

Geomorphic predictors of riparian vegetation in small mountain watersheds

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Abstract

Aims

Hydrogeomorphic processes operating at watershed, process zone and site scales influence the distribution of riparian vegetation. However, most studies examining the relationships between hydrogeomorphic processes and riparian vegetation are conducted at site scales. We quantified the relative importance of watershed, process zone and site geomorphic characteristics for predicting riparian plant community types and plant species abundances in four small mountain watersheds in central Nevada, USA.

Methods

We mapped riparian vegetation types and identified process zones (based on dominant geomorphic process and valley fill material) within the watersheds. We sampled sites in each combination of vegetation type and process zone ($n = 184$ sites) and collected data on watershed scale factors, valley and stream geomorphic characteristics and on plant cover of each geomorphic surface. Plant community types were defined by cluster and indicator species analyses of plant cover data, and related to geomorphic variables using ordination analysis (nonmetric multidimensional scaling). Linear mixed effects models were used to predict abundances of indicator species.

Important Findings

Variables describing position in the watershed (elevation, contributing area) that are related to gradients of temperature, moisture and stream discharge were of primary importance in predicting plant community types. Variables describing local geomorphic setting (valley width, stream gradient, channel sediments, geomorphic surface height) were of secondary importance, but accurately described the geomorphic setting of indicator species. The process zone classification did not include position in the watershed or channel characteristics and only predicted plant community types with unique geomorphic settings. In small mountain watersheds, predicting riparian vegetation distribution requires explicit consideration of scale and geomorphic context within and among watersheds in addition to site variables.

Keywords: Great Basin, multiscale, plant community analysis, process zone, riparian

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INTRODUCTION

Riparian ecosystems are a high priority for conservation and restoration efforts worldwide (Wohl *et al.* 2005). Although they occupy a small proportion of the landscape, riparian areas provide numerous ecosystem functions, including regulation of light and temperature regimes, habitat for aquatic and terrestrial biota and corridors for animal and plant dispersal (Naiman *et al.* 2005). Widespread degradation of rivers

and riparian communities has occurred due to anthropogenic activities such as water diversion, groundwater extraction, flood control, land use change and livestock grazing (Richardson *et al.* 2007). Effective management and restoration of degraded riparian areas requires understanding the relationships between hydrogeomorphic processes and riparian vegetation at appropriate scales (Wohl *et al.* 2005).

Hydrologic and geomorphic processes, such as flooding, erosion and sediment movement, structure and maintain the

physical template for riparian ecosystems (Gregory *et al.* 1991; Hupp and Osterkamp 1996; Steiger *et al.* 2005). Riparian plant species vary in their life history and physiological characteristics and species distributions are influenced by flood disturbance regimes (Naiman *et al.* 2005; Swanson *et al.* 1998), substrate characteristics and spatial and temporal variability in water availability (Castelli *et al.* 2000; Loheide and Gorelick 2007; Stromberg *et al.* 1996). Thus, hydrogeomorphic characteristics that can be related to particular physiological or life history traits are likely to be strong predictors of riparian species distributions.

Hydrogeomorphic processes operating at watershed, process zone and site or stream reach scales influence the extent and composition of riparian vegetation. Most studies that have developed predictors of the distribution of riparian vegetation have been conducted at site scales (Merritt and Cooper 2000; Stromberg *et al.* 1996). Studies conducted at watershed scales indicate that watershed characteristics exert direct effects on riparian vegetation (Chambers *et al.* 2004; Engelhardt *et al.* 2012; Sarr and Hibbs 2007) as well as indirect effects through constraints on valley and channel characteristics and hydrology (Baker 1989; Harris 1988; Shaw and Cooper 2008). Differences in watershed characteristics influence the hydrograph and flood disturbance regime via collection area for storm events, geologic factors that affect infiltration and erosion rates, overall gradient and drainage network development (Howard 1990; Kelson and Wells 1989; Patton 1988).

An understanding of the relative importance of watershed characteristics, process zones and site-specific characteristics on riparian vegetation can be used to prioritize management activities and select appropriate restoration treatments (Montgomery 1999). Quantifying longitudinal environmental variables that change along the length of the valley bottom within watersheds, including position in the watershed (e.g. elevation of a site, contributing area above a site) and site-specific characteristics, such as bedrock type, valley width, stream gradient and channel dimensions, provides a measure of among-site variation (Bendix 1994a; Montgomery 1999). Quantifying transverse variables that change perpendicular to the channel, including height above and distance from the stream channel, substrate texture and inundation frequency, provides an indication of within-site variation. Both sets of variables influence riparian species distribution and abundance via temperature and moisture regimes, potential discharge, disturbance intensity and substrate characteristics (Bendix 1994a; Friedman *et al.* 2006; Hupp and Osterkamp 1996; Yang *et al.* 2011).

Designating process zones within watersheds has the potential to improve predictive capacity. A process zone is a section of river defined by characteristic behaviors (e.g. erosion, deposition, transport), uniform structure in terms of geometry (channel shape and size), channel planform (shape when viewed from above) and assemblage of geomorphic units (pool, riffle, run) (Brierley and Fryirs 2000; Montgomery 1999). Because the magnitude and timing of geomorphic processes vary among process zones, process zones divide stream networks into distinct sections where

ecological communities are structured by unique hydrogeomorphic characteristics and disturbance regimes (Brierley and Fryirs 2005; Fryirs and Brierley 2001; Montgomery and Buffington 1997; Montgomery 1999).

In this study, our objective was to evaluate the relative importance of watershed, process zone and site geomorphic characteristics in predicting riparian plant community types and plant species abundances (i.e. floristic composition) in four small mountain watersheds in the semi-arid Great Basin. We investigated the importance of hydrogeomorphic influences on riparian vegetation across multiple levels of an ecological hierarchy (Poole 2002), where vegetation structure is the emergent outcome of physical and biological processes at the finest level (site), is constrained by physical characteristics at the coarsest level (watershed), and may be most predictable according to physical features at the focal or intermediate level (process zone).

METHODS

Study area

Study sites are located within four upland watersheds in the Toiyabe mountain range of central Nevada: Birch, Cottonwood, Kingston and San Juan Canyons (Fig. 1). The watersheds are relatively small (mean = 4475 ha, range = 2200–7292 ha), have high relief (mean = 1332 m, range = 1078–1574 m), and are characterized by narrow valleys and streams with generally high gradient, coarse, gravel-bed channels. Mean annual precipitation ranges from 20 cm at the base of the watersheds to 60 cm at the highest elevations and arrives primarily as winter snow with peak runoff in late May. Watersheds were selected to capture the geological complexity of the region.

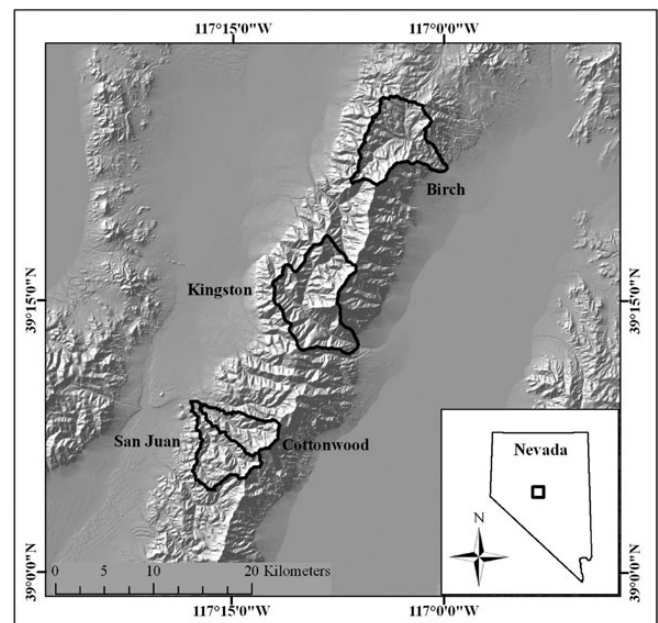


Figure 1: the locations of the four study watersheds in the Toiyabe Mountains of central Nevada, USA.

