Production of stream habitat gradients by montane watersheds: hypothesis tests based on spatially explicit path analyses

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Abstract: We studied how the features of mountain watersheds interact to cause gradients in three stream attributes: baseflow stream widths, total alkalinity, and stream slope. A priori hypotheses were developed before being tested in a series of path analyses using data from 90 stream reaches on 24 second- to fourth-order streams across a fifth-order Rocky Mountain watershed. Because most of the conventional least squares regressions initially calculated for the path analyses had spatially correlated residuals (13 of 15 regressions), spatially explicit regressions were often used to derive more accurate parameter estimates and significance tests. Our final working hypotheses accounted for most of the variation in baseflow stream width (73%), total alkalinity (74%), and stream slope (78%) and provide systemic views of watershed function by depicting interactions that occur between geomorphology, land surface features, and stream attributes. Stream gradients originated mainly from the unidirectional changes in geomorphic features that occur over the lengths of streams. Land surface features were of secondary importance and, because they change less predictably relative to the stream, appear to modify the rate at which stream gradients change.

Résumé : Notre étude vise à comprendre comment les caractéristiques des réseaux hydrographiques de montagne interagissent pour former des gradients dans trois des descripteurs des cours d’eau : la largeur du lit au débit de base, l’alcalinité totale et la pente. Nous avons élaboré des hypothèses a priori avant de les éprouver dans des analyses de pistes causales basées sur des données provenant de 90 sections de 24 cours d’eau d’ordres 2 à 4, appartenant à un système hydrographique d’ordre 5 des Rocheuses. Parce que les régressions conventionnelles par la méthode des moindres carrés calculées initialement pour l’analyse des pistes possèdent des résidus qui présentent entre eux des corrélations spatiales (13 des 15 régressions), nous avons utilisé des régressions spatialement explicites pour obtenir des estimations plus précises des paramètres et de meilleurs tests de signification. Nos hypothèses de travail finales expliquent la plus grande partie de la variation dans la largeur du lit au débit de base (73%), l’alcalinité totale (74%) et la pente du cours d’eau (78%); elles génèrent une représentation du fonctionnement du système hydrographique qui décrit les interactions entre la géomorphologie, les faciès terrestres et les caractéristiques du cours d’eau. Les gradients dans les cours d’eau apparaissent surtout à cause de changements unidirectionnels des caractéristiques géomorphologiques le long du cours. Les faciès terrestres ont une importance secondaire et, parce qu’ils changent de façon moins prévisible en rapport avec le cours, ils semblent modifier le rythme auquel les gradients des cours d’eau évoluent.

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Introduction

Stream ecologists have over the last century described patterns in lotic biotas relative to habitat gradients in streams (Shelford 1911; Huet 1959; Ward 1986). The ubiquity of these patterns led to the formulation of the River Continuum Concept (Vannote et al. 1980), which in part posits that lotic communities are structured by the quality and quantity of energy inputs to a stream and that these inputs result from interactions between the riparian zone and environmental gradients within a stream. The River Continuum Concept has become a dominant paradigm within stream ecology, but despite its explicit recognition of factors external to the stream and a trend toward broadscale management of stream systems, relatively few studies have examined linkages between stream habitats and surrounding landscapes.

Much of the work that links streams to their surroundings was conducted during the mid-twentieth century by geomorphologists working on stream energy expenditure theory (e.g., Leopold and Maddock 1953), and many authors have linked channel characteristics to broadscale variables such as watershed size or basin relief (Langbein 1947; Strahler 1957). More recently, fisheries scientists have related fish habitats to geomorphic and geologic traits of watersheds (Lanka et al. 1987; Nelson et al. 1992), while hydrologists and geohydrochemists have made similar advances in explaining stream flows (Thomas and Benson 1970; Zecharias and Brutsaert 1988) and water chemistries (Teti 1984; Close and Davies-Colley 1990). But despite the merit of these efforts, previous studies have oversimplified stream–watershed

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linkages by not including all of the factors that may affect a particular stream attribute in the same model. Additionally, no study has modeled the chains of causality that can be expected to link watershed features to instream habitats. We attempted to partially fill these voids by examining how watershed features interact to impinge upon streams and cause gradients in three habitat attributes important to lotic biotas: baseflow stream width, total alkalinity, and stream slope. Our objectives were to develop detailed hypotheses about the linkages between watersheds and stream attributes, use empirical data to test predictions generated by the hypotheses, and revise the hypotheses to derive an accurate and systemic understanding of how watersheds function to produce stream habitat gradients.

Stream gradient hypotheses

In this section, the hypothesis for each stream attribute is described and rationales are provided for the causal relationships among variables. To facilitate accurate modeling of these systems, the features characterizing the terrestrial landscape were divided into two classes. Geomorphic features pertain to size, shape, or orientation, whereas land surface features describe surficial or near-surface aspects of a watershed. Hypothesis 1 depicts the predicted causal structure among factors associated with baseflow stream width (Fig. 1), a variable that provides a measure of habitat volume during periods when competitive interactions are expected to be strongest (e.g., Gipson 1973). Stream width also helps determine the trophic status and community structure of streams by regulating the amount of sunlight incident upon a stream (Vannote et al. 1980).

A survey of the literature, combined with observations made while working in the field, suggested that baseflow widths were potentially affected by nine factors: cattle density, watershed size, aquifer storage, basin elevation, drainage density, watershed slope, tree abundance, soil compaction, and road density. In a mechanistic sense, baseflow widths should be positively affected by watershed size because larger land areas collect and concentrate more precipitation. Elevation is also expected to be an important determinant of stream flows in montane landscapes because the lapse rate of temperature with elevation and orographic lifting of air parcels cause greater condensation and precipitation at high elevations (Brooks et al. 1991). Therefore, if all other factors are held constant, the baseflow width of a stream flowing from a high-elevation basin should be greater than the width of a stream flowing from a low-elevation basin.

Once a water molecule enters a watershed, its probability of contributing to baseflow is affected by factors that alter the timing and intensity of precipitation runoff. Watersheds underlain by large amounts of geologic materials that provide aquifer storage should have greater baseflows because more precipitation will enter long-term storage and not immediately pass through the system. Conversely, land uses such as livestock grazing or timber harvest can expedite runoff and negatively affect baseflows by compacting soil layers and decreasing infiltration (Brooks et al. 1991; Meehan 1991). Watershed slope, road density, and drainage density are also expected to negatively affect baseflows because denser stream and road networks and greater hydraulic gradients in steep watersheds increase the throughput of precipitation (Carlston 1963; Zecharias and Brutsaert 1988; Jones and Grant 1996). Drainage density is in turn predicted to be positively affected by basin elevation and watershed slope because more precipitation will be available to form stream channels at high elevations, and this precipitation will be quickly concentrated in watersheds with steep slopes, thereby enhancing channel initiation and maintenance (Langbein 1947).

