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Development of an eco-geomorphic modeling framework to evaluate riparian ecosystem response to flow-regime changes

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ABSTRACT

Tools that provide decision makers with an understanding of ecosystem response to changes in streamflow attributes are necessary to balance human and ecosystem water needs. Flow response curves provide one such approach for informing management based on modeled relationships between environmental control (e.g., flood magnitude) and response (e.g., plant recruitment) variables, although unidirectional relationships may fail to capture the complex interactions between ecological and physical processes in riparian ecosystems. We take advantage of the linkage between plant functional traits important for (a) determining a plant's response to environmental conditions and (b) for predicting its impact on the flow of water and transport of sediment, to build a predictive model of riparian ecosystem dynamics. By using plant functional groups (i.e., guilds), our model accounts for process linkages among streamflow properties, physical processes, and plant community response. The model relies on a series of flow response curves built and tested with data collected along semiarid, canyon-bound rivers in Colorado. We built 2D hydrodynamic models and updated them with a flexible vegetation module to represent plant-hydraulic interactions for three study reaches. Plant guild distributions are well described by the model while predictions of the occurrence and direction of topographic change are less deterministic. Our work is among the first to develop response curves for both physical and ecological processes in the same framework. The shape of the resulting curves indicate that the functioning of riparian ecosystems is driven by nonlinear relationships and that clear, identifiable thresholds exist. As such, changes to the flow regime will have a differential impact on physical and ecological processes, depending on the nature of the shift. We discuss the strength and limitations of our model and make suggestions about its applicability to river management.

1. Introduction

Identifying ecosystem responses to the introduction or removal of a stressor or changes in available resources is critical for the effective management of natural systems (Ormerod et al., 2010), and tools to isolate important factors and translate scientific understanding into an ecosystem context can aid decision making (Schaeffer et al., 1988). Response curves link the response of an ecosystem property to environmental control variables in a single relationship (Potvin et al., 1990) and provide an important tool to bridge the gap between science and management (Wohl et al., 2015). Relationships built from empirical data are used to assess how a response variable reacts to a change in the control variable (e.g., Fig. 1). Characteristics of the response curve inform us on the functioning of ecosystems (Scheffer et al., 2001). For example, nonlinearities and inflection points may indicate thresholds that signify system sensitivity and resilience (Fig. 1).

Response curves are particularly useful in aquatic and riparian ecosystems (e.g., Bovee et al., 1998). In such settings, flow is the dominant driver of ecological and physical processes (Merritt et al., 2010), resulting in functional relationships between flow and ecosystem response. Control-response relationships have been used to predict changes in ecosystem properties as a result of deliberate (e.g., water development) or unintentional (e.g., climate change) shifts in flow attributes (King and Brown, 2010; Lytle et al., 2017). For example, flow response curves for individual fish species predicted the impact of flow depletions on fish assemblage structure in Michigan (Zorn et al., 2012). On the Bill Williams River, Arizona, flow response curves characterizing seedling survival, beaver dam integrity, and the dynamics of benthic macroinvertebrate groups have been tested for use in environmental flow decisions (Shafroth et al., 2010).

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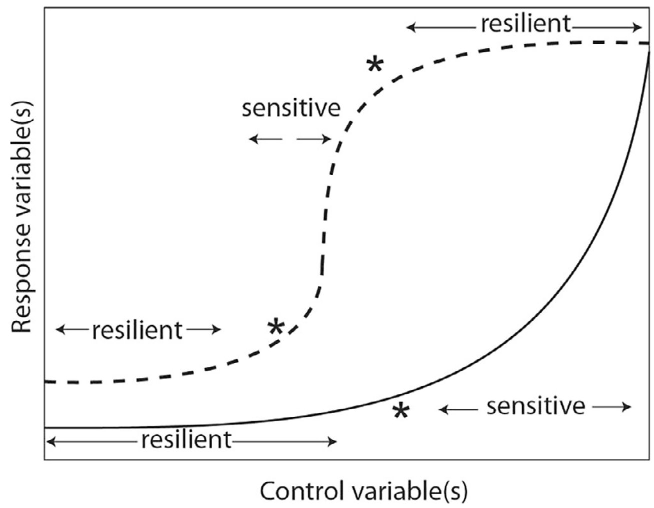

Fig. 1. Hypothetical response curves, the shape of which lends insight into ecosystem function. Both curves depicted here exhibit nonlinearities and inflection points. Asterisks identify conceptual thresholds that separate regions of the curve for which the response variable is resilient to changes in the control variable (i.e., with a change in the control variable, little change in the response variable occurs) from regions for which the response variable is sensitive to change (i.e., with a change in the control variable, a large change in the response variable occurs). Multiple thresholds may exist (e.g., dashed line) representing multiple regions of resilience and sensitivity.

Because of the process linkages and feedbacks between physical and ecological processes in aquatic and riparian ecosystems (Reinhardt et al., 2010), the complex response of these systems to changes in flow regimes are difficult to capture using response curves. Germination of riparian plants not only relies on flood peak timing and the rate of stage decline (Rood et al., 1998) but also the availability of unshaded, freshly deposited sediment (Scott et al., 1996). In turn, the recruitment of plant communities alters the physical processes that create suitable plant habitat (Corenblit et al., 2007). Moreover, the strength and direction of feedbacks between hydrogeomorphic processes and ecosystems vary temporally, for example with time since large floods and degree of maturity of riparian vegetation (Corenblit et al., 2007).

In this paper, we present an eco-geomorphic modeling framework that incorporates the interactions and feedbacks among flow, plants, and physical processes in riparian ecosystems. This modeling framework is built from a series of flow response curves, or curves for which attributes of the flow regime serve as one or more of the control variable(s). To date, response curves have been predominately used to describe changes in ecological attributes (e.g., species presence or distribution). Flow response curves also have strong potential for use in understanding controls on physical ecosystem attributes, and predicting shifts with a change in flow (Wohl et al., 2015). Our objectives in developing the eco-geomorphic modeling framework presented here are to tackle the challenge of building these relationships and, by using ecological and physical flow response curves in the same framework, to demonstrate the feasibility of applying a series of flow response curves to capture the integrative nature of riparian ecosystem response to shifts in flow attributes. Such a framework allows us to explore ecosystem functioning by identifying sensitivities and resiliencies. Additionally, with the use of relatively straightforward relationships between flows and ecosystem properties, this framework can inform decision-making about water allocation, changes in water due to climate change, and managing hydrographs for the benefit of riparian ecosystems. The example we use is for the Yampa and Green Rivers in Dinosaur National Monument, Colorado and Utah, USA where, as in many dryland river systems, climate change and upstream water use have the potential to substantially shift the flow regime in the coming decades (Yampa/White/Green Basin Implementation Plan, 2015).

To incorporate linkages between physical and ecological processes we rely on the relationship between functional plant traits important for describing how a plant will respond to abiotic stressors (ecological-response traits) and those traits important for determining how a plant alters the flow of water and transport of sediment (morphological-effect traits) (Lavorel and Garnier, 2002). Ecological-response and morphological-effect plant traits show similarities and correlations (Diehl et al., 2017a), and as a result, assemblages of species with similar combinations of traits (i.e., guilds) built from ecological response traits are likely to have a unique and consistent impact on fluvial processes. Data collected for 35 species along the Yampa and Green Rivers in Dinosaur National Monument in Colorado and Utah provide support for relationships among ecological-response and morphological-effect plant traits and fluvial processes (Diehl et al., 2017a). Using cluster analysis, Diehl et al. (2017a) identified 11 ecological-response guilds for the Yampa and Green Rivers. Morphological-effect traits were distinct (i.e., the range of values for the species within the guild) for 70% of the guild comparisons. As such, they demonstrated that ecological guilds are, in fact, morphologically unique and provided evidence that these morphologically-important groupings of plants have a distinct geomorphic signature.

The eco-geomorphic model we present here is built from three flow response curves that predict the response of plant-guild presence, total vegetation cover, and topographic response to a change in flow regime attributes. The use of flow response curves presents at least two basic challenges: quantifying the relationship between control and response variables, and identifying limitations in applying the flow response curves (Wohl et al., 2015). To address the first of these we use three years of data collected on the Yampa and Green Rivers to build statistical models that describe the relationship between flow and ecosystem properties. To identify limitations in the flow response curves, we apply the full eco-geomorphic model, based on the established relationships, to a fourth year of data. The model successfully identifies the spatial distribution of suitable plant guild habitat while having moderate success predicting the occurrence and direction of the geomorphic response to floods. We discuss insights derived from the model into the function of semiarid riparian ecosystems, as well as the model's utility in evaluating the impact of shifts to the flow regime on plant community dynamics and the evolution of landforms.

2. Yampa and Green Rivers

We work along the Yampa and Green Rivers; major tributaries to the Colorado River. Our analyses focus on three reaches, Harding Hole and Laddie Park on the lower Yampa, and Seacliff on the middle Green River, in Dinosaur National Monument (Fig. 2). These reaches are gravel-bedded and confined within bedrock canyons. The Harding Hole (slope of 0.004) and Laddie Park (slope of 0.007) reaches have incised meanders with tight bends in the bedrock, whereas the Seacliff reach (slope of 0.001) is debris-fan dominated; all reaches have mid-channel gravel bars. We focus on these gravel bars because of their susceptibility to vegetation establishment and expansion, deposition of fine-grained sediment, and changes in morphology (Manners et al., 2014; Van Steeter and Pitlick, 1998). Narrowing and simplification of the river channel has occurred within Dinosaur National Monument during the last century in large part from secondary channel aggradation (Alexander and Schmidt, 2007; Allred and Schmidt, 1999; Grams and Schmidt, 2002; Manners et al., 2014).