Birch Canyon is characterized by siliciclastic and intrusive igneous rocks (granite, quartz monzonite) and has discontinuous and localized incision. Cottonwood Canyon is primarily quartzite, and Kingston Canyon is primarily siliciclastic and carbonate (limestone). Both Cottonwood and Kingston are moderately incised with side valley fans that prograde onto the main channel. San Juan Canyon is characterized by volcanic rocks (welded and rhyolitic tuff) and deep incision (Germanoski and Miller 2004).

Woody vegetation along perennial stream reaches consists of narrow bands (10–20 m) of *Betula occidentalis*, *Salix exigua*, *S. lutea*, *Rosa woodsii*, *Populus angustifolia* and *P. tremuloides*. Meadows are characterized by wetland obligate and facultative graminoids and forbs (e.g. *Carex nebrascensis*, *Deschampsia cespitosa*, *Juncus arcticus* and *Symphyotrichum spathulatum*). *Artemisia tridentata* ssp. *tridentata* and *vaseyana* occur in dry meadows and along ephemeral stream reaches.

DATA COLLECTION

Geomorphic variables were quantified at three levels of investigation: watershed, process zone and site (Table 1). The four watersheds were delineated as previously described. Process zones were mapped along the main channel of each watershed and digitized in a Geographical Information System (GIS). Identification of four process zone types was based on predominant geomorphic process (erosion, deposition or transport) and valley fill material (Table 2; Miller et al. 2012). Process zones were delineated on 1:15 000–1:19 000 scale aerial photographs. Vegetation was field mapped on 1:3000 scale aerial photographs according to ecological types derived from Weixelman et al. (1996): aspen, birch, cottonwood, willow, sedge meadow, mesic meadow, sagebrush meadow and upland. A stratified design was used to locate three to five representative sampling sites in all combinations of process zone and vegetation type within each of the four watersheds ($n = 184$); not all combinations were present within each watershed. Photo-interpreted vegetation types were used only as strata for the sampling design, to ensure representative sampling. Plant community types used in the data analysis were derived from field sampling of plant species abundances (see below).

Geomorphology

Site-level geomorphic variables were measured along transects that were oriented perpendicular to the channel. Transects were of variable length so as to include all geomorphic surfaces from the channel thalweg to the valley floor, where geomorphic surfaces are defined as areal units of consistent elevation formed by a common fluvial process. Cross-sectional profiles were measured along transects with a leveled meter tape and stadia rod. Data were collected on riparian and valley widths, stream gradient, number of geomorphic surfaces and knickpoints. Particle size distribution and channel bed lithology were determined from a modified Wolman pebble count

Table 1: geomorphic variables measured at three levels of analysis: watershed, process zone and site

Variable	Description
<i>Watershed Level</i>	
Measured using GIS	
WSHD	Watershed (categorical)
AREA	Contributing area above the site (m ²)
ELEV	Elevation of the site (m)
S_LNGTH	Stream length of main channel above the site (km)
Measured in the field	
%SILT	% silt in the channel
%CARBS	% carbonate in the channel
%INTRS	% intrusive in the channel
%METASED	% metasedimentary in the channel
%QTZT	% quartzite in the channel
%SLCLT	% siliciclastic in the channel
%VOLCS	% volcanic in the channel
%SNDSTN	% sandstone in the channel
<i>Process zone level</i>	
PZ	Process zone type (categorical)
<i>Site level</i>	
Measured for each geomorphic transect	
W_WDTH	Water width (cm)
THAL	Thalweg depth (cm)
WD_RATIO	Width:depth ratio
I_WDTH	Width of channel incision (cm)
I_DPTH	Depth of channel incision (cm)
I_RATIO	Incised width:depth ratio
%FINES	% fine fragments in bank soil (<2 mm diameter)
D50	Channel bed D50 (mm)
D84	Channel bed D84 (mm)
S_GRAD	Stream gradient (%)
V_SLOPE	Valley slope parallel to the channel (%)
RIP_WDTH	riparian zone width (m)
VAL_WDTH	Valley floor width (m)
#SURFS	# of geomorphic surfaces
#KNICK	# of knickpoints within 20 m upstream and downstream of the site
Measured for each geomorphic surface	
SURF#	Surface position: 1st, 2nd, 3rd, etc
HEIGHT	Surface vertical height above channel (cm)
DIST	Surface horizontal distance from channel (cm)
WIDTH	Surface width perpendicular to channel (cm)

Watershed-level variables include descriptors of position within the watershed. The process zone variable identifies stream reaches with similar geomorphic process and valley fill material. Site-level variables describe quantitative characteristics of the local geomorphic setting, measured either for whole transects or for individual plots on geomorphic surfaces of differing elevation within transects.

Table 2: characteristics of main channel process zones occurring in the study watersheds

Process zone	Frequency	Valley fill composition	Dominant processes
Aggrading alluvial (AA)	Rare	Alluvium	Deposition, channel avulsion
Bedrock valley (BV)	Uncommon	Bedrock	Sediment transport, minimal deposition
Incised alluvial (IA)	Very common	Alluvium	Erosion, sediment transport, sediment storage
Incised colluvial (IC)	Common	Colluvium, fan material	Erosion, sediment generation, sediment transport

(Wolman 1954). Soil texture of the active channel bank was quantified by a bulked soil sample (~1 L soil combined from two holes dug on each side of the stream). Elevation, valley slope, contributing area and main channel length above each site were calculated from 10 m DEMs. The stream was categorized as perennial or ephemeral at each site, based on presence of visible flow above the stream bed throughout the year. Bedrock geology of each site was obtained from the USGS Geologic Map of Nevada (1:250 000; Crafford 2007).

Descriptions and units of geomorphic variables are in Table 1. Active channel width, depth and width:depth ratio, incised channel width, depth and width:depth ratio, as well as geomorphic surface width, height above channel and distance from channel, were derived from the cross-sectional profile. Incised channel depth was the vertical height from valley floor surface to channel thalweg, and incised channel width was the corresponding horizontal distance between valley floor surfaces. Channel bed D_{50} , D_{84} and percent composition of seven rock types were derived from Wolman pebble count data. Percentage of fine fragments (<2 mm diameter) in bank soil was determined by air drying the soil samples and passing them through a 2-mm sieve.

Vegetation

All vascular plants were identified to species and aerial cover was recorded in plots 1 m upstream and 1 m downstream of the geomorphic transect on all surfaces and at water's edge. Many surfaces were small, thus percentage aerial cover was recorded in a 0.25 m² plot for herbaceous species and a 1-m² plot placed at the same location for shrub species (Castelli *et al.* 2000; Weixelman *et al.* 1996). Percent cover was estimated using 12 categories: <1, 1–5, 6–15, 16–25, 26–35, 36–45, 46–55, 56–65, 66–75, 76–85, 86–95 and 96–100. Ground cover was recorded as total percentage of the 0.25 m² plot using 10 categories: vegetation, bare ground, gravel, rock, litter, woody debris, live roots and stems, moss, water and other.