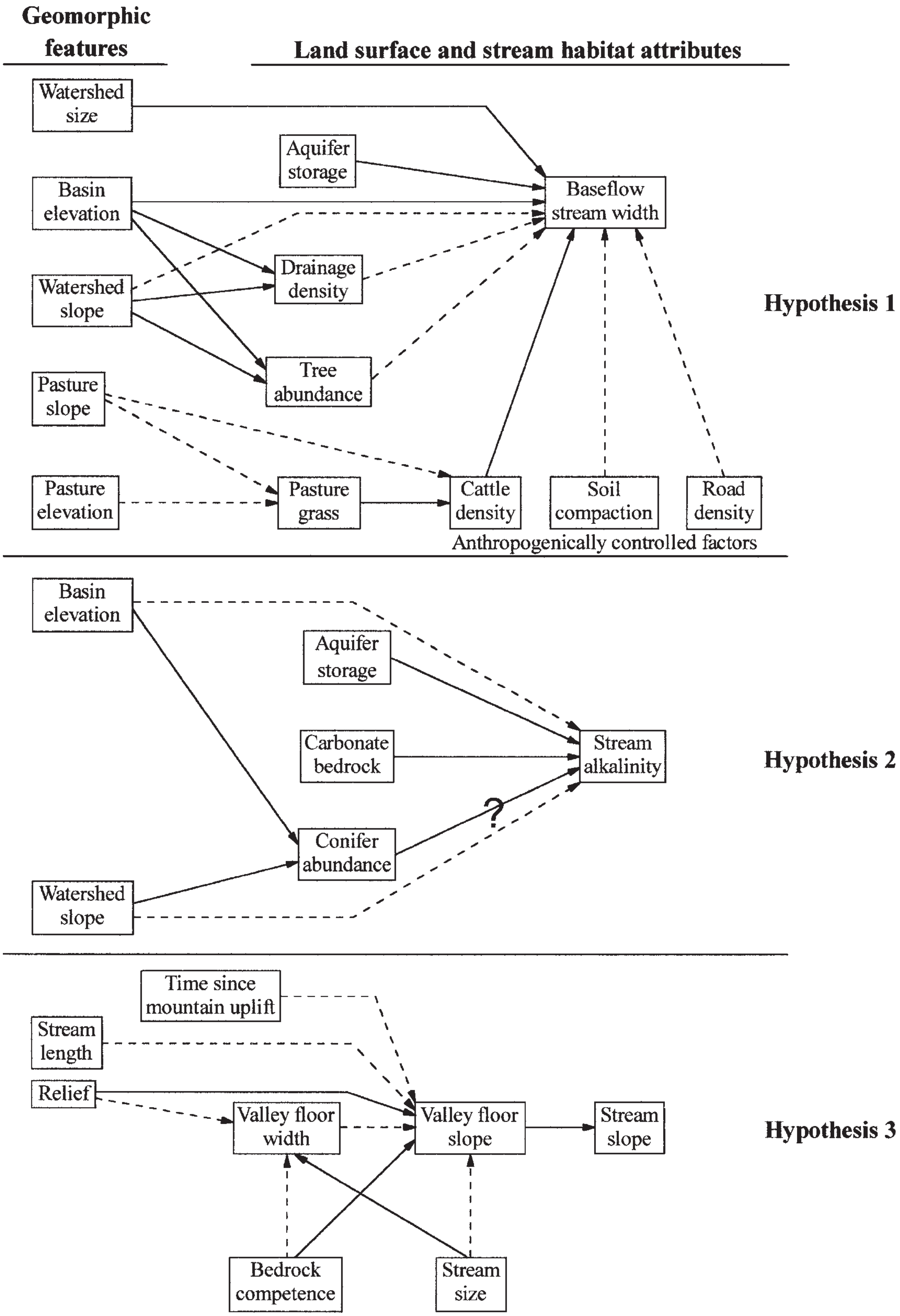
Evapotranspiration allows water to exit basins by a route other than stream flow (Brooks et al. 1991). Because trees transpire at greater rates than other vegetation types (Brown and Thompson 1965), watersheds with more trees should have lower baseflows. Tree abundance is in turn expected to be controlled by geomorphic characteristics that produce the mesic conditions needed by trees (Running 1984), and we predict that tree abundance will be positively related to basin elevation. Watershed slope is also expected to have a positive effect on tree abundance because topographic shading is greater in steeper watersheds.

The factors described above affect stream width by altering the amount of water in the channel. However, grazing by cattle and the associated bank destabilization can affect the physical structure of the channel (Belsky et al. 1999), and it is predicted that streams will be wider where cattle densities are greater. Although the distribution of cattle across a landscape is somewhat arbitrary given human intervention, our field observations suggest that cattle are generally grazed in areas amenable to their preferences for gradual slopes (Mueggler 1965) and grass forage (Odion et al. 1988). Grass abundance is expected to be controlled by the same geomorphic factors that regulate the abundance of trees, although slope and elevation should have negative rather than positive effects on grass abundance.

In the second hypothesis, we describe linkages among watershed features and stream alkalinity (Fig. 1), a measure of the nutrient content of water that has often been positively correlated with greater abundances of aquatic macroinvertebrates and fish (e.g., Krueger and Waters 1983; Kwak and Waters 1997). Although a causal relationship between alkalinity and stream biota is not well substantiated, speculations are that organisms in more alkaline waters use less energy for ionic regulation (Fiance 1978) or that alkalinity ions provide an important source of dissolved inorganic carbon that stimulates greater primary productivity (Krueger and Waters 1983).

In the pH range of most surface waters, alkalinity is determined almost entirely by the abundance of bicarbonate ions, which originate from the chemical weathering of bedrock-derived mineral soils by carbonic acid dissolved in groundwater (Drever 1997). Stream alkalinity should therefore be positively related to the abundance of carbonate bedrocks (i.e., limestone and dolomite) because these geologic materials weather into soils that can produce large amounts of bicarbonate ions (Drever 1997). Soil development is expected to relate to alkalinity because thick and finely dissected soils provide more surface area to yield bicarbonate ions, and these soils will lengthen soil–water contact time by slowing the movement of water through a hillslope (Drever and Zobrist 1992). Consequently, steep watersheds should have streams with low alkalinities because soil depth is inversely

Fig. 1. Hypotheses about factors that cause habitat gradients in small mountain streams. Arrows point in the direction of causality. If an arrow has a solid line, the relationship is predicted to be positive; if an arrow has a broken line, the relationship is predicted to be negative.



related to slope steepness (Carson and Kirkby 1972). Basin elevation is also predicted to negatively affect alkalinity because colder temperatures at high elevations slow biological and chemical processes that build soils (Drever and Zobrist 1992). Conversely, the amount of aquifer storage within a watershed should have a positive effect on alkalinities because greater storage will lengthen soil–water contact time and provide more opportunity for bicarbonate ions to enter solution.

The abundance of coniferous trees may affect alkalinity because the decomposition of conifer needles results in the development of acid soils (Nihlgard 1970). Water percolating through these soils becomes more acid, but the effect that this has on stream alkalinity depends on the composition of the underlying bedrock. In watersheds with carbonate substrates, low pHs increase weathering rates, which releases additional bicarbonate ions and leads to the alkalization of surface waters (Kilham 1982). But in watersheds overlying less soluble igneous or metamorphic bedrocks, weathering rates will not change appreciably, and stream alkalinities may actually decrease as greater acidities use some of the buffering capacity already present in the water (e.g., Sharpe et al. 1984).

Hypothesis 3 depicts the predicted causal structure between watershed features and reach-scale stream slope (Fig. 1), a variable that strongly affects the structure of habitats (Montgomery and Buffington 1997) and the attributes of lotic biotas (Isaak and Hubert 2000). The stream slope hypothesis differs from the previous two hypotheses in that the primary response variable is predicted to be entirely controlled by one factor, the slope of the underlying valley floor. As such, understanding how the longitudinal profiles of valley floors are formed should provide insight into the factors determining reach-scale stream slope.

During mountain-building episodes, uplift rates exceed the erosive capacity of a stream, but the magnitude of this exceedance decreases in a downstream direction as stream size and erosive capacity increase (Snow and Slingerland 1990). Downstream areas, therefore, are more quickly reduced than upstream areas, which results in the concave upward profile of most valley floors (Wheeler 1979) and suggests that stream size will negatively affect valley floor slope. Stream length is expected to have a similar negative effect on valley floor slope because the descent to baselevel can be spread over a greater distance in a longer stream. The amount of time since the mountain-building event is also predicted to have a negative effect on valley floor slope because weathering and erosive forces will gradually reduce the relief of a mountain range. Conversely, valley floor slope should be steeper where relief is greater because the amount of geologic material to be eroded increases as uplift magnitude increases.

The rate at which geologic materials weather and become susceptible to fluvial displacement can affect valley floor slope at two spatial scales. At the scale of the entire slope profile, greater bedrock competence will slow the rate at which a landmass erodes and should increase the steepness of the profile (Wheeler 1979). At a more restricted scale, variation in the competence of the individual geologic formations that a stream flows across can alter the width of a valley floor (e.g., Hupp 1982). Valley floor width will in turn have a negative effect on valley floor slope because streams can deposit more alluvium and build gently sloping floodplains in wider valleys. Valley floor width should be positively affected by stream size because larger streams not only carve wider valleys but transport and deposit more alluvium. Finally, relief is expected to have a negative effect on valley floor width because streams farther removed from baselevel are more likely to be downcutting and will create steep and incised valleys rather than alluvial valleys.