Riparian ecosystems in Dinosaur National Monument have been well described elsewhere (Merritt and Cooper, 2000; Uowolo et al., 2005). Species distributions represent the continuum of environmental conditions from the active channel, where early-successional species such as *Salix exigua* and *Carex emoryii* are found, up to intermediate floodplain benches with *Symphoricarpos occidentalis*, and then to upper surfaces with mature, late-successional floodplain trees and shrubs

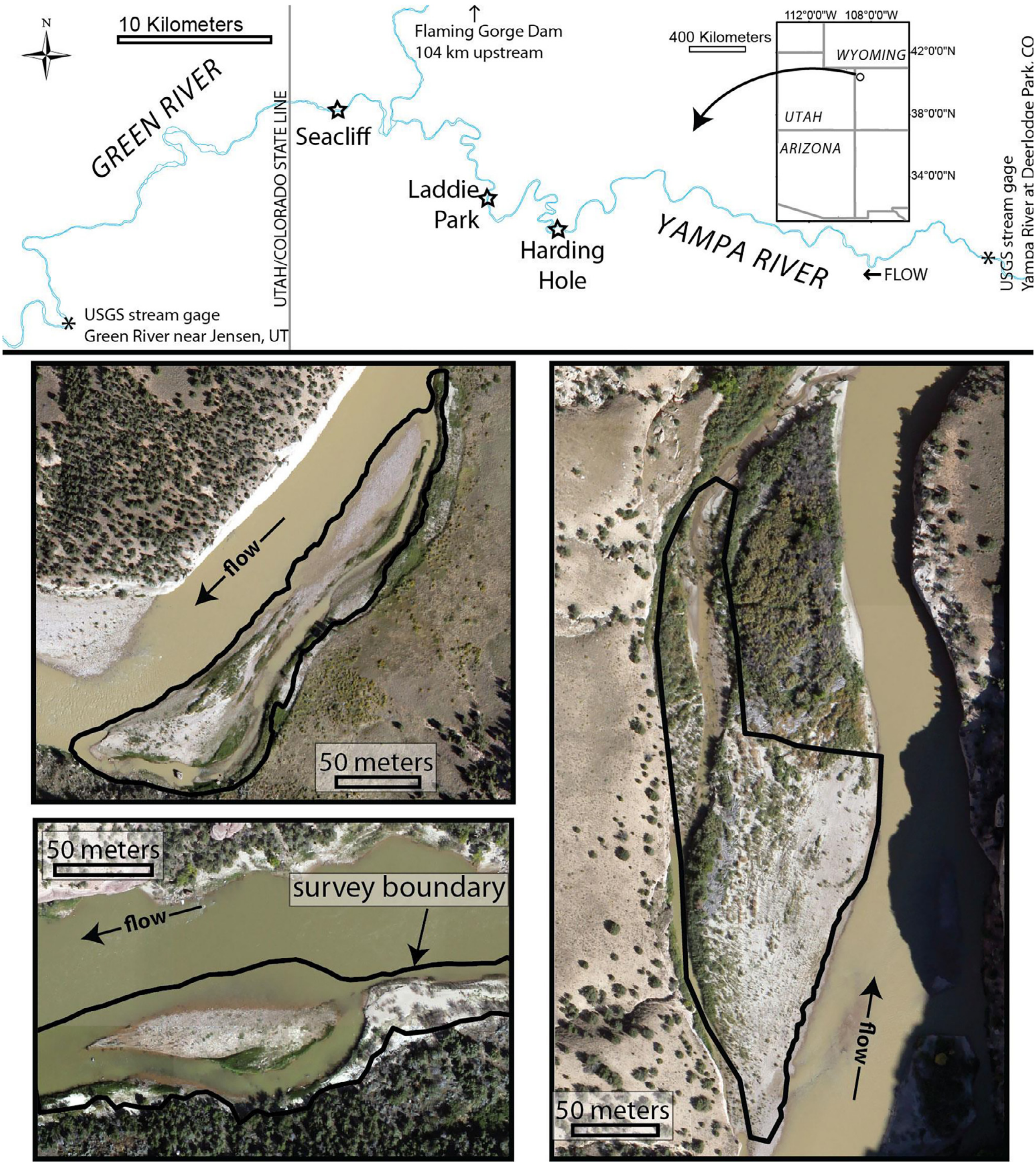

Fig. 2. Study area in northwestern Colorado, USA. Harding Hole (top left) and Laddie Park (right) are on the Yampa River, and Seacliff (bottom left) is on the Green River downstream from the confluence. The spatial extent of repeat surveys defined the study area boundary. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Merritt and Cooper, 2000). Our study reaches also have *Acer negundo*, *Celtis laevigata*, and the non-native shrub *Tamarix ramosissima* in the floodplain.

The natural flow regime of the Yampa River has maintained key ecological and physical processes both above and below the confluence of the Yampa and Green, where the Yampa contributes a natural flood pulse to the regulated Green and Colorado Rivers. Prior to the 1963 closure of Flaming Gorge Dam on the Green River, upstream from Dinosaur National Monument, the Green and Yampa had similar mean annual and peak flows. The hydrologic inputs to both systems are dominated by spring snowmelt floods, and annual peak flows occur between late April and June. The Yampa has retained most of its natural hydrology, although irrigation withdrawals deplete late summer flows in some years. In contrast, the Green River has lost much of its seasonal variability compared to pre-dam conditions. Upstream from the confluence with the Yampa, the two-year flood peak has been reduced by 57%; below the confluence the two-year flood peak is 23% less than it was prior to the closure of Flaming Gorge Dam (Schmidt and Wilcock, 2008). Flood timing, rate of change, daily minimum and maximum flows, and the sediment supply on the Green River have also been impacted by dam operations with later, smaller peaks and elevated baseflows (Grams and Schmidt, 2002; Merritt and Cooper, 2000; Vinson, 2001).

Our study reaches are co-located with long-term monitoring sites established and maintained by the National Park Service's Northern Colorado Plateau Network (NPS-NCPN) as part of an effort to detect physical and ecological changes to river channels as they begin to occur. Much of our data is derived from annual surveys, conducted by NPS-NCPN after the recession of the snowmelt flood, of plot-level vegetation and topography. As such, our work both relies on the monitoring program and strives to inform it.

3. Methods

To quantitatively link the flow regime to the structure and functioning of the riparian ecosystem along the Yampa and Green Rivers, we built a series of flow response curves. Ecological-response guilds present at our sites (Diehl et al. 2017a) are used to link flow, plant presence (represented with guilds), and geomorphic processes. We used data collected at the plot-scale on vegetation attributes and the topographic response to three flood events at Harding Hole, Laddie Park, and Seacliff, as recorded by US Geological Survey (USGS) stream gages near these sites. Hydrodynamic models were built to relate discharge histories from USGS gages to the hydrologic and hydraulic properties of the plot. We constructed statistical models from these relationships. We then tested and validated these models with an additional year of survey data from the same three sites.

3.1. Hydrology

To characterize variability in flow-related ecological and physical processes, we calculated the frequency of annual peak and daily discharges at the Yampa River at Deerlodge Park, Colorado (USGS gage #09260050) and the Green River at Jensen, Utah (USGS gage #09261000) (Fig. 2). We used a Log-Pearson Type III analysis to identify the return period of peak discharges for the post-Flaming Gorge Dam period, 1963–2016, and a flow duration analysis to identify the likelihood that a daily flow will be met or exceeded in any given year (i.e., exceedance probabilities). Because we use these exceedance probabilities as an indicator of water availability to riparian plants, we focus only on the growing season (April 26–October 10 based on the typical last/first freeze). Annual peak floods also occur during the growing season on the Yampa and Green Rivers and are associated with spring snowmelt. To account for the variable life histories of different plant communities, we calculated the exceedance probability of each flow for two time periods, 5 and 20 years, and translated the probability to the number of days inundated by multiplying by the number of days in the growing season (168 days). The number of days a plot is inundated based on the 5-year flow duration curve and 20-year flow duration curve is denoted in our models as *DaysInun5year* and *DaysInun20year*, respectively.

3.2. Riparian vegetation

We use riparian plant guilds to develop the eco-geomorphic modeling framework. A guild-based approach allows for generalization across large spatial and temporal scales (Merritt et al., 2010). From a list of 34 species and based on 7 functional traits, we identified 11 riparian vegetation guilds for the Yampa and Green Rivers (Diehl et al., 2017a). Eight of the 11 guilds are present at the three sites. Our work focuses on the six guilds that are present during floods and are therefore most likely to affect morphodynamics (Table 1).

Beginning in 2012, the NPS-NCPN collected annual plot-level (1 × 1 m) surveys at each of our three sites. These surveys record the total cover (%) of each species present. Topography was also surveyed each year. Survey methods included total station (2012 and 2013 at all sites, 2014 at Seacliff) and real-time kinematic GPS (RTK-GPS) (2014 at Harding Hole and Laddie Park, 2015 and 2016 at all sites). Plots span a gradient from the edge of the baseflow channel up to the floodplain. Each year, plots were randomly placed along systematic transects. Between 77 and 153 plots (mean = 95), were annually established at each site. We used vegetation surveys collected in 2014 to develop plant-related flow response curves, and those collected in 2015 to validate model predictions.