At sites with trees (*B. occidentalis* and *Populus* spp.), a 2-m belt transect was located parallel to the meter tape delineating the geomorphic transect, and aerial cover of tree species was ocularly estimated by surface using the same categories. The arithmetic mean of cover categories collected at upstream and downstream plots on each geomorphic surface were averaged for analysis of herbaceous, shrub and groundcover data. Species nomenclature follows the PLANTS database (USDA Natural Resources Conservation Service, April 2009).

Statistical analysis

We used species aerial cover values to define plant community types for each geomorphic surface, and to conduct ordination analysis of plant species distribution along underlying ecological and geomorphic gradients. Ordination analysis used non-metric multidimensional scaling (NMS) with the Bray–Curtis distance measure. Comparative studies with simulated data sets have shown NMS with the Bray–Curtis distance measure to be a robust and effective ordination method compared to principal components analysis and approaches based on correspondence analysis, particularly where ecological gradients are long and species response to gradients fails to consistently fit either a linear or symmetric unimodal form (Minchin 1987). Important environmental gradients were identified by interpreting the ordination axes and examining correlation coefficients with ordination site scores using Pearson's *r*.

To define plant community types, we conducted a hierarchical, agglomerative cluster analysis using the Bray–Curtis distance measure and flexible beta linkage method with $\beta = -0.25$. Rare species that occurred at less than 1% (4 or fewer) of sites were excluded after exploring the interpretability of cluster and ordination analysis with differing levels of rare species retention. The full data set resulted in an extremely sparse matrix with 95.4% empty cells and did not converge to a successful NMS solution. Omitting rare species was appropriate for our purpose of quantifying dominant patterns of variation in vegetation composition because indicators of uncommon habitats were not of major interest. All species cover values were arc-sine square root transformed to stabilize variance and reduce skew (Sokal and Rohlf 2012). The transformation resulted in a more interpretable cluster analysis with less chaining ($0.64 < 0.98$) and a stronger NMS analysis with lower stress ($0.21 < 0.24$). Indicator species analysis was used to determine an appropriate number of groups from the cluster analysis and to characterize the identified groups (Dufrene and Legendre 1997). The statistical significance of indicator values was evaluated by Monte Carlo tests with 1000 randomizations. We chose an optimal number of plant community types by comparing the sum of significant indicator values for multiple cluster levels and sums of positive and negative differences in all species indicator values between successive levels (Dufrene and Legendre 1997). Results of cluster and ordination analyses were used to identify the important geomorphic variables for structuring riparian vegetation.

A Kruskal–Wallis ranked analysis of variance was used to test for differences in geomorphic variables (Table 1) by process zone types (Table 2) with a Bonferroni correction for multiple tests. Multiple comparisons by the Bonferroni method were used to test for differences between specific combinations of process zones. To determine if the IA and IC process zones occurred at different elevations, elevation and process zone were sampled from the DEM and digitized maps with regular points spaced 10 m apart along the valley bottom, and compared with a Welch's *t*-test. Bivariate correlations between transect geomorphic variables were examined with Pearson correlation coefficients (*r*).

To determine riparian composition within each process zone, process zones and field-mapped riparian vegetation were sampled from the digitized maps for the same set of points used to compare process zone elevations. The vegetation composition of each process zone was assessed with relative frequency graphs for all four watersheds combined and separately for each watershed.

Linear mixed effects (LME) models predicting abundances of key riparian species were developed to test for improvement in predictive power when larger scale categorical effects (watershed, process zone, bedrock type) or quantitative longitudinal and transverse geomorphic characteristics (e.g. elevation, valley width, surface height) were included. LME models incorporated random effects of higher order variables that did not vary among plots within transects or among transects within watersheds, thus mitigating biases associated with predictors sampled at different spatial scales. Quantitative geomorphic characteristics were treated as fixed effects, and categorical variables were compared as fixed versus random effects. Transect was included as a random effect to account for correlation in cover among multiple plots within the same transect.

For each plant community type identified in the cluster analysis, the species with the highest indicator value was selected for LME modeling. Only five of seven plant community types had a strong indicator species with sufficient number of occurrences in sampled plots to be used in the analysis. Prior to analysis, species cover values were arc-sine square root transformed and highly skewed geomorphic variables were log transformed. LME models were developed by systematically including geomorphic variables that were most related to each plant community type in the NMS analysis. Ten to fifteen models, as well as the 'intercept-only' model, were developed for each species. Bivariate correlations between transect geomorphic variables were examined prior to developing LME models, and no models included any pair of geomorphic variables with a correlation coefficient ≥ 0.40 .

LME models were compared utilizing the Akaike's Information Criterion (AIC) statistic to calculate AIC differences (Δ_i) and Akaike weights (w_i) that indicate the relative likelihood of a given model (Burnham and Anderson 2002). Competitive LME models ($\Delta_i < 2$) with different fixed effects were also compared with likelihood ratio tests based on

maximum likelihood fits. Models with more parameters were considered a significant improvement at $P \leq 0.05$.

Cluster and ordination analyses were conducted using PC-ORD 5.10 (version 5.10, MjM Software, Gleneden Beach, OR, USA). All other statistical analyses were completed with S-PLUS 8.1 (version 8.1, TIBCO Software Inc., Palo Alto, CA, USA).

RESULTS

Riparian plant community types

The sampled geomorphic surfaces supported a total of 169 vascular plant species. Species were 27% graminoids, 58% forbs, 12% shrubs (includes *Salix* spp.) and 3% trees. Seven plant community types were identified from the cluster analysis of species covers on geomorphic surfaces: aspen, birch, willow, sedge meadow, mesic meadow, basin big sagebrush and upland (Fig. 2).

Two tree-dominated types occurred on ~35% of the geomorphic surfaces. The birch type occurred on 59 surfaces and was defined solely by presence of *B. occidentalis*. Birch sites had a sparse understory with high percentages of litter and woody debris groundcover, explaining the lack of strong association with additional plant species. The aspen type occurred on 102 surfaces and was indicated by presence of *P. tremuloides*, with *Aquilegia formosa* and *Symphoricarpos oreophilus* as common understory species. Shrub-dominated types occurred on about 50% of geomorphic surfaces. The willow type occurred on 98 surfaces and was defined by *S. lutea* and *S. exigua* with *P. pratensis* and *R. woodsii* as secondary components. The basin big sagebrush type occurred on 42 surfaces and was indicated by *A. tridentata tridentata* and *Leymus triticoides*. The upland type occurred on 90 surfaces and was indicated by *A. tridentata vaseyana*, *Chrysothamnus viscidiflorus* and *Bromus tectorum*. The two plant community types dominated by herbaceous species were less common and occurred on 15% of surfaces. The mesic meadow type was more common, occurred on 60 surfaces, and was indicated by *J. arcticus*, *C. nebrascensis* and *S. spathulatum*. The sedge meadow type occurred on 10 surfaces, and was indicated by *C. utriculata*, *Senecio hydrophilus* and *Phalaris arundinacea*.