Materials and methods

Study area

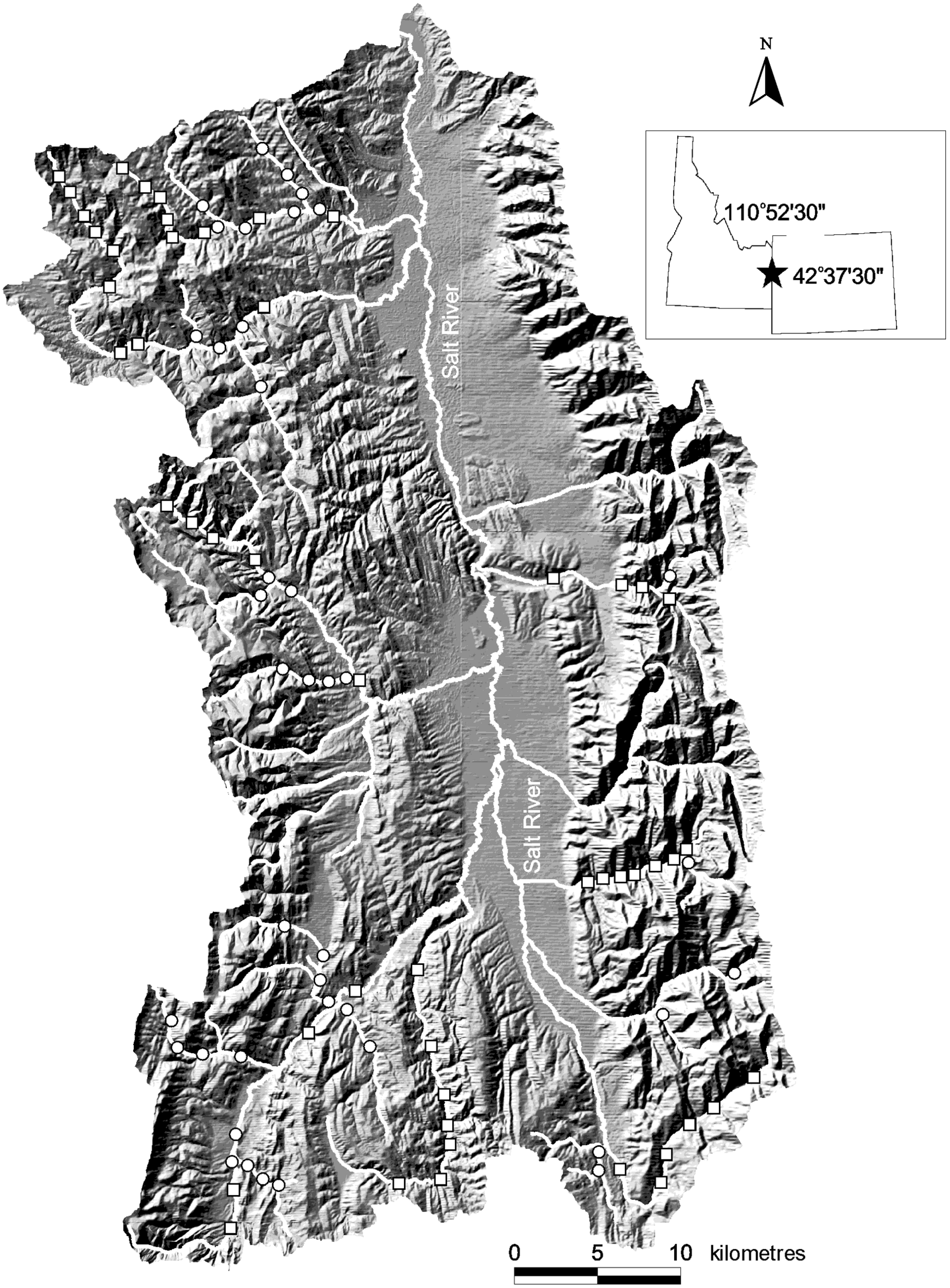
Data to test the hypotheses were collected from the 2150-km^2 Salt River watershed on the border between Idaho and Wyoming (42°37′30′′ latitude, 110°52′30′′ longitude). The Salt River watershed is part of the Middle Rocky Mountain physiographic province (Fenneman 1931) and is bordered by mountain ranges that differ markedly in morphology (Fig. 2). On the east side of the watershed, the rugged Salt River Range peaks at elevations exceeding 3300 m. The terrain in the Caribou and Webster ranges to the west and the Gannett Hills to the south is less rugged and elevations do not exceed 2800 m. Mountain massifs consist of uplifted sedimentary rock strata that have been convoluted to yield a complex bedrock geology comprising more than 40 geologic formations (Mitchell and Bennett 1979; Oriel and Platt 1980). Each formation contains a mixture of interbedded rock types that consists of various mudstones, conglomerates, shales, sandstones, limestones, and dolomites. Karstic structures occur within some of the formations, but obvious outflows from these structures affected none of the streams included in this study. Formation dates of the geologic formations range widely from the Mississippian to the Cretaceous ages, but the complement of rock types within the four mountain ranges exhibit distinct age distributions. Surficial geology consists primarily of colluvium overlain by thin soils, but bedrock outcrops are not uncommon hillslope features, and extensive alluvial deposits of Quaternary age fill the main river valley and downstream portions of some mountain valleys. Pleistocene glaciation occurred at the highest elevations in the Salt River Range, but did not extend to valley bottoms (Oriel and Platt 1980).

Characteristics of mountain streams differ with contrasts in mountain morphologies. Valleys in the Salt River Range are narrow and constrained, whereas valleys throughout other mountain ranges grade from constrained in upstream areas to unconstrained in downstream areas. Salt River Range streams have straighter channel patterns, larger substrate sizes, and steeper slopes than other streams. Hydrographs of all streams are typical for the Rocky Mountain region, with peak discharges driven by snowmelt in late May and June, followed by baseflows from late July into March.

The climate in the Salt River watershed is classified as cold with humid winters. Mean annual air temperature on the Salt River valley floor is 3.5°C, and monthly averages range from –9.1°C in January to 16.7°C in July (Owenby and Ezell 1992). Precipitation is evenly distributed throughout the year and comes as snow during cooler months and as rain during the remainder of the year. Annual precipitation averages 50 cm on the Salt River valley floor and over 100 cm at high elevations (Othberg 1984).

Land use in the Salt River watershed is indicative of geomorphic constraints and land ownership. Native grass communities in the privately owned main valley and the lower ends of alluviated mountain valleys have been converted to personal residences, pastures, and grain fields. Mountainous areas are owned and managed by the U.S. Forest Service and are used primarily for livestock grazing and recreation. Sheep grazing is common at the highest elevations, whereas cattle grazing is confined to the Gannett Hills and lower elevations in the Caribou and Webster ranges. Forestry

Fig. 2. Greyscale hillshade of a digital elevation model depicting the sample reaches and stream drainage network across the Salt River watershed. Locations marked with squares were sampled in 1996, and circles denote reaches sampled in 1997. The inset map shows the study area location on the border between Idaho and Wyoming, U.S.A.



activities have never constituted a major land use within the watershed, but unpaved roads have been constructed in most large drainages.

Data collection

Sampling was conducted at 50 reaches in 1996 and 40 reaches in 1997 on 24 second- to fourth-order streams (Fig. 2). Each reach consisted of a section of stream with consistent slope that averaged 180 m in length (range = 63–465 m). Sampling began in early July when snowmelt runoff subsided and continued until the middle of September when air temperatures cooled. A reach was sampled at every 50-m change in elevation along the length of a stream, and two reaches were sampled on the same stream near major tributary confluences: one upstream from the confluence and one downstream. Stream surveys began at the downstream end of each stream and progressed upstream except when time was limiting, in which case, one reach was sampled at the lower end of a stream (eight of 24 streams). No reaches were sampled downstream from reservoirs, major water withdrawals, or significant spring inputs, as these features would artificially alter gradients in stream habitats.

At each stream reach, wetted stream width was measured to the nearest centimetre along transects spaced at 10-m intervals and run perpendicular to the direction of stream flow, total alkalinity was measured with a water chemistry kit (test kit 24443-00, Hach, Loveland, Co.; mention of trade names does not imply endorsement by the University of Wyoming), and stream slope was measured with an Abney level as described in Isaak and Hubert (1999). Reach locations were identified using available landmarks and recorded on 1 : 24 000 scale topographic maps for later digitization.

Land surface and geomorphic variables were quantified for the watersheds upstream from sample reaches using a geographic information system (GIS). Coverages included 30-m resolution slope and elevation models, 1 : 24 000 scale stream hydrology, road, and vegetation coverages, a point coverage of reach locations, a 1 : 250 000 scale bedrock geology coverage, and a polygon coverage of U.S. Forest Service grazing allotment boundaries that contained information on the number of cattle and sheep grazed in each allotment. Completed coverages or data required to build them were acquired from the Caribou and Bridger–Teton national forests, published geologic maps (Mitchell and Bennett 1979; Oriel and Platt 1980), the Spatial Data and Visualization Center (2000) at the University of Wyoming, the Idaho Department of Water Resources (2000), and the Geospatial Data Center (2000). and the Idaho GAP Analysis Project (2000) at the University of Idaho.

