over Rock: Fluvial Processes in Bedrock Channels*, *Geophys. Monogr. Ser*, vol. 107, edited by J. Tinkler and E. Wohl, pp. 237–260, AGU, Washington, D. C.

Sklar, L., and W. E. Dietrich (2001), Sediment and rock strength controls on river incision into bedrock, *Geology*, *29*, 1087–1090, doi:10.1130/0091-7613(2001)029<1087:SARSCO>2.0.CO;2.

Snyder, N. P., K. X. Whipple, G. E. Tucker, and D. J. Merritts (2000), Landscape response to tectonic forcing: Digital elevation model analysis of stream profiles in the Mendocino triple junction region, northern California, *Geol. Soc. Am. Bull.*, *112*, 1250–1263, doi:10.1130/0016-7606(2000)112<1250:LRTTFD>2.0.CO;2.

Stock, J., and W. E. Dietrich (2003), Valley incision by debris flows: Evidence of a topographic signature, *Water Resour. Res.*, *39*(4), 1089, doi:10.1029/2001WR001057.

VanLaningham, S., A. Meigs, and C. Goldfinger (2006), The effects of rock uplift and rock resistance on river morphology in a subduction zone forearc, Oregon, USA, *Earth Surf. Processes Landforms*, *31*, 1257–1279, doi:10.1002/esp.1326.

Whipple, K. X. (2004), Bedrock rivers and the geomorphology of active orogens, *Annu. Rev. Earth Planet. Sci.*, *32*, 151–185, doi:10.1146/annurev.earth.32.101802.120356.

Wobus, C., K. X. Whipple, E. Kirby, N. Snyder, J. Johnson, K. Spyropolou, B. Crosby, and D. Sheehan (2006), Tectonics from topography Procedures, promise, and pitfalls, *Geol. Soc. Am. Spec. Pap.*, *398*, 55–74.

Wohl, E., and D. Merritt (2005), Prediction of mountain stream morphology, *Water Resour. Res.*, *41*, W08419, doi:10.1029/2004WR003779.

Wohl, E., and P. Pearthree (1991), Debris flows as geomorphic agents in the Huachuca Mountains of Southeastern Arizona, *Geomorphology*, *4*, 273–292, doi:10.1016/0169-555X(91)90010-8.