Geomorphic predictors of riparian vegetation

Variables indicating position within the watershed were the best predictors of riparian plant community types, followed by variables representing local or site geomorphic characteristics (Table 1). The NMS ordination of species composition resulted in a three-dimensional solution with final stress = 0.2113 and cumulative $R^2 = 61.2\%$. Most plant community types separated clearly along axis 3 (Fig. 3a) which was correlated with contributing area, stream length above sites, water width and percent carbonates in channels (Table 3). These variables primarily describe a gradient of site position related to discharge and flow dimensions. Aspen, mesic meadow and upland types occurred at sites with smaller contributing areas, and birch

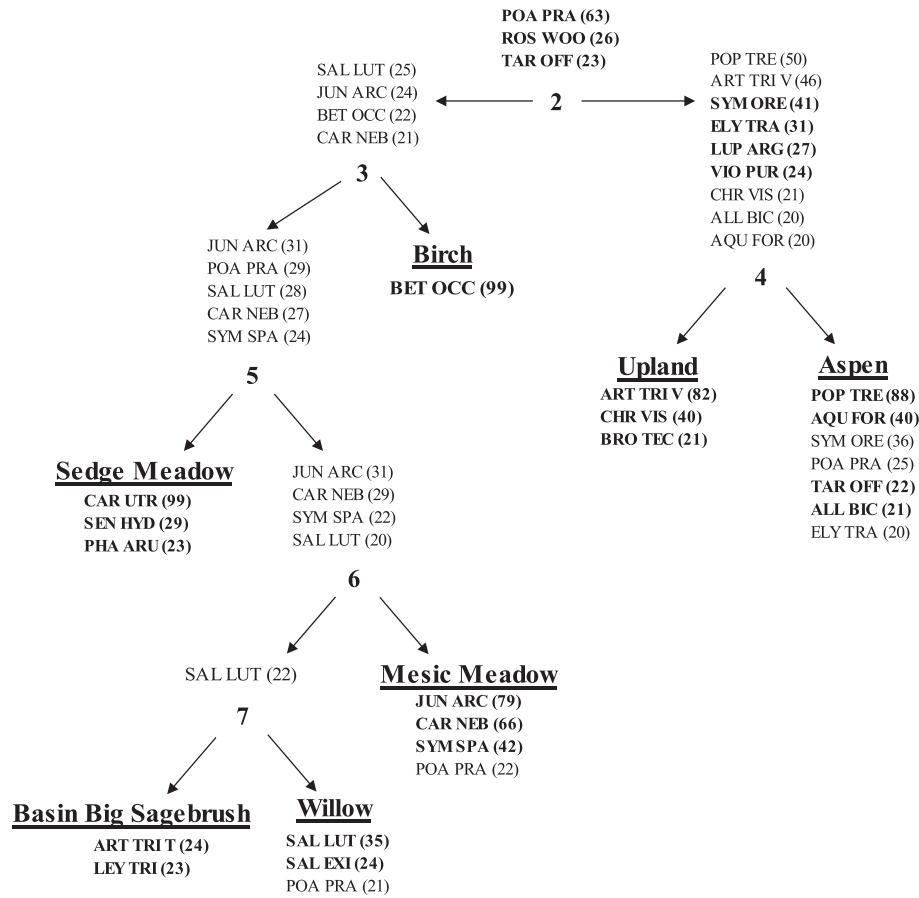


Figure 2: riparian plant community types and associated species obtained from a hierarchical, agglomerative cluster analysis and indicator species analysis of plant species percent cover at 461 geomorphic surfaces. Indicator values are in parentheses and all species with an indicator value $\geq 20\%$ are listed for each type where they occur. Maximum indicator values are in bold. ALL BIC = *Allium bisceptrum*, AQU FOR = *Aquilegia formosa*, ART TRI T = *Artemisia tridentata* ssp. *tridentata*, ART TRI V = *Artemisia tridentata* ssp. *vaseyana*, BET OCC = *Betula occidentalis*, BRO TEC = *Bromus tectorum*, CAR NEB = *Carex nebrascensis*, CAR UTR = *Carex utriculata*, CHR VIS = *Chrysothamnus viscidiflorus*, ELY TRA = *Elymus trachycaulus*, JUN ARC = *Juncus arcticus*, LEY TRI = *Leymus triticoides*, LUP ARG = *Lupinus argenteus*, PHA ARU = *Phalaris arundinacea*, POA PRA = *Poa pratensis*, POP TRE = *Populus tremuloides*, ROS WOO = *Rosa woodsii*, SAL EXI = *Salix exigua*, SAL LUT = *Salix lutea*, SEN HYD = *Senecio hydrophilus*, SYM ORE = *Symphoricarpos oreophilus*, SYM SPA = *Symphytotrichum spathulatum*, TAR OFF = *Taraxacum officinale*, VIO PUR = *Viola purpurea*.

and sedge meadow types occurred at sites with larger contributing areas. The basin big sagebrush and willow types were more variable indicating less sensitivity to contributing area.

Site elevation was most correlated with axis 2 (Table 3), which describes a gradient of site position within a watershed that is more closely related to temperature and precipitation. The aspen type occurred at the highest elevations, mesic meadow and willow types occurred at mid to high elevations, and birch, basin big sagebrush, sedge meadow and upland types occurred at low to middle elevations (Fig. 3b). Axis 1, the gradient most related to local geomorphic characteristics (e.g. valley width, stream gradient, D_{84} channel particle size, and surface height), explained the smallest proportion of variance in species composition (Table 3). Mesic meadow, sedge meadow and willow types were found on lower surfaces in wider, lower gradient valleys with smaller channel particle sizes (Fig. 3b). Aspen, birch and upland types occurred in narrower, steeper valleys, where channel particle sizes were

larger and height above the channel was moderate to high. The basin big sagebrush type was found in a greater range of settings, from wider, gentler sites to narrow, steeper sites.

Process zones were relatively poor predictors of riparian plant community types at watershed scales. The main channel in all four watersheds was classified predominantly into two process zone types. Incised Alluvial (IA) comprised 56% of the overall total channel length and Incised Colluvial (IC) comprised 41%. The two other types, Aggrading Alluvial (AA) and Bedrock Valley (BV) were rare, 2 and 1%, respectively, and did not occur in Cottonwood and San Juan Canyons.

Process zones differed significantly in valley and channel geomorphic characteristics (Table 4). The AA zone, where the dominant geomorphic process was sediment aggradation, was least incised and had the fewest geomorphic surfaces, smallest channel particle sizes, gentlest valley slopes and stream gradients and widest valleys. The incised zones, IA and IC, differed in that IC had significantly steeper gradients and narrower