3.3. Plot-scale hydrologic and hydraulic conditions

To understand plot-level hydrologic and hydraulic conditions including inundation properties and flow velocities for a wide range of discharges, we built 2D hydrodynamic models using FaSTMECH within iRIC (International River Interface Cooperative; Nelson et al., 2016) for each of the three study reaches. Topographic surfaces were built from three datasets. Topography in upland areas and colluvial and bedrock surfaces was derived from 2011 LiDAR data. The region around the vegetation plots was defined by RTK-GPS topographic surveys conducted by the NPS-NCPN in 2015. Bathymetric surveys for Harding Hole and Seacliff in 2015 were collected using an echo sounder with real-time kinematic (RTK-GPS), and for Laddie Park in 2011 using an ADCP with RTK-GPS. Pressure transducers installed at the downstream and upstream end of each reach were matched to gage records to define stage-discharge relationships and used to assign boundary conditions.

To represent plant-geomorphic feedbacks, we updated FaSTMECH with a flexible vegetation module. With this module, the increased roughness from riparian vegetation is accounted for as a drag force that is added to the drag from the bed to solve for the total drag, necessary to solve for depth and velocity. For each of several categories of vegetation types, one defines the height, frontal area (2D area of the plant that interacts with the flow), and drag coefficient of individual plants, and the plant density (number of plants/m^2). Height and frontal area may be static, or may be defined by a rating curve in order to account for the changing morphology of flexible plants as they pronate and streamline with increasing velocity. The density of plants is defined spatially, such that a vegetation category may have more than one plant density.

For application to our study sites, we defined five vegetation categories per model. Each category represented a unique plant guild because each site had five of the six guilds represented. The spatial distribution of the guilds and the density of plants were identified from vegetation plots surveyed in 2014. Based on observations of spatial variability in density for a given plant guild, we defined polygons of varying density for a single vegetation category. Plant characteristics, including plant height and the projected frontal area, for each category were based on the physical traits of the guild (Diehl et al., 2017a). To represent the dynamic nature of plants, we created height and frontal area rating curves for each guild using empirical formulations from Luhar and Nepf (2011, 2013) that relate the reconfiguration of a plant to the Cauchy number (Ca) and the buoyancy parameter (B). The Cauchy number is the ratio of hydrodynamic drag and the restoring force due to stiffness:

$$Ca = \frac{\rho U^2 A_{F0} h^2}{EI} \qquad (1)$$

where ρ is the density of water, U is downstream velocity in a uniform flow, A_{F0} is the projected area of the plant in still air, h is upright plant height, and EI is the flexural rigidity of the plant (Whittaker et al., 2015). The greater the flexural rigidity, the more rigid a plant stem. The buoyancy parameter is the ratio of the restoring force due to buoyancy and the restoring force due to stiffness:

Table 1
Summary of plant guilds identified in Diehl et al. (2017a) and used in the eco-geomorphic model.

Ecological Guild Name[a]	Example Species	Height (m)[c]	Flexural Rigidity (N m^2)[c]	Frontal Area (cm^2)[c]
Hydric Herb[b]	*Schoenoplectus pungens*	0.53	0.02	71.8
Hydric Pioneer Tree/Shrub Seedling	*Populus fremontii*	0.75	0.23	1323.9
Short Mesic Herb	*Glycyrrhiza lepidota*	0.66	0.05	171.3
Tall Mesic Herb	*Solidago gigantea*	1.18	0.20	536.9
Mesic Shrub/Tree	*Salix exigua*	2.13	4.20	2518.5
Xeric Late-Seral Shrub	*Tamarix ramosissima*	3.80	27.40	39126.6

[a] Two additional guilds, generalist annual and hydric fern ally, are present at the study sites but are not modeled here because they are absent during the typical high-flow months.
[b] Removed Conyza canadensis from guild described in Diehl et al. (2017a) because it was determined to be more of a generalist.
[c] Values represent average of all measurements made on individuals of species included in guild and are used to represent guild in hydrodynamic model.

$$B = \frac{(\rho - \rho_v) g A_{F0} d h^2}{EI} \tag{2}$$

where ρ_v is the stem tissue density, g is the gravitational constant, and d is the stem diameter. We measured EI and ρ_v for individual plants during a field campaign in summer 2015 and averaged for all species within a guild (Diehl et al., 2017a). We assumed $C_D = 0.8$, consistent with Whittaker et al. (2015). For more information on the two-dimensional hydrodynamic model, our approach to incorporating dynamic, flexible vegetation within the model, and examples of output, see Supplement Text A.1, Fig. A.1 and Figs. B.1–B.3.

We calibrated each model to surveyed water surface elevations by adjusting the bed roughness. Surveys were completed at flows ranging from at or below what we define as baseflow (the discharge that has a probability of being exceeded 50% of the time) to a discharge with an 8% exceedance probability. Discharges from baseflow to the 20-year flood were then modeled. We matched the predicted water surface to the upstream and downstream rating curves. The root mean square error (RMSE) of observed versus predicted water surface elevations ranged between 0.07 and 0.29 m for all sites and averaged 0.23 m for Laddie Park, 0.27 m for Harding Hole, and 0.22 m for Seacliff.

Water surface elevations and velocities for the range of flows modeled were exported from FaSTMECH and imported to ArcGIS in order to identify the hydrologic and hydraulic conditions of vegetation plots. For each plot, we calculated the inundating discharge, or that minimum discharge for which the modeled water surface is equal to or greater than the plot elevation. From the inundating discharge, we calculated the probability that a given plot was inundated in a given year based on a flow duration curve. The maximum velocity during a flood with a 3-year return period and a 20-year return period was identified from model output. We also calculated the flow-path distance at the flood peak for the 2013, 2014, and 2015 spring floods from hydrodynamic model output. The flow-path distance is defined as the 2-dimensional distance along a flow vector that water takes as it moves from the baseflow channel to an individual vegetation plot (Alsdorf et al., 2007) and is a proxy for sediment supply (see below). Streamlines, representing flow pathways, at peak discharge were exported from the model to calculate flow-path distance.

3.4. Flow response curve development

We use flow response curves to describe the relationship among flow properties, vegetation, and geomorphology. We developed three types of flow response curves: guild presence, plant distribution (presence and proportion cover), and topographic change as a result of a single flood event (Table 2). To build the curves, we used various types of generalized linear models in R (R Core Team, 2013), as described below. Plant presence and percent cover data collected at plots surveyed in 2014 were used to construct guild presence and proportion of plant cover curves. Topographic surfaces built with topographic survey data collected in 2012, 2013, 2014, and 2015 were used to construct the topographic change curves.

We modeled the presence of six guilds using logistic regression as a function of water availability and fluvial disturbance, the dominant selective pressures for riparian plants (Merritt et al., 2010). Water availability was represented by the number of days the plot is inundated in any given year during the growing season. This assumes that river stage and groundwater levels are closely coupled, a common assumption on arid and semi-arid rivers (Rood et al., 2003). Fluvial disturbance was represented by the maximum velocity the plot experiences for a flood of a given return period. Because of differences in the time-scale of response for different plant forms, we used one set of control variables for herbaceous and woody seedling guilds, and a second set for mature woody guilds. The presence of herbaceous plants and woody seedlings is more closely a function of the recent flow regime (e.g., Bagstad et al., 2005), whereas a mature woody plant integrates longer-term (e.g., decadal) hydrologic conditions (Stromberg, 2013). Additionally, woody species tend to respond over longer time-scales to altered water availability compared to herbaceous species (Reynolds et al., 2014), because woody plants typically have deeper and more extensive root systems. For herbaceous and woody seedling guilds, we therefore used as control variables the exceedance probability of the inundating flow for a flow duration curve developed from the past five years (*DaysInun5year*) and the maximum velocity during a flood with a 3-year return period (*3yrFloodVel*). For mature woody guilds, the control variables were the exceedance probability of the inundating flow for a flow duration curve developed from the past 20 years (*DaysInun20year)* and the maximum velocity during a 20-year return period flood (*20yrFloodVel*). Water availability and fluvial disturbance metrics were not correlated. To normalize the independent variables, maximum velocity and inundation duration, we took the fourth root.

The output of our logistic models is a probability of occurrence (between 0 and 1). Because our goal was to use the resulting curves to identify the likely presence of a guild given a set of hydrologic conditions, we converted the continuous output into a binary variable (presence or absence) based on a threshold probability of occurrence value. To identify this threshold, we calculated receiver-operating characteristic (ROC) curves that relate true positive (presence) predictions to true negative (absence) ones. From the ROC curve, we isolated the value that maximized these correct predictions. We also calculated the area under the ROC curve (AUC), which provides an index of overall model accuracy, independent of threshold selection. AUC values close to 1 indicate high performing models and a value of 0.5 is indicative of a model that is no more useful than a random guess (Fielding and Bell, 1997; Randin et al., 2006).

For some of the guilds, we suspected a modal (not monotonic) response to hydrologic drivers. Therefore, we tested linear and quadratic models, and we tested the inclusion of site as a categorical, random effect. Model selection primarily relied on Akaike Information Criteria (AIC), which balances goodness-of-fit based on the likelihood function with model parsimony. The model with the lowest AIC value, and those with a ΔAIC < 2 from that model, are considered to have substantial

Table 2
Summary of flow response curves.

