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Research article

Evaluation of the integrated riparian ecosystem response to future flow regimes on semiarid rivers in Colorado, USA

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ABSTRACT

Riparian ecosystems are shaped by interactions among streamflow, plants, and physical processes. Sustaining functioning riparian ecosystems in the face of climate change, growing human demands for water, and increasing water scarcity requires improved understanding of the sensitivity of riparian ecosystems to shifts in flow regimes and associated adaptive management strategies. We applied projected future flow regimes to an ecogeomorphic model of riparian and channel response to evaluate these interactions. We tested the hypothesis that components of the riparian ecosystem vary in their vulnerabilities to shifts in flow attributes and that changes in the representation of functional groups of plants result from interactions between ecological and physical drivers. Using the Yampa and Green Rivers in northwestern Colorado as our test system, we investigated ecogeomorphic response to (1) synthetic flow regimes representing continuous changes from baseline flows; and (2) future flow scenarios that incorporate changing climate, demand, and water-resource projects. For this region, we showed that riparian plant presence, composition, and cover are highly sensitive to the high flows that occur early in the growing season, but that shifts to low flows are also important, especially for determining the functional diversity of a riparian community. Future flow regimes are likely to induce vegetation encroachment on lower channel surfaces and to increase plant cover, which will be dominated by fewer functional groups. In particular, we predict a decrease in some mesic plants (shrubs and tall herbs) and an increase in presence and cover of late-seral, xeric shrubs, most of which are non-native species. Managing for high flows that occur early in the growing season must complement maintenance of adequate baseflows to maintain ecosystem functioning in the face of hydrologic alterations induced by climate change and human water demand.

Rebecca DiehlAndrew WilcoxJohn Stella

1. Introduction

Both water supply and water demand are changing in many regions due to a combination of human population growth and changes in climate and land use (Christensen et al., 2004; D'Odorico et al., 2018; Haddeland et al., 2014). These regional hydrologic changes often induce non-stationarity in river flow regimes and increased stress in dependent biotic communities (Milly et al., 2008; Poff et al., 1997). Sustaining aquatic and riparian ecosystems and their associated functions and services requires adaptive water management approaches that integrate an understanding of linkages among ecogeomorphic processes, although few such management frameworks exist (King and Brown, 2010; Tonkin et al., 2019; Wohl et al., 2015).

Riparian ecosystems are sensitive to flow regime shifts because of interactions and feedbacks among hydrology, plants, and their physical environment (Corenblit et al., 2007; Stella and Bendix, 2019). Water availability and inundation patterns during the growing season drive the creation and suitability of habitat for riparian species and regulate propagule dispersal, germination and establishment, and subsequent plant community dynamics (Scott et al., 1997; Mahoney and Rood, 1998; Corenblit et al., 2015). This is particularly true in arid and semiarid settings where water is the fundamental limiting resource (Stella et al., 2013; Diehl et al., 2017; Shafroth et al., 2000; Stromberg et al., 2010). Streamflow timing also affects riparian ecosystems, for example with respect to the congruence of high flows and seed-release or hydrochory (Merritt and Wohl, 2002; Stella et al., 2006).

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Flow regimes further influence riparian plant communities by governing physical processes that create and maintain channels and floodplains (Stella et al., 2011; Martínez-Fernández et al., 2018). Plant communities are adapted to the severity and frequency of disturbance, taking on growth forms that either tolerate or avoid high stresses associated with high velocities or long inundation periods (Puijalon et al., 2011). Frequent floods create bare substrates suitable for pioneer plant establishment within or near the active channel (Bertoldi et al., 2011; Scott et al., 1997), whereas larger floods activate higher surfaces with older or less flood-tolerant plants (e.g., Dean and Schmidt, 2011), uproot vegetation (Bywater-Reyes et al., 2015; Kui et al., 2014), and create or eliminate habitat via channel-planform alterations (Stella et al., 2011). Decreases in flood magnitude and frequency can result in a greater uniformity and cover of riparian plants, especially along previously unvegetated areas near or within the active channel, in turn reducing flood velocities and further altering channel morphology and associated plant distribution, composition and structure (Kui et al., 2017; Merritt and Cooper, 2000; Shafroth et al., 2002). Changes in riparian plant community composition have been documented along many rivers with altered flow regimes, although determining the relative influences of changes in magnitude, frequency, timing, and other flow attributes is difficult (Stella and Bendix, 2019). For example, on many rivers in the southwestern U.S., native cottonwood (*Populus* spp) and willow (*Salix* spp.) communities have declined and non-native tamarisk (*Tamarix* spp.) and Russian olive (*Eleagnus angustifolia*) have expanded concurrent with flow regime shifts due to both river regulation and climate change (Friedman et al., 2005; Kui et al., 2017; Merritt and Poff, 2010).

In this context, the objectives of our present study are to (1) evaluate the relationship among river flow attributes, the presence and cover of riparian plants, and the geomorphic effectiveness of floods for rivers in the semiarid western US, and (2) use this understanding to estimate the effects of projected future changes in river flow attributes on riparian ecosystems. First we quantified relationships between the flow regime and riparian ecosystem attributes using an ecogeomorphic model developed and described by Diehl et al. (2018). This model represents interactions and feedbacks among flow, plants, and geomorphic processes and was developed using empirically derived flow response curves based on observed linkages between flow regime attributes and ecogeomorphic properties of the riparian ecosystem. The model uses riparian plant guilds, or functionally similar groupings of species, to allow for greater taxonomic generalization than for a species-based model (Merritt et al., 2010). The ecogeomorphic model predicts, at a plot scale, how plant guilds adjust to changing flow regimes over multiple decades (Diehl et al., 2018).