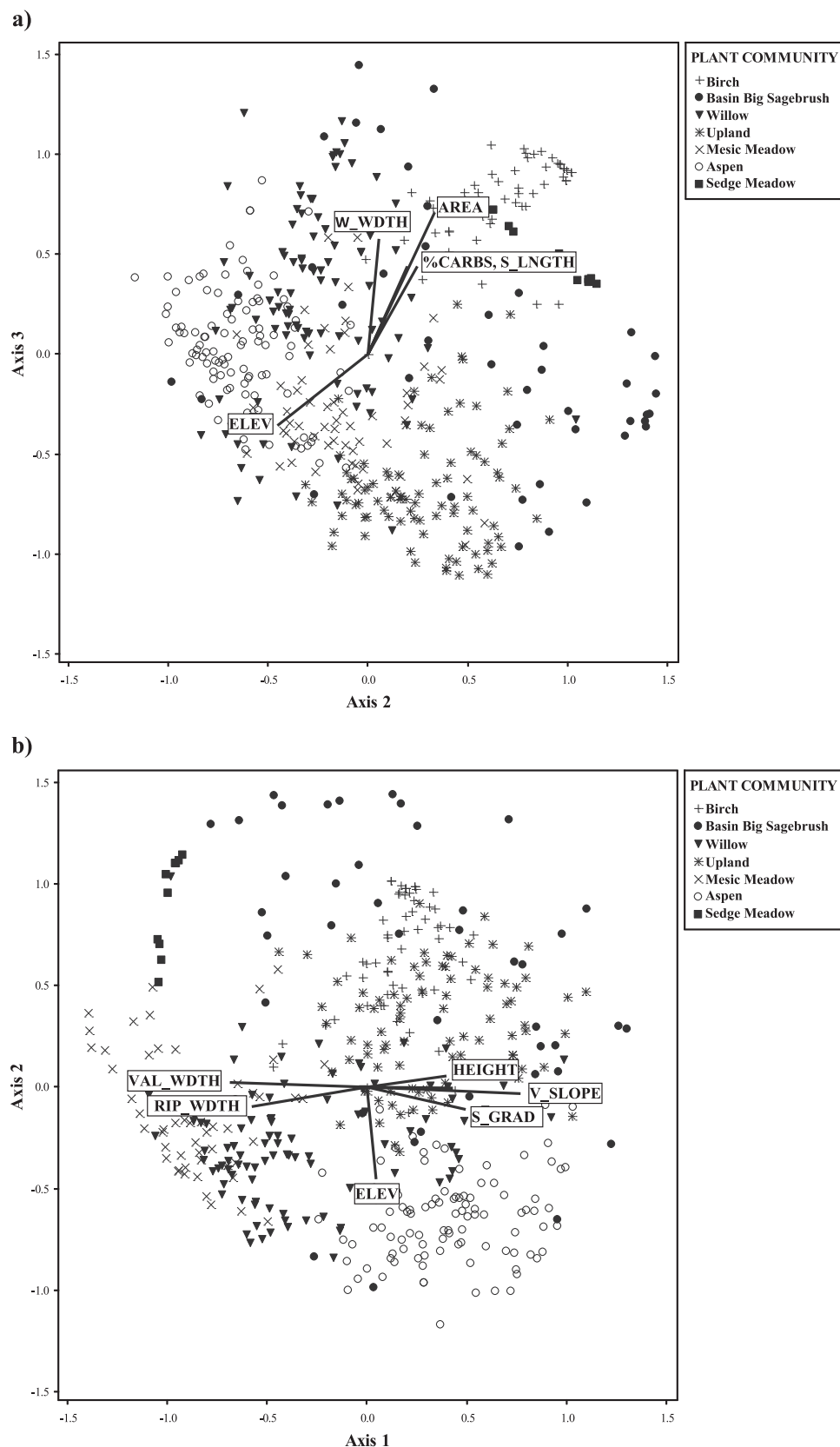


Figure 3 : NMS ordination of plant species composition on 461 geomorphic surfaces with surfaces coded according to plant community type. Joint plots show the direction and strength of relationships between geomorphic characteristics and ordination axes (a) 3 versus 2 and (b) 2 versus 1.

Table 3: proportion of variance represented by each NMS axis (R^2) and Pearson correlations (r) of geomorphic characteristics with each NMS axis for the 461 sampled geomorphic surfaces

Variable	Axis		
	2 ($R^2 = 0.23$)	3 ($R^2 = 0.22$)	1 ($R^2 = 0.17$)
AREA	0.360	0.520	-0.080
ELEV	-0.416	-0.372	0.133
S_LNGTH	0.276	0.412	-0.019
W_WDTH	0.142	0.468	0.063
THAL	0.309	0.254	-0.145
WD_RATIO	-0.240	0.100	0.202
I_WDTH	0.058	0.022	0.178
I_DPTH	-0.013	-0.018	0.235
I_RATIO	0.070	0.129	-0.071
%FINES	0.164	0.123	-0.233
D50	-0.128	0.124	0.366
D84	-0.049	0.195	0.406
%CARBS	0.310	0.410	0.058
%INTRS	0.075	0.190	0.134
%METASED	0.146	-0.013	-0.077
%QTZT	-0.295	-0.202	-0.021
%SLCLT	-0.042	-0.005	0.129
%SNDSTN	-0.039	0.003	-0.091
%VOLCS	-0.153	-0.062	0.189
%SILT	0.200	0.126	-0.291
WOODY	-0.017	0.361	0.211
S_GRAD	-0.204	0.177	0.434
V_SLOPE	-0.105	0.184	0.542
RIP_WDTH	-0.193	0.166	-0.471
VAL_WDTH	0.089	-0.252	-0.512
#KNICK	-0.122	0.102	0.267
WIDTH	-0.146	0.106	-0.140
DIST	0.162	-0.204	0.031
HEIGHT	0.141	-0.243	0.389

valleys and was more deeply incised than IA. However, channel material size and width:depth ratio did not differ between IC and IA. Also, approximately normal distributions and nearly identical elevation ranges of the two process zones indicated that they occurred in nearly equivalent proportions along elevational gradients within the watersheds. Geomorphic characteristics of BV were similar to those of IC, but BV sites tended to have the largest particle sizes and steep gradients, and occurred in the narrowest valleys.

The two most common process zones, IA and IC, had similar vegetation composition, although IC had slightly more woody vegetation (aspen and willow types) and less herbaceous-dominated vegetation (sedge meadow, mesic meadow and narrow mesic) than IA (Fig. 4). The AA zone, the lowest-gradient and widest zone, supported primarily willow with some sedge meadow vegetation. The BV zone, the steepest

and narrowest zone, supported primarily birch vegetation with some willow.

Geomorphic predictors of indicator species

Mixed effects models were developed for percent cover of *P. tremuloides*, *B. occidentalis*, *Artemisia tridentata vaseyana*, *S. lutea* and *J. arcticus*. These five species have different life histories and physiological traits, were strong indicators of plant community types (Fig. 2), and occurred at enough sites to permit predictive modeling. These species responded differently to quantitative variables describing position in the watershed (elevation, contributing area), site-level characteristics indicating valley and channel geomorphology (e.g. riparian width, stream gradient, width:depth ratio) and process zone. The best model of *P. tremuloides* cover included watershed, site elevation and measures of stream characteristics (width:depth ratio, stream gradient, thalweg depth) (Table 5). *Populus tremuloides* cover increased with greater channel width:depth ratios, stream gradients, thalweg depths and at higher elevations, particularly in Cottonwood and San Juan Canyons. In contrast, the best model of *B. occidentalis* cover included contributing area above the site, process zone, and bedrock as fixed effects (Table 5). *Betula occidentalis* cover increased with greater contributing area, was highest in the BV process zone, and higher in IC and IA process zones than the AA process zone (where the species did not occur). Average *B. occidentalis* cover was higher at sites on intrusive and quartzite bedrock, and lower at sites on carbonate and volcanic bedrock relative to sites on alluvium.

Artemisia tridentata vaseyana cover was best predicted by a model that included watershed and process zone as fixed effects in addition to surface height, riparian width and contributing area above the site (Table 5). *A. tridentata v.* cover was greater on higher surfaces in narrower riparian corridors and at sites with less contributing area; *A. tridentata v.* cover was lowest in the IC process zone. The best model of *S. lutea* cover included surface height, percent volcanic rock in the channel, incised channel width:depth ratio and bedrock type (Table 5). *Salix lutea* cover was highest on lower surfaces, at sites with larger incised width:depth ratios and at sites on volcanic bedrock but with less volcanic rock in the channel. Finally, *J. arcticus* cover was best modeled as a function of riparian width, water width and process zone (Table 5). *J. arcticus* cover was greater at sites with wider riparian corridors and narrower stream channels. Mean *J. arcticus* cover was greatest in the IA process zone, intermediate in IC and BV process zones, and lowest in the AA process zone.