Curve	Regression Type	Formula	Random Factor	Threshold Value[a]	Classification Rate[b]	AUC Value[c]
Guild Presence						
Hydric Herb[d]	logistic, mixed	3yrFloodVel + DaysInun5yr	site	0.19	0.75	0.81
Hydric Pioneer Tree/Shrub Seedling	logistic, mixed	3yrFloodVel + 3yrFloodVel^2 + DaysInun5yr	site	0.61	0.64	0.67
Short Mesic Herb	logistic	3yrFloodVel + 3yrFloodVel^2 + DaysInun5yr + DaysInun5yr^2	N/A	0.26	0.71	0.72
Tall Mesic Herb	logistic	3yrFloodVel + 3yrFloodVel^2 + DaysInun5yr + DaysInun5yr^2	N/A	0.31	0.59	0.65
Mesic Shrub/Tree	logistic, mixed	20yrFloodVel + DaysInun20yr + DaysInun20yr^2	site	0.21	0.83	0.66
Xeric Late-Seral Shrub	logistic, mixed	20yrFloodVel + DaysInun20yr	site	0.05	0.67	0.61
Plant Distribution						
Presence	logistic	20yrFloodVel + DaysInun20yr	N/A	0.89	0.74	0.71
Proportion of Cover[e]	beta, mixed	20yrFloodVel + DaysInun20yr + GuildProp	site	N/A	0.87	N/A
Topographic Change						
Seacliff	linear, mixed	Flow_Path_Distance * Max_Vel + CoverXGuildProp	year	[f]	0.84	N/A
Laddie Park	linear, mixed	Flow_Path_Distance * Max_Vel + Cover * Max_Vel	year	[g]	0.51	N/A
Harding Hole	linear, mixed	Flow_Path_Distance * Max_Vel + Cover * Max_Vel	year	[h]	0.85	N/A

[a] Value used as threshold between presence (greater than cutoff) and absence (less than cutoff).
[b] Proportion of plots with a correct prediction.
[c] Calculated as the area under the receiver operating characteristic curve.
[d] Modeled the absence of this guild; the inverse of the resulting model predicted presence.
[e] Predicts values between 0 and 1, or 0% and 100% vegetation cover.
[f] 0.02 m threshold for deposition and −0.20 m threshold for erosion.
[g] 0.20 m threshold for deposition and 0 m threshold for erosion.
[h] 0.10 m threshold for deposition and −0.05 m threshold for erosion.

empirical support. In selecting the best model, we also considered other factors including model accuracy, by taking into account AUC values, and professional judgement. Supplement C Tables C.1–C.6 show a list of candidate models and model selection results.

We added an additional restraint to the resulting guild presence curves. Although some guilds are likely to have a greater probability of presence when inundated for the majority of the growing season, inundation for the entire growing season, on average, does not create optimal growing conditions. Based on observations from our data, plots inundated more than 75% of the growing season predominately lacked vegetation. We automatically assigned a zero probability of guild presence to plots inundated for 126 days or more. This threshold was chosen to differentiate suitable from unsuitable habitat as a function of inundation duration and the resulting anoxic, uninhabitable soils.

To describe plant distributions, we first modeled the likely presence of vegetation using logistic regression. For those plots with vegetation present, we then described the percentage of plant cover in each plot using beta regression (Table 2). Plots with vegetation cover less than 2% were considered to be essentially unvegetated and were coded as 0. Predictor variables included *DaysInun20yr* and *20yrFloodVel*, for both presence and density models. Because small plants are more likely to occupy a smaller proportion of a plot than large plants, we also included the presence of each of the six guilds (*GuildProp*) in the density model. All independent variables included in these models were uncorrelated. We also included *site* as a random variable. We converted the continuous output from the presence model into a binary variable (bare or vegetated) based on a threshold probability of occurrence value. To identify this threshold, we calculated a ROC curve and identified the value that maximized true positive (presence) and true negative (absence) predictions. We also calculated the AUC value to evaluate presence/absence model accuracy. To gage the success of the proportion cover model, we categorized plots whose total cover of the ground area was between 2 and 25% as "sparse" and > 25% as "dense".

The third flow response curve predicts the topographic response of a vegetated plot to a flood event. Changes in fluvial topography are a function of the balance between the capacity of the river to move sediment (i.e., transport capacity) and the caliber and availability of sediment, both on the bed and upstream (i.e., sediment supply). Vegetation alters the transport capacity by changing the magnitude and/or spatial distribution of velocity and turbulence. Plant morphology and density determine the magnitude and direction of these shifts (Manners et al., 2015; Yager and Schmeeckle, 2013). Morphodynamic predictions are challenging because of spatial variability and nonlinearity in sediment transport processes (Rennie and Church, 2010; Wilcock, 2001). Prediction of topographic changes within vegetated regions is further complicated by uncertainty in the partitioning of shear stress between plants and the bed (Nepf, 2012; Wilcox et al., 2006). Despite these complexities, we attempt to build flow response curves that characterize the well-established linkages between hydraulic variables and sediment transport and morphodynamics (Parker, 2004), and between plant variables and river channel topography (Bertoldi et al., 2011; Bywater-Reyes et al., 2017).

For each of the three sites, we built a separate model that describes the likely plot-scale topographic response (i.e., response variable) given the transport capacity, sediment supply, and vegetation characteristics (i.e., control variables), which were site-specific. We defined the topographic response for each surveyed plot (*topo*) as the difference between post- and pre-flood elevations (Diehl et al., 2017a). Elevations were extracted from continuous surfaces built from each year's survey points. Vegetation plots surveyed prior to the flood event were matched with the corresponding topographic response (i.e., 2014 vegetation survey is associated with topographic response to the 2015 flood). To account for survey and interpolation errors and uncertainty, we only considered changes in bed elevation that were greater than 20 cm. For each of the three sites, we evaluated a set of 16 linear candidate models, which included uncorrelated predictor variables, and were built to describe observations collected for three flood events (2013, 2014, 2015). We compared candidate models and chose the model with the most empirical support (i.e., the lowest AIC value). Supplement Tables C.7–C.9 show a list of candidate models and model selection results.

To designate transport capacity in the linear models, we include the maximum velocity a plot experiences during a flood (*Max_Vel*); velocity described more of the variability in the topographic response than bed shear stress. The sediment supply is represented by proxy with the variable flow-path distance (*Flow_Path_Dist)*, defined as the distance water must travel from edge of the baseflow channel to the plot at peak flood conditions. Sediment transport capacity diminishes as water leaves the main channel, and we assume that distance from the baseflow channel edge is inversely related to sediment concentrations (Walling and He, 1998). We expect that the relationship between *Flow_Path_Dist* and sediment concentrations differs depending on flow velocities, as represented by the interaction term *Max_Vel:Flow_Path_Dist*.

To describe the role of vegetation, we tested the total surveyed vegetation cover of a plot, *Cover*, a value between 0 and 100. We also tested the importance of the proportion of plants within a plot comprised of each guild (*GuildProp*, between 0 and 1), by multiplying *GuildProp* by *Cover (GuildPropXCover)*. The role of plants in altering the topographic response may also be influenced by the sediment transport rate, as represented by the term *Cover:Max_Vel*. Finally, we included the elevation above the baseflow channel (*Elev_Abv_BF*) as a descriptor of multiple processes, including the duration of inundation, the flow strength, and the character of the vegetation community (Diehl et al., 2017a).

To account for the differences in temporal characteristics of floods (i.e., hydrograph shape) between years (*year*), we used a mixed effects model. The variable *year* was treated as a random variable and the remainder as fixed. Because we are only interested in the occurrence and direction of change, we identified thresholds in the predicted model output delineating no change, deposition, and erosion, corresponding to small, large positive, and large negative topographic responses, respectively. Thresholds were identified as those values that optimized the true positive prediction of three possible topographic responses.

3.5. Eco-geomorphic model application and validation

In order to validate the eco-geomorphic model, we applied the series of flow response curves to the three sites using hydrologic and hydraulic data that represented the conditions leading up to, and during, the 2016 snowmelt flood event. We tested the predicted guild presence and topographic response using plot-scale plant surveys collected in 2015 and bed elevation changes from topographic surveys collected in 2015 and 2016.

To apply the eco-geomorphic model, we first modeled the likely presence of plants, and then the distribution of the six plant guilds for conditions prior to the 2016 flood (Table 2). Given the likely presence of the plant guilds, we determined the proportion of plant cover. Finally, we used the topographic change curve to predict the occurrence and direction of change in the bed elevation as a result of the hydraulic conditions and plant cover.

4. Results

4.1. Guild presence and plant cover flow response curves

For plant-guild presence curves identified using logistic models, classification rates for the fitted data compared to the observed data varied from 0.59 to 0.83 (Table 2; Fig. 3). AUC values ranged from 0.61 to 0.80, indicating adequate to good model performance (Randin et al., 2006).

The resulting curves are consistent with the hypothesized habitat preference of each guild (i.e., hydric, mesic, or xeric). Hydric guilds are most likely to occupy plots inundated for most if not all of the growing season. With increasing inundation duration, the likelihood of plant-guild presence increases relatively rapidly (Fig. 3A and B). The xeric guild is found in dry areas (Fig. 3F). The response curve for the xeric guild is highly nonlinear, with an abrupt threshold between presence and absence at a point where a plot is inundated for only 2–3 days during a typical growing season. Between plots regularly inundated and rarely inundated during the growing season, conditions are optimal for mesic guilds (Fig. 3C–E). These curves have a distinct peak between 0 and 50 days of inundation.

Water availability was a stronger predictor of guild presence or absence than fluvial disturbance, especially for hydric and xeric guilds, based on the shape of the curves. Our model predicts the likely presence of plants within hydric and xeric guilds for a wide range of fluvial disturbance strengths, from very low velocities to 4 m/s based on the range of velocities modeled (Fig. 3A, B, F). In contrast, mesic guilds are most likely to be found in areas with low to moderate velocities (Fig. 3C–E). Mesic guilds are more responsive to shifts in the maximum velocity than hydric or xeric guilds, and the shape of the curve differs among the mesic guilds.