The calculation of most land surface and geomorphic variables is described in detail in Isaak and Hubert (2001) and brief descriptions are provided in Table 1. Some variable constructs, however, require additional explanation. Grazing by sheep and cattle, for example, was the only land use at the study area with the potential to compact soil layers across broad areas. As such, soil compaction was estimated by dividing the total weight of domestic livestock (mean weights of 55 kg for sheep and 320 kg for cows were used) that grazed each watershed by the size of the watershed. The aquifer storage variable was impossible to quantify directly because of an absence of data on the water-holding capacities of geologic formations. Instead, we used the area of unconsolidated Quaternary alluvial deposits divided by watershed area as a surrogate measure because these deposits provide significant inputs of water to streams during baseflow periods (Smuin 1990) and are conspicuously depicted on geologic maps. Cattle density, pasture grass, pasture slope, and pasture elevation were quantified at the scale of a grazing allotment in accord with the resolution at which these data were available. Additionally, pasture grass was calculated by dividing the allotment area covered by grassland at an elevation lower than 2400 m by the area of the grazing allotment. The elevation limit was imposed because alpine meadows often exist above the treeline, but sheep were grazed in these areas rather than cattle.

In the stream slope hypothesis, valley floor slope was quantified from 1 : 24 000 scale topographic maps by digitizing the distance of the valley floor between the elevation contours that bounded a stream reach and dividing this distance by the concurrent drop in elevation. Using Grant and Swanson's (1995) definition of a valley floor as the valley width at an elevation 3 m above the streambed, valley floor width was calculated as an average from three elevation transects that were evenly spaced over the length of a reach and were interpolated from the elevation model. The complexities of the bedrock geology underlying the study area and an absence of weathering rate data made it impossible to quantify the effect that the competence of the bedrock adjacent to each sample reach would have on valley floor width. However, we were able to estimate the effect of bedrock competence on valley floor slope using a surrogate measure based on the rank-ordered age of the set of geologic formations that composed each mountain range. This measure was predicated on the belief that the oldest sedimentary rocks would have been overlain by the greatest amount of overburden and become most strongly lithified.

Data analysis

Path analysis (Wright 1934; Mitchell 1993) was used to analyze each hypothesis. To conduct each path analysis, regressions were calculated for response variables in a manner that was structured by the hypothesis. Five regressions were required for the initial path analysis of Hypothesis 1, one each for baseflow stream width, cattle density, grass abundance, tree abundance, and drainage density (Fig. 1). The direct effect (DE), or the amount of change in a response variable attributable to a predictor, was estimated as a partial regression coefficient that was standardized to facilitate comparisons of effect strengths within and among the different regressions that composed a hypothesis (unstandardized coefficients can be found in Isaak (2001)). The overall accuracy of a hypothesis was assessed by comparing the correlation matrix predicted by a hypothesis with the correlation matrix derived from the empirical data (Table 2). Predicted correlations were calculated as described in Sokal and Rohlf (1995) and plotted against observed correlations before the strength of this bivariate relationship was quantified with a simple Pearson correlation. We also used procedure CALIS (SAS Institute Inc. 1989) to calculate a χ^2 measure of model fit for each hypothesis. The χ^2 statistic was slightly biased because the CALIS procedure used aspatial parameter estimates rather than spatially explicit parameter estimates (discussed below), but it still provided a useful tool for assessing the accuracy of each hypothesis.

Assumptions regarding the distribution of residual errors derived from the regression models were checked using tests for normality and homoscedasticity, and departures from linearity were assessed using scatterplots and residual plots. If assumptions were violated, the necessary variable transformations were applied (see Table 2). Linear regression models also require that residuals be independent, but temporally correlated residuals could occur where response variables exhibited trends in time over the course of data collection efforts (e.g., baseflow stream widths decreasing during a sample season due to gradual declines in aquifer discharge). To test for time effects, sample year (interyear variation), sample date (intrayear variation), and both year and date terms were iteratively included as predictors in the appropriate regressions. Where time effects were apparent, these terms were retained to control for this nuisance variation.

Given the spatial dimension of the data set, violations of the independence assumption were also possible if the size of regression residuals were related to the distance between sampling locations. The residuals derived from least squares regressions were tested for spatial correlation using Moran's *I* (Moran 1948) and a row standardized spatial weights matrix based on the inverse of the stream distance between sample locations. Results using a spatial weights matrix based on the inverse of straight-line distance were

Table 1. Descriptive statistics for variables in a data set used to test hypotheses about factors that cause habitat gradients in small mountain streams.

Variable[a]	*N*	Mean	SD	Minimum	Maximum
CATTLE	90	6.2	10.5	0.0	37.5
PAS_SLOP	90	15.9	4.9	1.0	26.0
PAS_GRAS	90	28.4%	24.3%	1.6%	100.0%
PAS_ELE	90	2246	204	1892	2649
WAT_SIZE	90	40.9	41.4	1.6	256.1
BAS_ELE	90	2394	178	2124	2904
WAT_SLOP	90	17.0	4.2	10.6	27.1
D_DEN	90	1.33	0.18	0.80	1.70
ROADS	90	0.50	0.29	0.0	1.07
AQUIFER	90	4.11%	5.31%	0.0%	23.8%
SOIL_COM	90	3056	1831	519	8352
TREE	90	67.0%	13.4%	30.6%	91.2%
STR_WID	90	4.33	1.66	1.25	8.84
CONIFER	90	42.9%	14.4%	16.3%	78.0%
CARBNAT	90	53.1%	26.1%	0.0%	100.0%
STR_ALK	90	197	42	82	286
BEDROCK	90	2.33	1.12	1	4
VFLR_WID	90	96.8	82.6	40	603.3
R_RELIEF	90	0.36	0.15	0.09	0.81
STR_LENG	90	82.0	32.3	24.0	126.7
VFLR_SLOP	90	2.82%	1.83%	0.48%	9.60%
STR_SLOP	90	2.20%	1.67%	0.19%	10.14%

[a] CATTLE, cattle density within a grazing allotment (cows·km^{-2}); PAS_SLOP, mean grazing allotment slope (°); PAS_GRAS, proportion of a grazing allotment covered by grassland at an elevation of less than 2400 m; PAS_ELE, mean grazing allotment elevation (m); WAT_SIZE, watershed size (km^2); BAS_ELE, mean basin elevation (m); WAT_SLOP, mean watershed slope (°); D_DEN, density of streams within a watershed (km·km^{-2}); ROADS, density of roads within a watershed (km·km^{-2}); AQUIFER, proportion of a watershed with Quaternary alluvial deposits; SOIL_COM, total weight of domestic livestock grazed within a watershed divided by watershed size (kg·km^{-2}); TREE, proportion of a watershed covered by trees; STR_WID, wetted stream width at reach location (m); CONIFER, proportion of a watershed covered by conifers; CARBNAT, proportion of a watershed with carbonate bedrock; STR_ALK, total stream alkalinity at reach location (mg·L^{-1}); BEDROCK, bedrock competence (rank ordered age of geologic materials composing four mountain ranges); VFLR_WID, width of valley floor adjacent to a reach (m); R_RELIEF, elevation difference between a reach and the mouth of the Salt River (km); STR_LENG, stream distance between a reach and the mouth of the Salt River (km); VFLR_SLOP, slope of valley floor underlying a reach; STR_SLOP, water surface slope of a reach.

nearly identical and are not reported. When spatial nonindependence was detected, SpaceStat 1.90 (Anselin 1998) was used to estimate spatially explicit maximum likelihood regressions that took the spatial juxtaposition of observations into account and thereby minimized or eliminated the lack of independence among residuals. Because the spatial regressions minimized violations of the independence assumption, they should have provided the most accurate results, and inference was based on spatial regressions when these models were estimated. To facilitate model comparisons, Akaike's Information Criterion (AIC) (Akaike 1981) was calculated and R^2 values were calculated as the squared correlations between predicted and observed values.