DISCUSSION

Riparian vegetation is most commonly investigated at the scale of individual streams or stream reaches, but relatively few studies have considered the context of riparian vegetation within higher order ecohydrological systems including stream networks or topographically complex watersheds

Table 4 : Kruskal–Wallis χ^2 and P values and means $\pm$ standard errors for geomorphic variables by process zone

Variable	Kruskal–Wallis χ^2	P	Process zone (n)			
			AA (13)	IA (104)	IC (64)	BV (3)
Water width (cm)	5.76	0.12	223.77 $\pm$ 22.88	171.73 $\pm$ 7.83	171.33 $\pm$ 11.17	197.33 $\pm$ 21.73
Thalweg depth (cm)	12.63	0.006	33.77 $\pm$ 6.62	15.53 $\pm$ 0.85	14.77 $\pm$ 1.11	23 $\pm$ 3.51
Width:depth ratio	4.26	0.23	12.08 $\pm$ 3.28	13.87 $\pm$ 0.8	14.31 $\pm$ 1.19	9.19 $\pm$ 2.01
Incised width (cm)	40.5	<0.001	283.08 $\pm$ 21.89 a	666.55 $\pm$ 36.45 b	773.36 $\pm$ 48.84 b	569.33 $\pm$ 85.66 ab
Incised depth (cm)	26.71	<0.001	47.02 $\pm$ 7.92 a	162.94 $\pm$ 7.85 b	198.71 $\pm$ 9.6 c	187.1 $\pm$ 26.8 bc
Incised width:depth ratio	11.33	0.01	7.92 $\pm$ 1.51	4.39 $\pm$ 0.22	4.09 $\pm$ 0.25	3.04 $\pm$ 0.09
# of terraces	15.01	0.002	1.69 $\pm$ 0.13 a	2.69 $\pm$ 0.08 b	2.66 $\pm$ 0.14 b	3 $\pm$ 0.58 b
Bank fines (%)	2.64	0.45	61.65 $\pm$ 7.52	52.7 $\pm$ 14.59	51.11 $\pm$ 1.84	53.60 $\pm$ 9.35
Channel bed D_{50} (mm)	22.33	<0.001	14.2 $\pm$ 4.22 a	37.87 $\pm$ 1.97 b	44.68 $\pm$ 3.55 b	54.68 $\pm$ 18.23 b
Channel bed D_{84} (mm)	32.51	<0.001	21.11 $\pm$ 7.58 a	74.15 $\pm$ 4.86 b	98.13 $\pm$ 8.62 c	124.64 $\pm$ 30.79 bc
% Silt	23.17	<0.001	41.85 $\pm$ 13.36 a	1.77 $\pm$ 0.37 b	1.34 $\pm$ 0.38 b	2 $\pm$ 1.15 b
% Carbonate	5.61	0.13	0 $\pm$ 0	1.87 $\pm$ 0.79	4.87 $\pm$ 1.63	0 $\pm$ 0
% Intrusive	13.8	0.003	3.54 $\pm$ 3.22	2.56 $\pm$ 0.71	3.42 $\pm$ 1.32	62.67 $\pm$ 6.57
% Metasedimentary	1.96	0.58	36.56 $\pm$ 11.23	20.99 $\pm$ 3.02	20.99 $\pm$ 3.86	1.33 $\pm$ 0.67
% Quartzite	13.39	0.004	20.5 $\pm$ 6.98	51.79 $\pm$ 3.06	42.94 $\pm$ 3.69	34.67 $\pm$ 5.7
% Sandstone	11.25	0.011	0.48 $\pm$ 0.34	1.9 $\pm$ 0.3	0.89 $\pm$ 0.25	0 $\pm$ 0
% Siliciclastic	3.95	0.27	0 $\pm$ 0	0.38 $\pm$ 0.15	0.22 $\pm$ 0.12	0.67 $\pm$ 0.67
% Volcanic	15.49	0.001	0.46 $\pm$ 0.33 a	20.51 $\pm$ 2.8 ab	26.68 $\pm$ 3.72 b	0.67 $\pm$ 0.67 ab
Stream gradient (%)	36.68	<0.001	1.68 $\pm$ 0.39 a	2.84 $\pm$ 0.21 ab	4.77 $\pm$ 0.37 c	6.28 $\pm$ 0.32 bc
Valley slope (%)	49.13	<0.001	0.34 $\pm$ 0.12 a	1.79 $\pm$ 0.12 b	2.83 $\pm$ 0.16 cd	4.39 $\pm$ 0.29 d
Riparian width (m)	36.32	<0.001	84.23 $\pm$ 9.06 a	38.41 $\pm$ 3.48 b	17.02 $\pm$ 0.92 c	11 $\pm$ 1 bc
Valley width (m)	72.69	<0.001	88.15 $\pm$ 8.31 a	71.12 $\pm$ 4 a	32.92 $\pm$ 1.69 b	20 $\pm$ 2.52 b
# of knickpoints	17.36	<0.001	0.08 $\pm$ 0.08 a	0.38 $\pm$ 0.08 a	0.53 $\pm$ 0.12 a	3.67 $\pm$ 0.67 b

χ^2 values in bold are significant at $P \leq 0.002$ based on the Bonferroni correction for multiple tests. Significant differences among process zones are indicated by different letters using the Bonferroni multiple comparisons method.

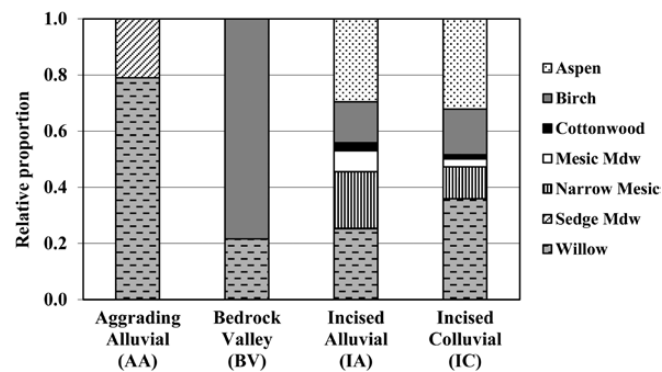


Figure 4: relative proportion of seven riparian plant community types occurring in four process zones, based on process zone and plant community type sampled by points regularly spaced every 10 m along the valley bottom (all watersheds combined).

(Douda 2010; Dunn *et al.* 2011; Engelhardt *et al.* 2012). Our study demonstrates the importance of the higher order watershed context for explaining site-specific plant community composition on small geomorphic surfaces along mountain streams. In contrast to our initial prediction, we found that both riparian plant community types and species were better

correlated with watershed-level variables than either process zone or site-level variables. Watershed characteristics such as morphometry (size and shape), bedrock composition and effective precipitation determine not only channel and valley characteristics but also hydrologic regimes and thus can have strong top-down influences on patterns of riparian vegetation (Baker 1989; Engelhardt *et al.* 2012; Shaw and Cooper 2008). Previous research in the study watersheds that used remote sensing showed that watershed geomorphology was strongly related to the extent and composition of the riparian vegetation (Engelhardt *et al.* 2012). In this study, watershed-level variables including bedrock type and position in the watershed (elevation, contributing area) were generally the best predictors not only of riparian plant community types but also of individual species.