The plant distribution curve indicated that larger velocities and greater inundation durations resulted in less likelihood of vegetation (presence model), and when vegetation was present less vegetation cover (proportion cover model) (Table 3). For plots that had mature woody guilds (i.e., mesic shrub/tree guilds and xeric late-seral shrub guilds), plant cover was 20–70% more likely to be dense than with hydric herb, tall mesic herb, and hydric pioneer tree/shrub seedling guilds present. The presence of the short mesic herb guild also contributed to a greater likelihood of a densely covered plot, likely because this guild predominately grows at our sites in dense rhizomatous clumps. The classification rate for the plant distribution curve was, on average, 81% (74% for the presence model and 87% for the density model) (Table 2).

4.2. Topographic change flow response curve

The topographic change flow response curves predict the bed elevation response of a vegetation plot to a single flood event. At all three sites, the top models, or those with the lowest AIC values, included control variables that describe the sediment transport capacity (*Max_Vel*), the sediment supply (*Flow_Path_Dist*), and the effect of vegetation (*Cover* or *CoverXGuildProp*) (Table 2; Supplement Tables C.1–C.8). Although *Cover* was in the top models for all three sites, *CoverXGuildProp* was only important at the Seacliff site. We found, however, that the interaction between *Max_Vel* and cover was important at Harding Hole and Laddie Park (i.e., the importance of *Cover* on the topographic response changes with a change in *Max_Vel*). Interannual differences were significant in all models ($p < 0.001$; -2 log likelihood ratio test). The average classification rates for the topographic change models was 73% and ranged from 51% to 85% (Table 2).

Variables that represent the transport capacity and sediment supply describe the majority of the variability in the Harding Hole and Laddie Park models (68% and 54%, respectively, based on model sum of squares) (Table 4). In contrast these abiotic factors account for only 4% of the variability in the Seacliff model. Therefore, abiotic factors were more important for determining the occurrence and direction of topographic change at the Yampa River sites, Harding Hole and Laddie Park, and vegetation characteristics had a relatively greater influence on the topographic response at Seacliff (Fig. 4). The regression relationships shown in Fig. 4A and B assign a value of 0 to *Cover*, thereby isolating the impact of abiotic factors.

With increasing velocity, the model predicts that plots located at Harding Hole and Laddie Park are more likely to be depositional (Fig. 4A). The relationship between deposition and velocity is mediated by distance from the channel (i.e., there is an interaction between *Max_Vel* and *Flow_Path_Dist*): plots located farther away from the channel edge (i.e., 100 m *Flow_Path_Dist*) are more likely to be depositional than those located close to the channel edge (i.e., 0 m) (Fig. 4A). At Seacliff, in contrast, the model suggests that where vegetation cover is held at zero, topographic changes are unlikely across the range of maximum velocities and flow-path distances considered here (Fig. 4B).

Plant cover influences the topographic response at Seacliff and Laddie Park but has relatively little impact on the topographic response at Harding Hole (Table 4; Fig. 4C and D). Increasing cover at Laddie

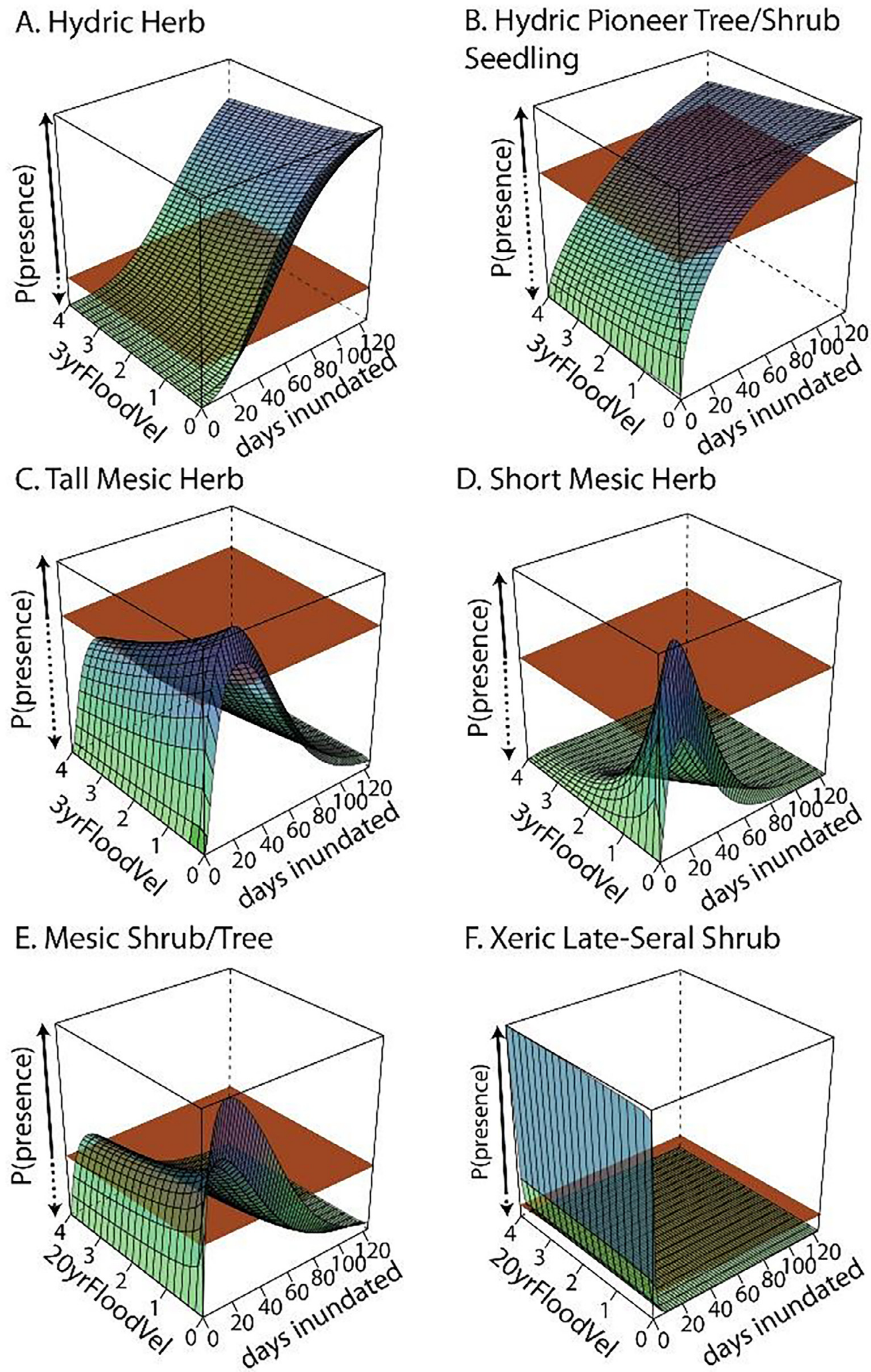

Fig. 3. Guild Presence flow response curves for the six plant guilds present at our study sites that influence geomorphic processes during floods. Orange plane represents the threshold value, above which we expect that guild to be present and below which growth of that guild is unlikely. The probability that a guild will be present in a plot (y axis; solid line indicates likely presence, dashed line likely absence) is a function of the maximum velocity during the flood with a 3-year return period or the flood with a 20-year return period and the number of days the plot is inundated during the growing season based on a typical year for the past 5 years (herbaceous plants and seedlings; A–D) or 20 years (mature woody plants; E–F). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Park increases the likely occurrence of deposition; densely vegetated plots are highly likely to be depositional (Fig. 4C). At Seacliff the occurrence and direction of bed elevation change with increasing cover depends on the composition of plant guilds present. For example, with increasing cover of the hydric herb guild, there is a greater likelihood of deposition within the plot. In contrast, for increasing cover of the short mesic herb guild and the xeric late-seral shrub guild, there is a greater likelihood of erosion.

4.3. Model evaluation

We applied the full eco-geomorphic model to the hydrologic, hydraulic, and topographic conditions present, leading up to, and during, the 2016 snowmelt flood. For the 307 vegetation plots surveyed in 2015, the guild presence curves had an average classification rate of 69% and AUC values that ranged from 0.62 to 0.80 (Table 5). The short mesic herb curve had the highest classification rate, 78%. For guilds

Table 3
Model parameters for the two models that were used to construct the plant distribution curve.

Variable	Coefficient[b]	Standard Error	p-value
Presence			
Intercept	6.50	1.49	< **0.01**
20yrFloodVel[a]	−0.89	1.20	0.46
DaysInun20yr[a]	−1.33	0.71	**0.06**
Proportion of Cover			
Intercept	−0.69	0.31	< **0.01**
20yrFloodVel[a]	−0.52	0.23	**0.03**
DaysInun20yr[a]	−0.77	0.15	< **0.01**
Guild Prop			
Hydric Herb	1.17	0.40	< **0.01**
Hydric Pioneer Tree/Shrub Seedling	1.02	0.16	< **0.01**
Short Mesic Herb	2.92	0.24	< **0.01**
Tall Mesic Herb	1.26	0.27	< **0.01**
Mesic Shrub/Tree	2.59	0.27	< **0.01**
Xeric Late-Seral Shrub	6.60	0.77	< **0.01**

[a] Variables transformed by taking fourth root in order to satisfy assumption of normality.
[b] Estimated value for variable within models.

other than the xeric late-seral shrub, prediction rates were higher for the absence of a guild, rather than the presence. The plant distribution curve had an average classification rate of 66% (71% for the presence model and 60% for the proportion cover model). The AUC value for the plant presence model (0.90) indicates a reliably predictive model.