Multicollinearity, which results from correlations among the predictor variables in a multiple regression, can lead to unreliable parameter estimates and significance tests when correlations are strong. The effects of multicollinearity were monitored using standard diagnostic tests such as variance inflation factors, condition indices, and tolerance values (SAS Institute Inc. 1989). When problems arose, the predictor variable or variables most responsible were either deleted or included with subsets of predictors in an alternative regression for which multicollinearity problems were less severe.

Results

Much of the variation in baseflow stream widths was explained by predictors included in the initial hypothesis (R^2 = 0.74) (Fig. 3, 1A). Stream widths were affected most by a large positive effect from watershed size (DE = 0.63, p < 0.01), a negative effect from soil compaction (DE = –0.29, p < 0.01), and small positive effects from aquifer storage (DE = 0.13, p = 0.05), basin elevation (DE = 0.15, p = 0.04), and tree abundance (DE = 0.18, p = 0.01). The effects of road density and watershed slope on baseflows were not estimated due to multicollinearity problems that resulted from strong correlations between watershed slope and several other predictors and between roads and basin elevation. For other response variables in this hypothesis, the abundance of grass within a pasture had much of its variation explained by moderate negative effects from pasture slope (DE = –0.39, p < 0.01) and pasture elevation (DE = –0.49, p < 0.01). In turn, grass abundance had a positive effect on cattle density (DE = 0.23, p = 0.07). Problems with multicollinearity in the regression for tree abundance led to the deletion of basin elevation as a predictor variable, but watershed slope had a positive effect on trees (DE = 0.25, p = 0.04). Finally, drainage density was unaffected by either watershed slope (DE = –0.01, p = 0.99) or basin elevation (DE = –0.15, p = 0.45).

As would be expected given the number of small and insignificant effects in the original stream width hypothesis,

Table 2. Correlations among variables in a data set used to test hypotheses about factors that cause habitat gradients in small mountain streams.

Variable	CATTLE	PAS_SLOP	PAS_GRAS^a	PAS_ELE	WAT_SIZE	BAS_ELE	WAT_SLOP	D_DEN^a	ROADS	AQUIFER	SOIL_COM
CATTLE	—										
PAS_SLOP	**–0.49**	—									
PAS_GRAS^a	**0.52**	**–0.76**	—								
PAS_ELE	**–0.42**	**0.77**	**–0.67**	—							
WAT_SIZE	0.11	**–0.32**	**0.28**	**–0.39**	—						
BAS_ELE	**–0.33**	**0.63**	**–0.48**	**0.82**	**–0.34**	—					
WAT_SLOP	**–0.39**	**0.72**	**–0.61**	**0.60**	**–0.21**	**0.77**	—				
D_DEN^a	0.05	**–0.30**	0.13	**–0.24**	**0.22**	**–0.23**	**–0.26**	—			
ROADS	**0.42**	**–0.58**	**0.51**	**–0.63**	0.11	**–0.72**	**–0.68**	0.03	—		
AQUIFER	**0.29**	**–0.37**	**0.50**	–0.20	**0.37**	–0.10	**–0.22**	0.18	0.00	—	
SOIL_COM	**0.46**	**–0.53**	**0.67**	**–0.33**	0.08	**–0.39**	**–0.69**	0.11	**0.52**	**0.23**	—
TREE	**–0.20**	0.18	**–0.31**	**–0.21**	–0.05	**–0.26**	0.11	0.03	**0.21**	**–0.39**	**–0.26**
STR_WID	–0.12	0.02	–0.17	–0.07	**0.67**	0.01	**0.22**	0.20	**–0.26**	**0.23**	**–0.39**
CONIFER^a	**–0.32**	**0.64**	**–0.27**	**0.41**	**–0.24**	**0.55**	**0.69**	**–0.43**	**–0.33**	–0.11	**–0.34**
CARBNAT	0.01	0.16	–0.08	0.09	0.01	**0.22**	**0.44**	0.03	–0.04	0.11	–0.19
STR_ALK	**0.44**	**–0.54**	**0.56**	**–0.55**	**0.23**	**–0.70**	**–0.68**	**0.23**	**0.66**	**0.23**	**0.53**
BEDROCK	–0.15	**0.51**	–0.17	**0.48**	–0.12	**0.62**	**0.69**	**–0.41**	**–0.40**	0.15	**–0.30**
VFLR_WID^a	0.09	**–0.35**	0.16	**–0.33**	**0.45**	–0.15	–0.07	0.18	0.06	**0.26**	–0.08
R_RELIEF	**–0.25**	**0.38**	**–0.28**	**0.73**	**–0.49**	**0.80**	**0.32**	–0.17	**–0.43**	–0.11	–0.04
STR_LENG	0.15	0.07	**0.26**	**0.40**	–0.10	**0.48**	0.09	**–0.21**	–0.08	**0.30**	**0.33**
VFLR_SLOP^a	**–0.28**	**0.45**	**–0.37**	**0.45**	**–0.69**	**0.46**	**0.38**	**–0.33**	**–0.32**	**–0.45**	–0.20
STR_SLOP^a	**–0.25**	**0.48**	**–0.42**	**0.46**	**–0.69**	**0.45**	**0.43**	**–0.40**	**–0.27**	**–0.41**	**–0.24**

Note: Correlation values in bold type have probability values less than 0.05 and were calculated assuming no spatial correlation. See Table 1 for definitions of variables.

[a] Transformation applied to meet regression assumptions. PAS_GRAS = $\sqrt{x}$, D_DEN = $(x^{2.63} - 1)/2.63$, CONIFER = arcsin x, VFLR_WID = $-1/x$, VFLR_SLOP = $\log_{10} x$, and STR_SLOP = $(x^{0.115} - 1)/0.115$.

the data structure that it predicted differed strongly from the structure observed in the empirical data ($\chi^2 = 170.35$, df = 35, $p < 0.01$). A scatterplot of the observed and predicted correlations also indicated that, despite a strong bivariate correlation ($r = 0.93$, $p < 0.01$), many correlation pairs plotted well away from the 1:1 line (Fig. 3, 1A).

The stream width hypothesis was revised by deleting drainage density and cattle density and using basin elevation rather than watershed slope as a predictor of tree abundance (Fig. 3, 1B). Additionally, road density was included as a predictor of stream width, and the linkage to basin elevation was dropped to avoid problems with multicollinearity. After these revisions, Hypothesis 1B was simpler than its predecessor and it explained a similar amount of variation in baseflow widths ($R^2 = 0.73$). A large decrease in the difference between the predicted and observed correlation matrices ($\chi^2 = 40.54$, df = 6, $p < 0.01$) suggested that 1B was an improvement over 1A, but both of the new paths included in this hypothesis were of negligible importance.

In a further revision of the stream width hypothesis, road density and the path from basin elevation to tree abundance were deleted and paths were reinserted from watershed slope to tree abundance and from basin elevation to stream width (Fig. 3, 1C). The overall fit of 1C was similar to 1B ($\chi^2 = 53.38$, df = 6, $p < 0.01$), but it seemed a more plausible representation of the study system because all of the predictors had statistically improbable effects.

In the alkalinity hypothesis, multicollinearity problems masked the effect of basin elevation when it was included with watershed slope in the initial regression. Therefore, the pathway from basin elevation to alkalinity was dropped and this regression was recalculated. The four remaining predictors accounted for 72% of the variation in stream alkalinity (Fig. 4, 2A), mostly due to a negative effect from watershed slope (DE = –0.44, $p < 0.01$) and a small positive effect from carbonate bedrock (DE = 0.19, $p < 0.01$). Stream alkalinity appeared to be unaffected by aquifer storage (DE = –0.03, $p = 0.67$) or conifer abundance (DE = –0.07, $p = 0.43$). The bivariate relationship between the correlations predicted by this hypothesis and the empirically derived correlations was strong ($r = 0.96$, $p < 0.01$), although the χ^2 statistic suggested some discrepancies ($\chi^2 = 12.31$, df = 2, $p < 0.01$).

The alkalinity hypothesis was revised by dropping conifer abundance, aquifer storage, and the path between watershed slope and stream alkalinity. A path was added from basin elevation to alkalinity (Fig. 4, 2B), which, in the absence of watershed slope, proved to be a strong linkage (DE = –0.77, $p < 0.01$). In Hypothesis 2C, we reinserted the path between watershed slope and alkalinity because despite problems with multicollinearity, a model containing both causal factors seemed most realistic on theoretical grounds. In the absence of aquifer storage and conifer abundance, multicollinearity simply suppressed the estimated effect sizes of basin elevation (DE = –0.25, $p < 0.01$) and watershed slope (DE = –0.29, $p < 0.01$). Hypothesis 2C accounted for more of the variation in stream alkalinity than either of its predecessors ($R^2 = 0.74$), had effects that concurred with a priori predictions, and had closely matched data structures ($r = 0.99$, $p < 0.01$). A χ^2 test of overall model fit could not be calculated because no degrees of freedom are available for this test in a fully specified path model (i.e., paths exist from every predictor to every response variable).