Position in the watershed may be an especially important predictor of hydrogeomorphic processes and riparian vegetation in mountainous regions as elevation and contributing area change rapidly due to high relief and drainage density (Baker 1989; Miller *et al.* 2012). Increasing elevation is associated with cooler temperatures and lower potential evapotranspiration (Friedman *et al.* 2006), less flood disturbance (Duhovnikoff *et al.* 2005) and decreased response potential to changes in

Table 5: AIC analysis of linear mixed effects models evaluating the influence of geomorphic characteristics on the percent cover of five riparian plant species

Species	Fixed effects	Random effects	<i>k</i>	<i>w_i</i>	LogLik
<i>Populus tremuloides</i>	WD_RATIO (+), S_GRAD (+), THAL (+), ELEV (+), WSHD	Transect	10	0.28	185.45
<i>Betula occidentalis</i>	AREA (+), BDROCK, PZ	Transect	12	0.55	287.10
<i>Artemisia tridentata vaseyana</i>	HEIGHT (+), R_WDTH (-), AREA (-), WSHD, PZ	Transect	12	0.55	446.59
<i>Salix lutea</i>	HEIGHT (-), %VOLCS (-), I_RATIO (+), BDROCK	Transect	11	0.39	226.43
<i>Juncus arcticus</i>	R_WDTH (+), W_WDTH (-), PZ	Transect	8	0.34	837.92

The best models ($\Delta_i = 0$) for each species are presented. Transect was always included as a random effect. Direction of effect is indicated in parentheses next to each continuous variable. *k* = number of model parameters, *w_i* = AIC weight of model *i*, and LogLik = log-likelihood value (fit by maximum likelihood). WSHD = watershed, PZ = process zone, BDROCK = bedrock.

sediment supply or discharge (Montgomery and Buffington 1997). As expected, we found that elevation and contributing area were correlated with channel dimensions such that channel width and channel depth both increased in the downstream direction. Stream power, the energy available to transport sediments, generally increases in proportion to contributing area and channel size (Bull 1979). Elevation and unit stream power were important predictors of among-site variability in riparian vegetation in arid watersheds of southern California (Bendix 1994b, 1999). In our study aspen and upland plant community types were located at higher elevations with smaller contributing areas, birch and sedge meadows were at lower elevations with larger contributing areas, and mesic meadow and willow were intermediate. Site geomorphic characteristics, specifically valley width, stream gradient, channel sediments and height above the stream channel, were of secondary importance to plant species composition in the analyses. However, these variables did describe the local geomorphic setting of the different plant community types. Similar to previous research, meadow and willow types occurred in larger valleys on lower surfaces of streams with low gradients and fine particle sizes, while aspen, birch and upland types were located in narrow, steep valleys on higher surfaces of streams with larger particle sizes (Chambers *et al.* 2004).

Process zones have been suggested to be strong predictors of riparian vegetation in watersheds that exhibit distinct erosion, transport and deposition zones along elevation gradients in mountainous regions (Montgomery 1999; Montgomery and Buffington 1997). In our study, geomorphic characteristics of the rarer process zones, AA and BV, differed quantitatively from the other process zones for key attributes, including incision depth, stream gradient, valley width, and channel bed particle sizes. These differences resulted in distinctive geomorphic conditions and vegetation composition. However, colluvial reaches indicative of erosion were not limited to the upper elevations of the watershed and the two dominant process zones, IC and IA, failed to adequately differentiate plant community types. Process zones were distinguished solely on the valley fill material and the dominant geomorphic processes (erosion, deposition, transport), and did not incorporate either position in the watershed or channel characteristics. As a result both colluvial and alluvial

reaches were distributed throughout the watersheds at similar elevations in association with large side-valley fans that prograded into the main channel. Thus, disturbance processes operating in the IA and IC zones as delineated probably were not fundamentally different. Position in the watershed has been shown to be an important predictor of riparian vegetation in other mountainous watersheds (Baker 1989, 1994a; Harris 1988). Thus, to consistently predict vegetation types in small mountain watersheds, process zone classifications need to account for larger scale factors and incorporate position in the watershed, specifically contributing area and elevation.

Mixed effects models were most successful in explaining the abundance of indicator plant species when they included a combination of watershed- and site-level variables. Riparian plant species distributions depend on life history and physiological traits and are influenced by both watershed and site variables including temperature and effective precipitation, disturbance regimes, substrate characteristics and water availability (Naiman *et al.* 2005). Watershed characteristics and process zones had a greater influence on woody riparian species than on herbaceous species such as *J. arcticus*. *Populus tremuloides* is a facultative riparian species associated with cooler temperatures and extended water availability from snowmelt at higher elevations in arid watersheds (Weixelman *et al.* 1996). This widespread species occurred in watersheds with perennial streams at higher elevations that had steep gradients but fairly wide channels and thus higher water availability. *S. lutea* is a disturbance-tolerant species that had the highest cover on sites with volcanic bedrock and incised streams. Watersheds underlain by volcanic rocks have short lag times and high peak flows (Amacher *et al.* 2004; Germanoski and Miller 2004) which are hydrograph properties that are conducive to frequent flooding (Chambers *et al.* 2004; Engelhardt *et al.* 2012). Larger contributing area and BVs were associated with higher abundance of *B. occidentalis* which occurs on sites with high susceptibility to flood events (Friedman *et al.* 2006; Weixelman *et al.* 1996), erosion and rock slides (Harris 1988). *Artemisia tridentata v.* is a widespread upland species that occurs in riparian corridors at moderate to high elevations in geomorphic settings with relatively deep water tables (Chambers *et al.* 2004). In this study, it was most abundant on higher terraces in watersheds with narrow,

ephemeral streams at higher elevation. The only herbaceous species, *J. articus*, is a riparian obligate characteristic of mesic meadow ecosystems that was associated with the alluvial process zone and wider riparian corridors and stream widths.

Riparian plant species composition and the abundance of indicator species were strongly related to the geomorphic context including watershed and bedrock type, and to geomorphic characteristics including contributing area, elevation, valley confinement and stream gradient. Variables describing position in the watershed (e.g. elevation, contributing area) that are related to gradients of temperature, moisture and stream discharge were of primary importance in predicting overall plant species composition. Variables describing the local geomorphic setting (e.g. valley width, stream gradient, channel sediments, geomorphic surface height) were of secondary importance. A process zone classification that was based only on valley width and dominant geomorphic processes did not consistently predict plant community type. We expect these findings to apply generally to riparian vegetation in small mountain watersheds globally, and that the relative importance of watershed context or position in a hydrologic network for predicting riparian plant community structure should increase for watersheds with greater topographic diversity and steeper ecohydrological gradients.

These results indicate that a hierarchical approach which includes watershed-level morphometric and geological characteristics, hydrogeomorphic position within watersheds and reach scale geomorphic characteristics can improve our capacity to explain and predict patterns of riparian vegetation in small mountain watersheds. Our findings inform riparian ecosystem management by highlighting the importance of top-down hierarchical constraints on local vegetation distribution and providing boundary conditions for potential vegetation responses to site-specific ecological restoration.

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REFERENCES

Amacher MC, Kotuby-Amacher J, Grossl PR (2004) Effects of natural and anthropogenic disturbances on water quality. In Chambers JC, Miller J (eds). *Great Basin Riparian Ecosystems - Ecology, Management and Restoration*. Washington, DC: Island Press, 162–95.