Modeled distributions of the six guilds are consistent with their hypothesized habitat preference. Hydric guilds are most likely to grow at low elevations and nearer the channel, while the xeric guild only has a small likelihood of growing on the floodplain, and mesic guilds are expected to grow in intermediate locations (Fig. 5). Fig. 5 shows the modeled distributions, and observed presence/absence, of the six guilds at Seacliff. Areas that did not meet the threshold for the likely presence are blank (Table 2). In Fig. 5, where the predicted probability exceeds the threshold, we normalized the values (range rescaled to 0–1.0). Observed patterns are generally consistent with predicted ones. For example, the short mesic herb guild was documented growing in the area where our model predicted the likely presence, as well as growing in plots just upstream and offshore of the predicted area.

The topographic response curve had a total classification rate (averaged over the three models) of 64%. The model developed for Seacliff and Harding Hole had relatively high classification rates, predicting 76% and 73% of the occurrence and direction of topographic change in response to the 2016 flood, respectively (Table 5). Laddie Park had an overall prediction rate of 44%. At all of the sites, the model had the most success predicting the occurrence of no topographic change, with greater variability in their success to predict erosion or deposition. Although spatially variable, some trends in the erosional and depositional patterns were captured by model predictions (e.g., Fig. 6). Many elevated vegetated surfaces on mid-channel bars experienced deposition, and erosion commonly occurred along the edge of floodplain or channel bar surfaces. The Seacliff model correctly predicted deposition on the mid-channel bar and erosion along floodplain and bar edges.

5. Discussion

5.1. Model performance: strengths and limitations

Our eco-geomorphic model of riparian ecosystem dynamics relies on a series of flow response curves that together describe the coupled response of plants and physical processes to changes in the flow regime. The straightforward nature of flow response curves makes them attractive for use in ecosystem studies, and for application to environmental decision making (Shafroth et al., 2010). Our curves captured much of the variability in the plant community response, but classification rates for the erosional or depositional response were lower.

Unexplained variability in our response variables may be attributed to control variables not included in the models and/or to complexity not captured by logistic models. Guild presence curves identify suitable habitat based on the selective pressure of water availability and fluvial disturbance. Within suitable areas, other factors such as soil textural properties (Auble et al., 1994), groundwater levels, biotic competition (Wisz et al., 2013), pathogens and other forms of mechanical disturbance (e.g., herbivory) contribute to the success of plants. As a result, in some guild models, predictions of plant absence were more accurate than predictions of presence. Additionally, in many plots more than one plant guild was surveyed, such that one guild (e.g., larger, more rigid species) may veil the effect of another guild (e.g., smaller, more flexible plants) on modeled topographic response.

Changes in topography during floods are affected by complex relationships among sediment transport capacity (including as affected by vegetation) and sediment supply, which are challenging to comprehensively represent in flow response curves. Sediment transport capacity and supply vary spatially and temporally, within and between flood

Table 4
Model parameters for the three models that were used to construct the topographic change curve.

Variable	Seacliff			Laddie Park			Harding Hole		
	Coefficient	Sum of Square	p-value	Coefficient	Sum of Square	p-value	Coefficient	Sum of Square	p-value
Intercept	−0.007		0.91	−0.631		0.20	−0.317		< **0.01**
Flow_Path_Dist[a]	0.699	0.025	0.71	5.154	1.519	**0.05**	3.687	0.464	< **0.01**
Max_Vel[b]	0.022	0.002	0.14	0.938	1.566	**0.05**	0.290	0.288	< **0.01**
Flow_Path_Dist[a]:Max_Vel[b]	−1.125	0.046	**0.04**	−6.634	1.619	**0.04**	−3.490	0.196	< **0.01**
Cover	[c]			0.068	2.005	**0.02**	0.008	0.159	< **0.01**
Cover:Max_Vel[b]	[c]			−0.092	2.027	**0.02**	−0.009	0.196	< **0.01**
CoverXhydric herb	0.007	0.020	0.19	[c]			[c]		
CoverXhydric pioneer tree/shrub seedling	−0.019	0.811	< **0.01**	[c]			[c]		
CoverXshort mesic herb	−0.003	0.364	< **0.01**	[c]			[c]		
CoverXtall mesic herb	0.002	0.007	0.45	[c]			[c]		
CoverXmesic shrub/tree	0.003	0.000	0.95	[c]			[c]		
CoverXxeric late-seral shrub	−0.037	0.432	< **0.01**	[c]			[c]		
Model Sum of Squares		1.71			8.74			1.81	
Residual Sum of Squares		1.94			59.09			3.12	

[a] Flow path distance is in km.
[b] The fourth root of maximum velocity was used.
[c] Variables not included in site models.

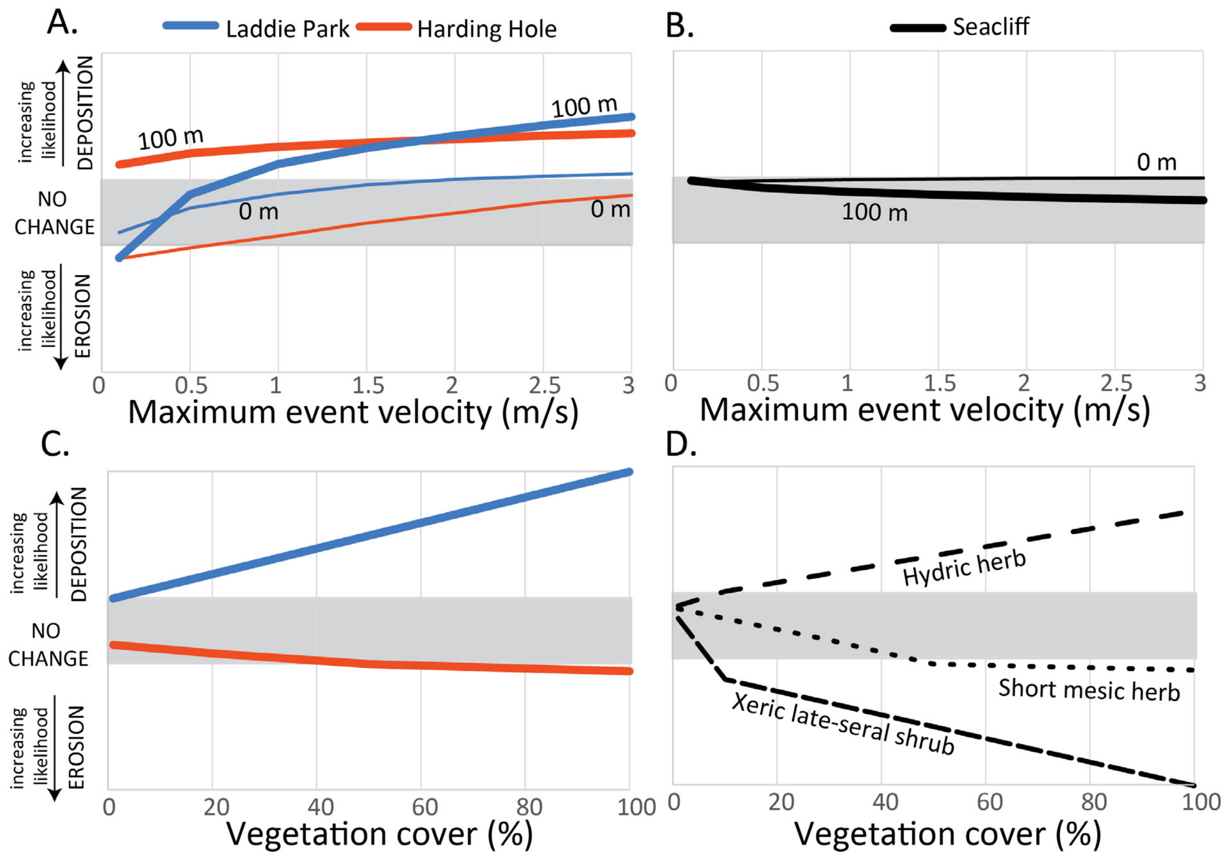

Fig. 4. Relationship between abiotic (A, B) and biotic factors (C, D) and the likely occurrence of plot-scale erosion and deposition, derived from the topographic response curve for the Yampa River sites (A, C) and the Seacliff site on the Green River (B, D). In (A) and (B), where vegetation cover is set to zero and likelihood of erosion or deposition with increasing velocity is shown for two flow-path distances (0 m and 100 m), relationships differ among sites. Deposition becomes increasingly likely with increasing velocity for Harding Hole and Laddie Park (A), but plots at Seacliff are unlikely to experience topographic change for any value of Max_Vel or Flow_Path_Dist (B). In (C) and (D), where Max_Vel is set to 1 m/s and Flow_Path_Dist is 100 m, increasing vegetation cover has minimal impact at Harding Hole but increases the likelihood of deposition at Laddie Park (C), whereas at Seacliff the impact of increasing cover depends on the guild present (D). The curves shown here are normalized, based on their thresholds (see Table 2), to have a similar range of values in order to more accurately compare the trends. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

events (Morehead et al., 2003), and are difficult to directly measure (Hicks and Gomez, 2016). Metrics such as flow-path distance, which we used as a proxy for sediment supply in our topographic response curves (after Walling and He, 1998), may not adequately represent plot-scale conditions experienced by plants. Additionally, topographic change resulting from bank erosion, as occurred at our sites, is challenging to model and predict and may not be well represented by variables such as maximum velocity, the measure of transport capacity we used. Variables such as wetting history, pore water pressure (or matric potential), bank stratigraphy, root morphology of plants, and sediment sizes of bank material all can influence bank erosion (Fox and Wilson, 2010; Simon and Collison, 2002).

Response curves developed from empirical data are, by their very nature, most applicable to the hydroclimatic and geomorphic setting, and plant community, in which the data were collected. We worked along canyon-bound, semiarid rivers. Our observations occurred at sites with mid-channel bars for which floodplains are relatively limited in spatial scope and community diversity. By using guilds, we have extended the applicability of our work to areas or time periods in which flow factors differ, and areas where there may be functionally similar plants, but entirely different floras (species) (Merritt et al., 2010).