In the slope hypothesis, valley floor slope had a large ef-

TREE	STR_WID	CONIFER^a	CARBNAT	STR_ALK	BEDROCK	VFLR_WID^a	R_RELIEF	STR_LENG	VFLR_SLOP^a	STR_SLOP^a
—										
0.14	—									
0.25	–0.02	—								
0.24	0.10	**0.54**	—							
0.11	–0.18	**–0.38**	–0.02	—						
–0.14	0.08	**0.81**	**0.61**	**–0.36**	—					
0.03	**0.37**	**–0.24**	0.06	0.12	–0.08	—				
–0.42	**–0.33**	**0.23**	–0.05	**–0.52**	**0.32**	**–0.30**	—			
–0.55	**–0.26**	**0.32**	**0.27**	0.02	**0.57**	–0.18	**0.58**	—		
0.06	**–0.45**	**0.38**	–0.01	**–0.46**	**0.22**	**–0.49**	**0.49**	0.03	—	
0.09	**–0.45**	**0.39**	0.01	**–0.50**	**0.24**	**–0.40**	**0.45**	–0.01	**0.88**	—

fect on stream slope (DE = 0.88, $p < 0.01$) that explained most of its variation ($r^2 = 0.78$) (Fig. 5). In turn, much of the variation in valley floor slope was explained by large effects from stream length (DE = –0.69, $p < 0.01$) and relief (DE = 0.53, $p < 0.01$) and smaller effects from bedrock competence (DE = 0.45, $p < 0.01$), stream size (DE = –0.39, $p < 0.01$), and valley floor width (DE = –0.27, $p < 0.01$). Seventeen percent of the variation in valley floor width was explained by a positive effect from stream size (DE = 0.32, $p < 0.01$) and a smaller effect from relief (DE = –0.17, $p = 0.16$). In a modification of the a priori hypothesis, time since uplift was excluded from consideration because the mountain ranges at the study site were uplifted simultaneously. The χ^2 statistic suggested some difference between data structures (χ^2 = 15.02, df = 7, $p = 0.04$), but a scatterplot of the predicted and observed correlations indicated only slight discrepancies ($r = 0.99$, $p < 0.01$). In a minor revision of this hypothesis, the weak path between relief and valley floor width was deleted, but no improvements in overall model fit were observed (χ^2 = 18.62, df = 8, $p = 0.02$; $r = 0.98$, $p < 0.01$).

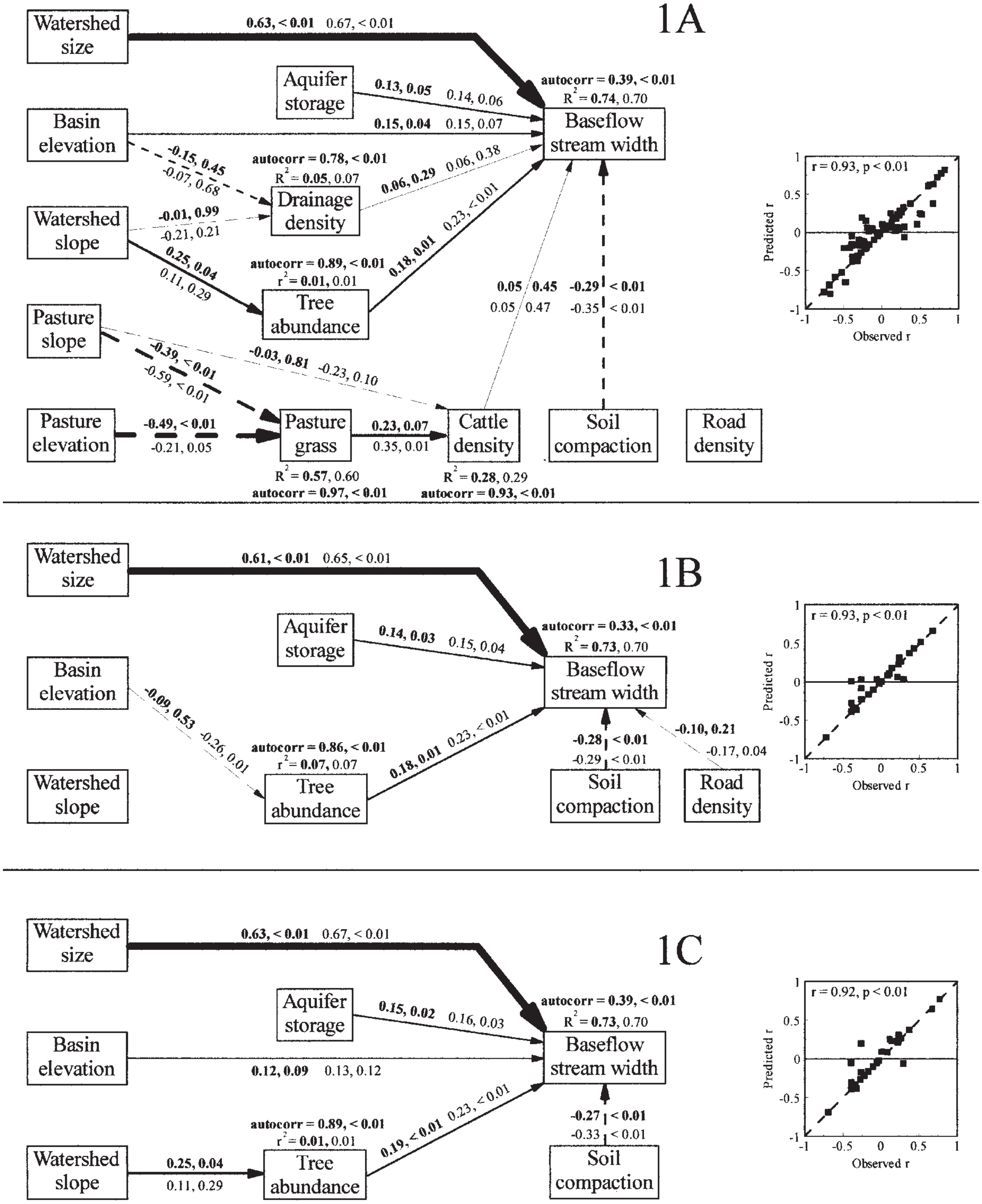
Spatially correlated residuals were common derivatives of conventional least squares regressions as indicated by the significance of Moran's I values for most of these regressions and the subsequent significance of autocorrelation coefficients in the spatial regressions (Table 3). Autocorrelation coefficients indicated that the strength of autocorrelation present in the regression data sets ranged widely, from nonexistent for stream slope and valley floor slope regressions, to moderately strong for four regressions of stream width and valley floor width, to very strong in the remaining nine regressions. In all cases, autocorrelation parameters were positive, indicating that proximal stream reaches contained similar information. The spatial regressions tended to decrease the magnitude of parameter estimates (8 increased, 27 decreased, and 3 remained constant), and the amount of change in parameter estimates was positively related to the strength of autocorrelation ($r = 0.66$, $p < 0.01$). AIC values always suggested that the spatial regressions were an improvement over the least squares regressions, and differences between the parameter estimates were sometimes large enough to qualitatively change inferences.

Discussion

The final versions of the hypotheses provide systemic views of watershed function by depicting interactions that occur between geomorphology, land surface features, and stream attributes. The hypotheses also suggest that most of the variation in baseflow stream widths, stream alkalinity, and stream slope can be explained by characteristics of the surrounding watershed. This result indicates a tight linkage between mountain streams and the terrestrial setting and allows insight into the origin of gradients in small mountain streams. Of the two classes of watershed descriptors, geomorphic features had the strongest effects on stream attributes, and gradients appear to arise primarily from the unidirectional changes in geomorphic features that occur over the lengths of streams. Land surface features were of secondary importance and, because they change less predictably relative to the stream, appear to modify the rate at which stream gradients change.