- Baker WL (1989) Macro- and micro-scale influences on riparian vegetation in western Colorado. *Ann Assoc Am Geogr* **79**:65–78.
- Bendix J (1994a) Scale, direction, and pattern in riparian vegetation-environment relationships. *Ann Assoc Am Geogr* **84**:652–65.
- Bendix J (1994b) Among-site variation in riparian vegetation of the southern California Transverse Ranges. *Am Midl Nat* **132**:136–51.
- Bendix J (1999) Stream power influence on southern California riparian vegetation. *J Veg Sci* **10**:234–52.
- Brierley GJ, Fryirs K (2000) River styles, a geomorphic approach to catchment characterization: implications for river rehabilitation in Bega Catchment, New South Wales, Australia. *Environ Manag* **25**:661–79.
- Brierley GJ, Fryirs K (2005) *Geomorphology and River Management: Applications of the Rivers Styles Framework*. Malden, MA: Blackwell Publishing.
- Bull WB (1979) Threshold of critical power in streams. *Geol Soc Am Bull* **90**:453–64.
- Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference – A Practical Information Theoretic Approach*, 2nd edn. New York, NY: Springer.
- Castelli RM, Chambers JC, Tausch RJ (2000) Soil-plant relations along a soil-water gradient in Great Basin riparian meadows. *Wetlands* **20**:251–66.
- Chambers JC, Tausch RJ, Korfmacher JL. et al. (2004) Effects of geomorphic processes and hydrologic regimes on riparian vegetation. In Chambers JC, Miller J. (eds). *Great Basin Riparian Ecosystems - Ecology, Management and Restoration*. Washington, DC: Island Press, 196–231.
- Crafford AEJ (2007) *Geologic Map of Nevada*. USGS Survey Data Series 249, 46, 1 plate.
- Douda J (2010) The role of landscape configuration in plant composition of floodplain forests across different physiographic areas. *J Veg Sci* **21**:1110–24.
- Douhovnikoff V, McBride JR, Dodd RS (2005) *Salix exigua* clonal growth and population dynamics in relation to disturbance regime variation. *Ecology* **86**:446–52.
- Dufrene M, Legendre P (1997) Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecol Monogr* **67**:345–66.
- Dunn W, Milne B, Mantilla R. et al. (2011) Scaling relations between riparian vegetation and stream order in the Whitewater River network, Kansas, USA. *Landscape Ecol* **26**:983–97.
- Engelhardt BM, Weisberg PJ, Chambers JC (2012) Influences of watershed geomorphology on extent and composition of riparian vegetation. *J Veg Sci* **23**:127–39.
- Friedman JM, Auble GT, Andrews ED. et al. (2006) Transverse and longitudinal variation in woody riparian vegetation along a montane river. *Western North Am Nat* **66**:78–91.
- Fryirs K, Brierley GJ (2001) Variability in sediment delivery and storage along river courses in Bega Catchment, NSW, Australia: implications for geomorphic river recovery. *Geomorphology* **38**:237–65.
- Germanoski D, Miller JR (2004) Basin Sensitivity to channel incision in response to natural and anthropogenic disturbance. In Chambers JC, Miller J. (eds). *Great Basin Riparian Ecosystems - Ecology, Management and Restoration*. Washington, DC: Island Press, 88–123.
- Gregory SV, Swanson FJ, McKee WA. et al. (1991) An ecosystem perspective of riparian zones. *Bioscience* **41**:540–51.
- Harris RR (1988) Associations between stream valley geomorphology and riparian vegetation as a basis for landscape

- analysis in Eastern Sierra Nevada, California USA. *Environ Manag* **12**:219–28.
- Howard AD (1990) Role of hypsometry and planform in basin hydrologic response. *Hydrol Process* **4**:373–85.
- Hupp CR, Osterkamp WR (1996) Riparian vegetation and fluvial geomorphic processes. *Geomorphology* **14**:277–95.
- Kelson KI, Wells SG (1989) Geologic influences on fluvial hydrology and bedload transport in small mountainous watersheds, northern New Mexico, USA. *Earth Surf Proc Land* **14**:671–90.
- Loheide SP, Gorelick SM (2007) Riparian hydroecology: A coupled model of the observed interactions between groundwater flow and meadow vegetation patterning. *Water Resour Res* **43**:W07414. doi:10.1029/2006WR005233
- Merritt DM, Cooper DJ (2000) Riparian vegetation and channel change in response to river regulation: A comparative study of regulated and unregulated streams in the Green River Basin, USA. *Regul Rivers Res Manag* **16**:543–564.
- Miller JR, Lord ML, Villarroel LF *et al.* (2012) Structural organization of process zones in upland watersheds of central Nevada and its influence on basin connectivity, dynamics, and wet meadow complexes. *Geomorphology* **139–140**:384–402.
- Minchin PR (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* **69**: 89–107.
- Montgomery DR (1999) Process domains and the river continuum. *J Am Water Resour Assoc* **35**:397–410.
- Montgomery DR, Buffington JM (1997) Channel-reach morphology in mountain drainage basins. *Geol Soc Am Bull* **109**:596–611.
- Naiman RJ, Décamps H, McClain ME (2005) *Riparia – Ecology, Conservation, and Management of Streamside Communities*. Burlington, MA: Elsevier Academic Press.
- Patton PC (1988) *Drainage basin morphometry and floods*. In: Baker V, Kochel R, Patton P (eds). *Flood Geomorphology*. New York, NY: John Wiley & Sons, 51–64.
- Poole GC (2002) Fluvial landscape ecology: addressing uniqueness within the river discontinuum. *Freshwater Biol* **47**:641–60.
- Richardson DM, Holmes PM, Esler KJ, *et al.* (2007) Riparian vegetation: degradation, alien plant invasions, and restoration prospects. *Divers Distrib* **13**:126–39.
- Sarr DA, Hibbs DE (2007) Woody riparian plant distributions in western Oregon, USA: comparing landscape and local scale factors. *Plant Ecol* **190**:291–311.
- Shaw JR, Cooper DJ (2008) Linkages among watersheds, stream reaches, and riparian vegetation in dryland ephemeral stream networks. *J Hydrol* **350**:68–82.
- Sokal RR, Rohlf FJ (2012) *Biometry*. 4th edn. New York, NY: Freeman & Co.
- Steiger J, Tabacchi E, Dufour S. *et al.* (2005) Hydrogeomorphic processes affecting riparian habitat within alluvial channel floodplain river systems: A review for the temperate zone. *River Res Appl* **21**:719–37.
- Stromberg JC, Tiller R, Richter B (1996) Effects of groundwater decline on riparian vegetation of semiarid regions: The San Pedro, Arizona. *Ecol Appl* **6**:113–31.
- Swanson FJ, Johnson SL, Gregory SV. *et al.* (1998) Flood disturbance in a forested mountain landscape: Interactions of land use and floods. *Bioscience* **48**:681–89.
- Weixelman D, Zamudio D, Zamudio K. *et al.* (1996) *Central Nevada Riparian Field Guide*. Utah: USDA Forest Service.
- Wohl E, Angermeier PL, Bledsoe B. *et al.* (2005) River restoration. *Water Resour Res* **41**:W10301.
- Wolman MG (1954) A method of sampling coarse river-bed material. *Trans Am Geophys Union* **35**:951–56.
- Yang J, Dilts TE, Condon LA. *et al.* (2011) Longitudinal- and transverse-scale environmental influences on riparian vegetation across multiple levels of ecological organization. *Landscape Ecol* **26**:381–95.