5.2. Structure and functioning of riparian ecosystem

The shape of a flow response curve informs us about the variables that govern ecosystem function (Wohl et al., 2015) (e.g., Fig. 1). Linear curves indicate proportional ecosystem responses to shifts in control variables. Flow response curves are often nonlinear, however (Phillips, 2006), such that the coupled riparian ecosystem response is highly dependent on the magnitude and type of shift in control variables. In some situations, small shifts in environmental conditions have a large impact on plant-guild presence and the likely topographic response suggesting a sensitivity, while other shifts have little to no effect, suggesting a resilience (Bejarano et al., 2012). An increase in maximum event velocities (i.e., higher magnitude events), for example, is likely to have a large impact on the likely presence of mesic guilds (i.e., sensitive) and little impact on hydric guilds (i.e., resilient).

All of our curves were nonlinear and some exhibited apparent thresholds. Plant-guild presence curves were steeper along the water availability axis than the maximum velocity axis (Fig. 3), suggesting that the availability of water was a stronger driver for determining the likely presence of plant guilds than was disturbance strength for the conditions modeled. Auble et al. (1994, 2005) demonstrated that the occurrence of riparian plant species is governed, in large part, by the inundation duration of the surfaces on which they grow. This was especially true for wet (hydric) or dry (xeric) guilds. The species comprising these guilds have been selected for more extreme environments (Banach et al., 2009; Pockman and Sperry, 2000). Mesic guilds, however, were sensitive to disturbance strength, and the tolerance of higher velocities depended on stem flexibility. Differences in the maximum velocity for rigid and flexible stems is suggestive of the avoidance-tolerance tradeoff, a theory describing the two strategies plants use to

Table 5
Results from application of guild presence and plant distribution curves to the hydrologic and hydraulic conditions prior to the 2016 flood event, compared with the 2015 vegetation survey results, and of application of the topographic change curve to the 2016 flood, and compared with the difference between the 2016 and 2015 surveys.

Response Curve	Classification Rates				AUC Value
Guild Presence[a]	Presence[c]	Absence[d]		Overall	
Hydric Herb	0.50	0.69		0.63	0.69
Hydric Pioneer Tree/ Shrub Seedling	0.50	0.64		0.58	0.62
Short Mesic Herb	0.38	0.90		0.78	0.76
Tall Mesic Herb	0.53	0.69		0.63	0.69
Mesic Shrub/Tree	0.50	0.82		0.78	0.80
Xeric Late-Seral Shrub	0.81	0.72		0.73	0.80
Plant Distribution[a]					
	Bare[c]	Vegetated[d]			
Presence	0.92	0.68		0.71	0.90
	Sparse[e]	Dense[f]			
Proportion Cover	0.58	0.85		0.60	N/A
Topographic Change[b]	No Change	Erosion	Deposition		
Seacliff	0.83	0.42	0.17	0.76	N/A
Laddie Park	0.48	0.12	0.47	0.44	N/A
Harding Hole	0.85	0.03	0.08	0.73	N/A

[a] Evaluation based on 2015 vegetation plots, 307 total.
[b] Evaluation based on full areal coverage at individual site.
[c] Presence is defined as a true positive, in which both the observed and predicted condition is presence.
[d] Absence is defined as a true negative, in which both the observed and predicted condition is absence.

survive the frequently disturbed river habitat (Puijalon et al., 2011). Rigid plants can resist high forces, and are therefore tolerant, whereas flexible plants minimize forces exerted on them by pronating and streamlining, thereby avoiding mechanical disturbance. Our sites were in locations that were on average wider than the surrounding canyons because we wanted to model areas with a wide range of guilds present. Other places in the canyon have a steep gradient, higher water velocities, fewer guilds, and less vegetation overall. In these settings the influence of velocity on plant-guild presence could outweigh the influence of water availability.

From our response curves, we differentiated suitable and unsuitable environmental conditions for plants and conditions likely to alter channel/floodplain bed elevations from those for which the bed is likely to remain relatively unchanged. Thus, some of the response curves developed for the eco-geomorphic model also have clear thresholds. Thresholds are used to differentiate between states (e.g., presence-absence of vegetation, change-no change in topography), and represent a change in process (Groffman et al., 2012). Thresholds in the guild presence curves separate suitable from unsuitable habitat, defined by hydrologic and hydraulic conditions. The absence of vegetation is a strong indicator of an active channel or one that is inundated for most of the year (Osterkamp and Hupp, 1984). Transition from active channel to floodplain occurs when there is a loss of active channel processes (i.e., regular inundation and regular re-working of channel bed). Plots that were unvegetated had, on average, 25% greater velocities and were inundated for 50% more of the growing season, than vegetated plots.

Vegetation cover has been shown to be a distinct driver of plant-mediated geomorphic processes (Bennett et al., 2002). We found that plant cover strongly controlled the topographic response at Seacliff, but did little to influence the response at Harding Hole. Abiotic factors described a greater proportion of the variability in the Harding Hole and Laddie Park models. Differences in site models may be attributed to differences in the hydrologic and sediment regimes of the Yampa and Green Rivers. Flaming Gorge Dam on the Green River regulates flows and alters sediment discharges (Andrews, 1986; Grams and Schmidt, 2005), whereas the Yampa maintains key flow components of its natural hydrology. Recent experimental work has suggested that when sediment supply is low relative to transport capacity, plants have a greater impact on the magnitude of change compared to when a sediment balance exists (Diehl et al., 2017b).

Differences in the sediment balance of the Yampa and Green may also explain the relationship between velocity, flow-path distance, and the topographic response on the two rivers. Because the sediment supply is more likely to be in balance with the transport capacity on the Yampa River, increasing peak velocity likely results in greater concentrations of sediment transported, and thus available for deposition during flood recession, farther away from the channel.

The unique topographic signature for each guild at Seacliff following a flood event may be explained, in part, with observations of how plant morphology determines a plant's influence on sediment mechanics (Diehl et al., 2017b; Whittaker et al., 2013). Large rigid plants can induce erosion, especially when stems are sparse (Perignon et al., 2013). Water accelerates around stems, causing the bed to scour locally (Temmerman et al., 2005). At the scale over which our data were collected and the predictive model constructed (i.e., the plot-scale), increasing cover of a late-seral guild such as the xeric one, likely indicates the presence of larger, rather than a greater number of, individual plants within a plot. When plants are flexible, increasing cover may instead lead to greater roughness, hydraulic energy loss, and increased deposition (Diehl et al., 2017b).

Thresholds may be indicative of hysteresis in the relationship between control and response variables (Beisner et al., 2003). Once a threshold is crossed, a return to a previous state is less likely (Scheffer et al., 2001). In the co-adjustment of plant communities and fluvial landforms, the removal of plants by scour represents a threshold phenomenon that has hysteretic characteristics. Scour of the bed around vegetation reduces the drag force necessary to dislodge a plant (Bywater-Reyes et al., 2015; Kui et al., 2014). Once removed, the hydraulic conditions shift, altering suitable habitat, and opening up space for a functionally similar (or different) guilds. Future development of a response curve that describes the conditions necessary to remove plants could aid riparian ecosystem management.

5.3. Predicting riparian ecosystem change with the eco-geomorphic model

Mounting pressure on water resources and associated threats to biodiversity (Barnett and Pierce, 2009; Vörösmarty et al., 2010) create a need for tools to evaluate the impact of flow-regime changes on riparian ecosystems. Our eco-geomorphic model can help evaluate general shifts in the plant community and in flood event morphodynamics. Because we built this model from empirical flow response curves, scenarios of altered flow attributes may be translated to the relevant control variables in order to apply the curves.

Our eco-geomorphic model accounts for some of the important interactions between ecological and physical processes that complicate eco-geomorphic predictions (Reinhardt et al., 2010). For example, in our model, guild presence relies on disturbance strength (Polzin and Rood, 2006) represented by the maximum event velocity, but flow velocities are dependent on roughness characteristics, including the morphology and density of plants. Iterative application of plant-guild presence curves based on output of a hydraulic model would help identify the likely presence of plant guilds given a change in flow regime attributes due to changes in management strategies and/or climate change effects on streamflow. Additionally, the shift in plant-guild presence, and as a result, flow velocities, impacts the topographic response. With these feedbacks accounted for, the model correctly predicted the presence of tall and short mesic herb guilds (Fig. 5), and deposition after the 2016 flood (Fig. 6). Some interactions or feedbacks, such as the co-adjustment of vegetation and topography across flood