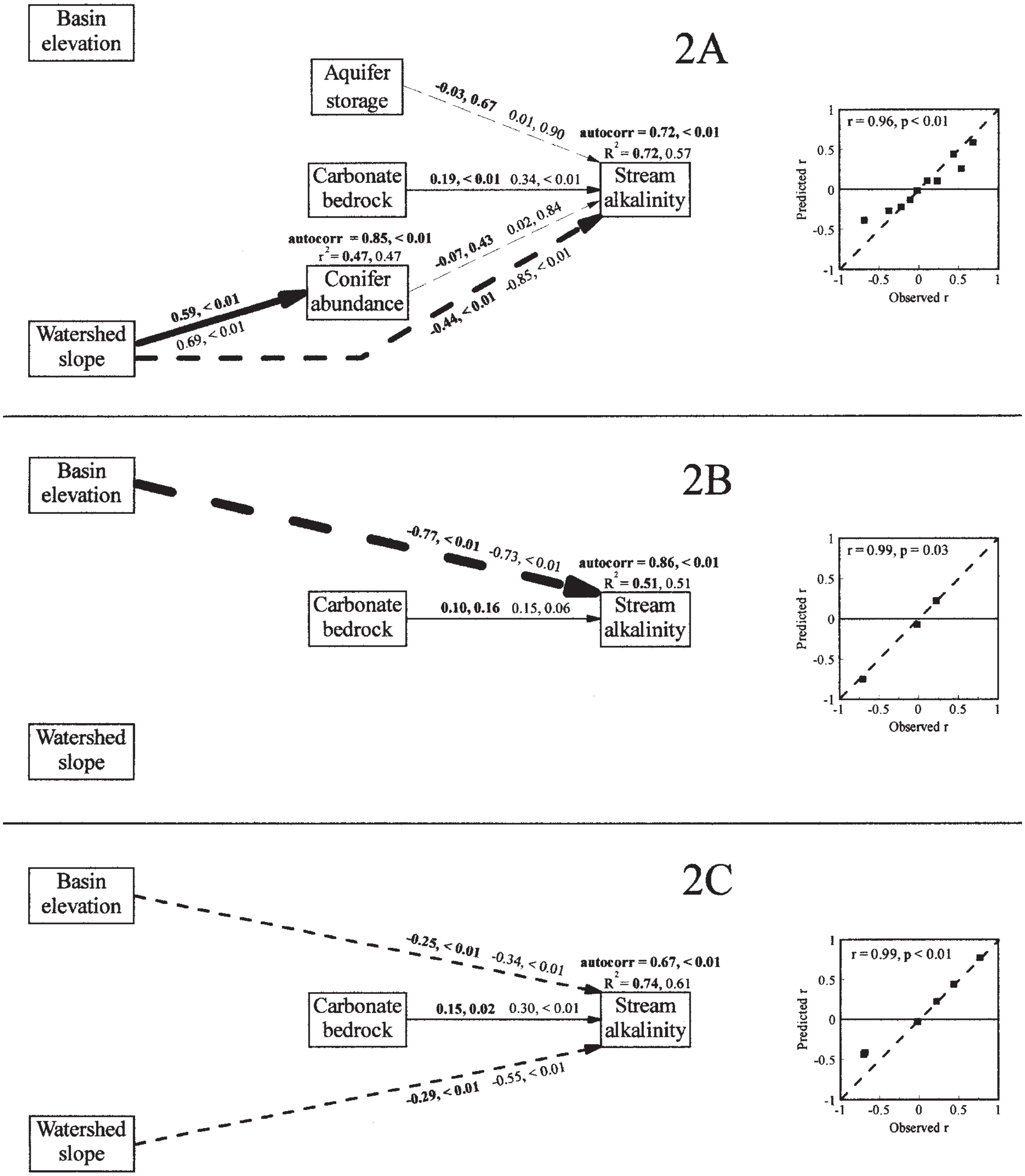
This study also provides inference regarding the relative importance of the specific causal factors affecting each stream attribute. In the stream width hypothesis, watershed size had a positive effect that was greater in magnitude than all other factors. Tree abundance, basin elevation, and aquifer storage had smaller positive effects. A positive effect from trees was unexpected given the frequency with which

Fig. 3. Path diagrams for three versions of a hypothesis about factors that affect baseflow stream widths of small mountain streams. The width of an arrow is proportional to the strength of an effect that a predictor variable has on a response variable. Numbers next to arrows are standardized partial regression coefficients and probability values derived from spatially explicit regressions (bold type) and conventional least squares regressions. Numbers next to response variables are the autocorrelation coefficients for the spatial regressions and the variation explained by the spatial regressions (bold type) and least squares regressions.



negative effects have been observed (Bosch and Hewlett 1982), but the convoluted and sometimes karstic geology at the study area may have interacted in an unknown manner with tree abundances to produce the observed pattern. Regardless, the positive effect from trees seems anomalous and suggests that the hydrology of the study area was somewhat unique. The effect of aquifer storage on stream widths was positive, as predicted, but it is not known how accurately

Fig. 4. Path diagrams for three versions of a hypothesis about factors that affect total stream alkalinity of small mountain streams. The width of an arrow is proportional to the strength of an effect that a predictor variable has on a response variable. Numbers next to arrows are standardized partial regression coefficients and probability values derived from spatially explicit regressions (bold type) and conventional least squares regressions. Numbers next to response variables are the autocorrelation coefficients for the spatial regressions and the variation explained by the spatial regressions (bold type) and least squares regressions.



this effect was estimated given that the area of unconsolidated alluvial deposits was used as a surrogate measure. Although alluvium apparently does make contributions to baseflows, a measure that accounted for hydrologic contributions from all geologic formations would have been desirable.

Several factors had no effect on stream width. The absence of a drainage density effect was not expected given the large negative effects previously observed (e.g., Carlston 1963). However, most earlier studies were conducted in the relatively old and mesic mountainous landscapes of eastern North America, where drainage densities are two to seven times greater and probably serve a more important hydrologic role. Road densities were also low relative to other studies (e.g., King and Tennyson 1984; Jones and Grant

Fig. 5. Path diagram for a hypothesis about factors that affect reach-scale stream slope of small mountain streams. The width of an arrow is proportional to the strength of an effect that a predictor variable has on a response variable. Numbers next to arrows are standardized partial regression coefficients and probability values derived from spatially explicit regressions (bold type) and conventional least squares regressions. Numbers next to response variables are the autocorrelation coefficients for the spatial regressions and the variation explained by the spatial regressions (bold type) and least squares regressions.

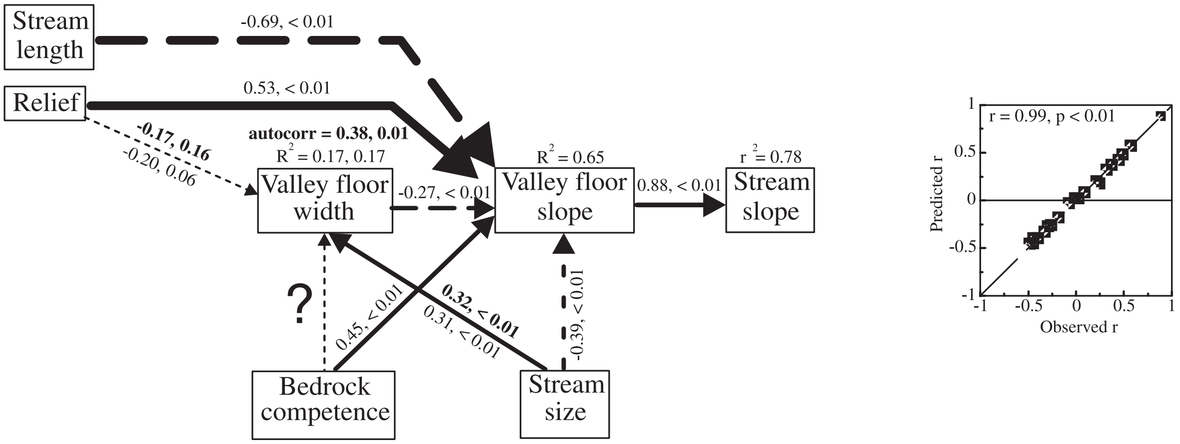


Table 3. Summary of spatial autocorrelation measures and model fits for conventional least squares regressions and spatially explicit regressions.

		Least square regressions				Spatially explicit regressions			
Hypothesis	Response variable	Moran's I	Probability value	R^2	AIC[a]	Autocorrelation coefficient	Probability value	R^2	AIC[a]
1A	STR_WID	0.12	<0.01	0.70	255	0.39	<0.01	0.74	248
	CATTLE	0.42	<0.01	0.29	652	0.93	<0.01	0.28	562
	PAS_GRAS	0.56	<0.01	0.60	–91.4	0.97	<0.01	0.57	–187
	TREE	0.42	<0.01	0.01	–105	0.89	<0.01	0.01	–155
	D_DEN	0.30	<0.01	0.07	20.5	0.78	<0.01	0.05	–6.74
1B	STR_WID	0.08	0.03	0.70	251	0.33	<0.01	0.73	247
	TREE	0.38	<0.01	0.07	–110	0.86	<0.01	0.07	–151
1C	STR_WID	0.12	<0.01	0.70	253	0.39	<0.01	0.73	246
2A	STR_ALK	0.26	<0.01	0.57	863	0.72	<0.01	0.72	836
	CONIFER	0.44	<0.01	0.47	–124	0.85	<0.01	0.47	–171
2B	STR_ALK	0.44	<0.01	0.51	869	0.86	<0.01	0.51	821
2C	STR_ALK	0.31	<0.01	0.61	851	0.67	<0.01	0.74	827
3	STR_SLOP	0.03	0.48	0.78	–13.2				
	VFLR_SLOP	–0.01	0.53	0.65	–58.7				
	VFLR_WID	0.14	0.01	0.17	–687	0.38	0.01	0.17	–692

Note: Spatially explicit regressions were estimated when residuals derived from least squares regressions were not independent. See Table 1 for definitions of variables.

[a] Smaller values indicate better model fits.

1996), which probably explains the negligible effect observed in this study. There was no empirical support for the effect of cattle density on stream width due to changes in channel structure, despite compelling evidence to the contrary from field exclosure experiments (Belsky et al. 1999). This inconsistency, however, may stem from differences in the way studies were conducted. In exclosure studies, the effect of cattle is examined over a limited area and in isolation from all other factors. Conversely, our study attempted to include all of the factors affecting stream width across a broad area and thereby assessed the effect of cattle grazing relative to other factors. When the results of both study types are viewed together, indications are that despite local impacts of cattle grazing, these effects do not translate to landscape-level effects on stream width. Regardless, the combined effects of cattle and sheep on soil compaction do suggest that livestock have some role in determining broad-scale patterns in baseflow widths. This role may be subtler than the direct channel modifications that cattle are typically credited with because it occurs in the uplands and arises from a spatially distributed mechanism, but the effect of soil compaction was second in magnitude only to watershed size. As the effect of soil compaction was also negative, grazing by domestic animals appears to decrease the volume of stream habitat during a period that is critical for stream biota.

Results from the stream alkalinity hypothesis suggest that carbonate bedrock had a positive effect on alkalinities, but this water chemistry attribute was affected most by basin elevation and watershed slope. Unfortunately, collinearity problems stemming from the strong correlation between these predictors precluded an accurate assessment of individual effects. Data sets collected in other areas may provide better insight, but the morphology of mountainous watersheds ensures that basin elevation and watershed slope will often be strongly correlated. Stream alkalinity was unaffected by aquifer storage, a result that may be inconclusive given the way aquifer storage was quantified and that most bicarbonate production occurs in the mineral soil layer of hillslopes (Drever 1997). Conifer abundance also had no effect on stream alkalinity, but this relationship is expected to vary among watersheds due to differences in geologic materials.

The causal structure predicted to occur among factors associated with stream slope was largely substantiated by this study. Stream slope had most of its variation explained by the slope of the underlying valley floor, and all of the variables predicted to affect valley floor slope did so. The largest effects on valley floor slope were attributable to stream length and relief, which supports predictions made by earlier researchers (Leopold and Maddock 1953; Cherkauer 1972). Bedrock competence also had a sizeable effect on valley floor slope, despite the crude manner in which competence was quantified. It is unknown how a more accurate measure might affect this parameter estimate, but better resolution would probably provide additional explanatory power.

Spatial autocorrelation

Spatially correlated residuals occurred in most of the least squares regressions that were calculated. Although our sampling design may have contributed to the near ubiquity of autocorrelation within the data, there is no reason to think that other sampling designs could have circumvented this problem and still provided a sufficient sample size and representative correlational structure. In fact, given the tendency for many variables to exhibit gradients or patchiness, violation of the independence assumption is probably a feature common to many linear models based on data generated from a GIS or collected in the field. For the present, however, the frequency with which this assumption is violated will remain unknown until testing for spatially correlated residuals becomes common. Such tests were not easily conducted until recently, but GIS and spatial statistical software (summarized at <www.ai-geostats.org>) now make the detection and incorporation of spatial patterns a routine matter, and these tools should become integral to the development of linear models based on data with a spatial component.

Within the context of this study, spatial autocorrelation was an extraneous consideration that had to be addressed before accurate inference could be drawn. Some anecdotal insights are possible, however, given the frequency with which autocorrelation occurred. Autocorrelation was always positive (i.e., similarity among sites was negatively related to distance), which makes intuitive sense given the variables being modeled, and we suspect that when present, positive autocorrelation will be the norm. Although standard error estimates were not presented, spatial regressions usually provided smaller standard errors than least squares regressions (see Isaak 2001). This result probably occurred because the inclusion of space as a predictor reduced residual variation and facilitated the estimation of more precise parameter estimates for other predictors. Lastly, the amount of change in a parameter estimate between least squares regressions and spatial regressions was directly related to the strength of autocorrelation, indicating that estimation errors were greater when autocorrelation was stronger.

Utility of path analysis

This study was greatly facilitated by path analysis, which despite being closely allied with regression modeling offers several advantages that allow researchers to draw novel inferences. First, many study systems are inherently complex and characterized by chains of causality and interdependence (Christensen et al. 1996). As such, factors that seem to have little direct relevance to a response variable may exert control over that variable through an intermediary. Because conventional regression models have no provisions for dealing with this situation, the result is that such insights are either missed entirely or are erroneously portrayed via a direct effect of a predictor on a response variable. Path analysis, by contrast, has an inherent capacity to deal with this complexity through the interlinkage of regression models. Second, path diagrams present the results of a path analysis in a data-rich, but intuitive format that makes it easy to understand the evolution of a hypothesis, the types of effects that predictors have on response variables, and the relative importance of each predictor. Third, advances in covariance structure analysis (Bollen and Long 1993) have made it possible to compare a predicted data structure with an empirical data structure, thereby providing an assessment of the overall accuracy of a hypothesis and facilitating comparisons among competing hypotheses. Lastly, because path analysis is a causal modeling technique, it requires that a very detailed and very explicit hypothesis be developed before the analysis is conducted. Researchers are thus forced to develop a deep level of familiarity with a study system and to include a plausible mechanism with each pathway included in a hypothesis. This step makes all aspects of the thinking associated with a hypothesis clear and discourages blind data snooping and the weak post hoc explanations that often result.

Despite the opportunities that path analysis offers for a more rigorous application of the scientific method, and that it has become a staple technique in the social science and evolutionary genetics fields (see introductory sections in Klem (1995) and Petraitis et al. (1996)), path analysis has rarely been used within the aquatic sciences. As aquatic systems are not inherently simpler than study systems in other fields, there seems to be no logical reason for this situation. The only limitation of path analysis relative to conventional regression modeling is that a body of knowledge sufficient to develop a comprehensive a priori hypothesis must exist. Whether this requirement is met can only be judged by researchers with expertise in a particular field, but path analysis would seem to be a technique that interested researchers could easily apply given excellent introductory articles (Mitchell 1993; Klem 1995) and widespread familiarity with regression modeling.

Conclusion

We developed and tested hypotheses about how the features of mountain watersheds interact to cause gradients in three stream attributes. By placing broadscale factors with the potential to affect stream attributes into probabilistic models, an assessment of the relative importance of each factor across a montane landscape was derived. In all cases, geomorphic features appear to be the primary determinants of habitat gradients, and land surface features were of secondary importance. This work adds a spatial component to the River Continuum Concept that had been lacking and highlights the importance of linkages between terrestrial and aquatic realms. Although our hypotheses would seem to have some generality given the mechanisms involved, these models have only been tested with data from one study area, and caution must be exercised in their interpretation until replicate tests are conducted. Of particular interest would be tests in other Rocky Mountain landscapes where underlying geologies are relatively simple or in other physiographic regions where the ranges of predictor variables might differ markedly. Such tests would yield insights into the mechanisms involved in the production of stream gradients and the spatial domains over which these relationships hold.

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