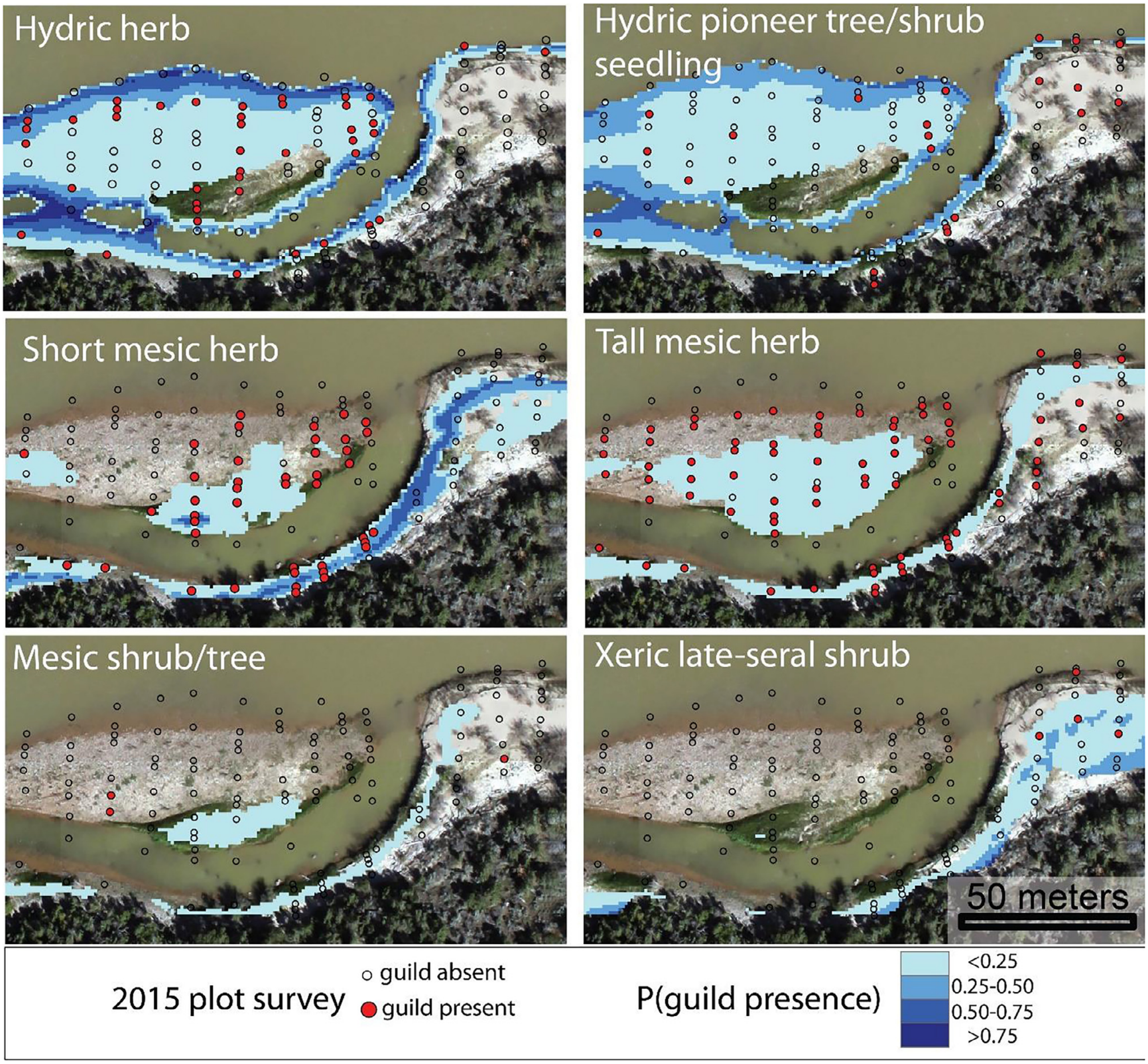

Fig. 5. Observed and predicted guild presence for the six guilds. Observed presence and absence of guilds is as surveyed in 2015 at the Seacliff site. Suitable habitat, as predicted by the six guild presence curves, is shown with blue shading, which covers areas where predicted probability exceeds the presence threshold; values are normalized to range between 0 and 1.0. Flow is from right to left. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

events, are not robustly represented in our model (See van Oorschot et al., 2017; Vesipa et al., 2015).

River systems respond to a shift in flow attributes over a range of spatial and temporal scales. Often, vegetation predictions are made for the reach or watershed, and at the plant community level at decadal time-scales, or longer, because these coarse scales integrate processes (Wu and David, 2002). Shifts in flow regimes often include multiple features, such as an increase in baseflows, a decrease in the magnitude of the largest floods, and an increase in the clustering of dry years (e.g., Magilligan and Nislow, 2005). Our eco-geomorphic model makes predictions at the reach-scale about shifts in plant communities over decadal time scales, but focuses on topographic changes at the scale of a single flood event. Modeling approaches such as ours that use field data to develop flow response curves can help predict conditions under which channels may be resilient or sensitive to change and in turn can inform management efforts.

6. Conclusion

We built a coupled eco-geomorphic model of riparian ecosystem dynamics that relies on a series of flow response curves and provides insights into the structure and functioning of riparian ecosystems. Flow response curves have proven useful for evaluating and predicting ecological and physical processes as they relate to the flow regime. However, their unidirectional nature is a limitation for understanding systems characterized by complex interactions and feedbacks. Our model relies on the linkage between ecological-response and morphological-effect traits of plants to incorporate process linkages between ecological and physical components. The model consists of a series of curves built from plant and topographic observations matched to flow-related attributes and include 1) individual curves for each plant guild that predicts their likely presence or absence, 2) a curve describing the density of plant coverage, and finally 3) a curve to predict the topographic response of a vegetated plot given abiotic factors and the

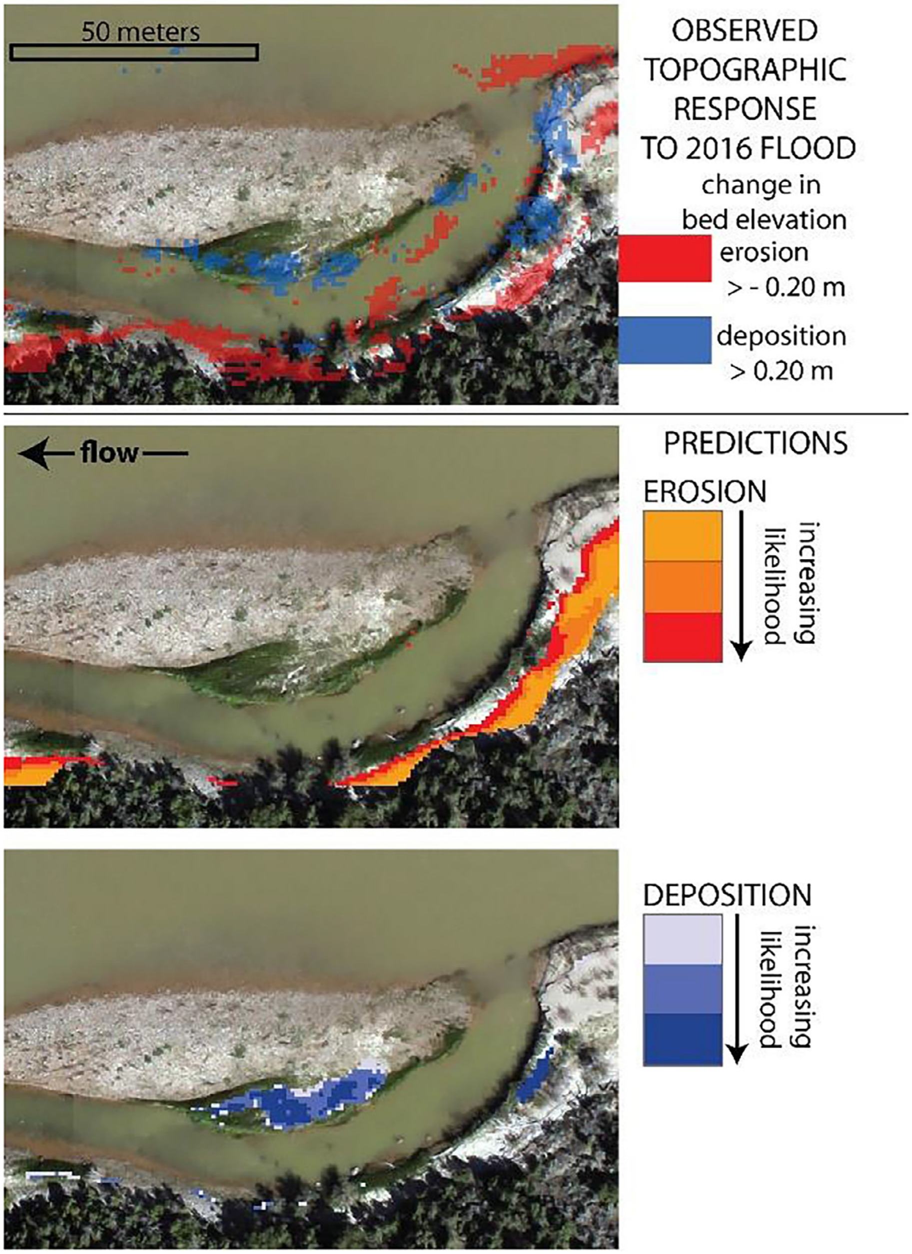

Fig. 6. Observed and predicted topographic response from the 2016 flood event at the Seacliff site. In the bottom two panels, we only show areas that are likely to experience erosion (middle) or deposition (bottom) based on thresholds identified in curve development. Because the topographic response curve is composed of linear models, the predicted values give a sense of the likelihood that an area will be erosional or depositional. Predicted values that are less (more negative) than the erosional threshold, are shown as being more likely to be erosional. Predicted values that are greater (more positive) than the deposition threshold, are shown as being more likely to be depositional.

predicted presence and cover of plant guilds. Our eco-geomorphic model predicted the spatial distribution of the riparian plant community along the semiarid, partially confined setting of the Yampa and Green Rivers in Dinosaur National Monument, with high accuracy. By incorporating this understanding into the topographic response curves, the model predicted some of the trends in physical processes. Our modeling provided indications of ecosystem sensitivity, whereby small changes to the flow regime can have consequential effects on the plant community and in turn, physical processes, and of the resilience of some ecosystems to change. Quantification of the relationships between flow attributes and ecosystem response, and formalization of these relationships into an eco-geomorphic model, will help river managers assess the impact of future changes in climate or river management.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecoleng.2018.08.024.

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