The responses of riparian plants and physical processes to shifts in flow attributes are often nonlinear (Dean and Schmidt, 2011; Manners et al., 2014), and the shape of a flow response curve provides insight into the behavior of individual riparian ecosystem attributes (Diehl et al., 2018). For example, the flow response curves in Diehl et al. (2018) ecogeomorphic model suggested the presence of thresholds in the response of some ecosystem attributes, including plant guild presence and cover, to changes in flow regimes. As such, we hypothesize that changes to attributes of the flow regime (e.g., changes to low versus high flows), will have variable impacts on different ecosystem attributes, and that these impacts will be manifested by shifts in the spatial distribution and cover of plant functional groups. To address this hypothesis, we first use the Diehl et al. (2018) ecogeomorphic model to predict shifts in the riparian community, including changes to the distribution and presence of guilds, at three sites on the Yampa and Green Rivers, Colorado, under a range of hydrologic regimes that represent a continuum of changes from the current regime. We then apply this framework to one of these sites and evaluate the integrated riparian ecosystem response to three flow scenarios developed by the State of Colorado to guide future surface-water appropriations (Gallaher et al., 2013). Evaluating likely changes using these two approaches provides insight into which flow attributes drive changes in the riparian vegetation community, including site-scale and plot-scale cover, and the relative abundance of different plant guilds under different future scenarios.

2. Water resources in the Colorado River Basin

The ecogeomorphic model we apply here was developed from data collected on the Yampa and Green Rivers in western Colorado, which are in Dinosaur National Monument and are part of the Upper Colorado River Basin (UCRB). River hydrographs in the UCRB are dominated by snowmelt from the Rocky Mountains (Christensen et al., 2004) and have several consistent attributes. Peak snowmelt floods historically arrived to the Yampa and Green Rivers between mid-May and early June. Following the recession of spring snowmelt floods, groundwater sustains baseflow throughout the summer and fall, interrupted occasionally by runoff derived from late-summer convective thunderstorms.

Water supply, irrigation, and hydropower collectively place heavy demands on water resources in the UCRB, and streamflow on most rivers in the basin is controlled by dams, diversions, and pumping projects (Schmidt, 2008). Within our study area, Flaming Gorge Dam regulates streamflow on the Green River. The Yampa River remains relatively unregulated, with no major dams or diversions (Grams and Schmidt, 2002; Manners et al., 2014; Richter et al., 1995).

The UCRB has already experienced hydrologic drying, with observed decreases of annual-mean discharge at a rate of 9.3% per °C of warming (Milly and Dunne, 2020). Climate change affects river flows in the UCRB by a combination of direct and indirect mechanisms including decreased reflection of solar radiation by snowpack associated with snow loss, enhanced rates of plant evapotranspiration, reservoir evaporation, snow sublimation, and soil-moisture depletion, as well as by altering the seasonal timing of precipitation and high stream flows (Milly and Dunne, 2020; Woodhouse et al., 2016). Some studies suggest that enhanced precipitation will offset runoff decreases directly associated with warmer temperatures, especially in the warm season. Modeling informed by data from the early 21st century drought in the western US, however, indicates that even with the uncertainty in temperature shifts and in the direction and magnitude of precipitation change, runoff is likely to decrease by 35–55% by the end of the century (Udall and Overpeck, 2017). Maintaining current water allocations and deliveries in the UCRB in the face of likely decreases in runoff and increases in consumptive use will exacerbate future supply and demand imbalances (Barnett and Pierce, 2008; Reclamation, 2012).

The Colorado Water for the 21st Century Act, passed in 2005 by the state of Colorado, mandates completion of a water-needs assessment and an analysis of available unappropriated water for each major river basin in the state, as well as proposed projects or methods for meeting those needs. As part of these assessments, future flow scenarios that incorporate projections of consumptive water demands, climate, and water-resource projects were developed for the Yampa and White River Basins, Colorado, which are significant tributaries of the Green River within the UCRB (Fig. 1; Yampa/White/Green BIP, 2015). Consumptive demands are projected to grow in the region, as incorporated into the scenarios, with increases of 98–237% relative to 2008 demands (Yampa/White/Green BIP, 2015). Climate projections are represented in the future flow scenarios as ranges of annual water supply, spanning wet to dry, as well as an average condition similar to historical average annual water supply. The future flow scenarios also include existing and proposed reservoirs that store water and control downstream flow and diversions, representing these water-resource projects as either implemented (all) or not implemented (none). In this paper we evaluate three of the future flow scenarios identified in the Basin Implementation Plan (BIP) (Yampa/White/Green BIP, 2015), as described in section 3.3 below. These scenarios represent realistic flow regimes that rivers in the Yampa and White River Basins may experience in the future and incorporate the most up-to-date information from models and forecasts at the time the BIP was written. These models and forecasts will continue to be updated based on new techniques or information (e.g.,

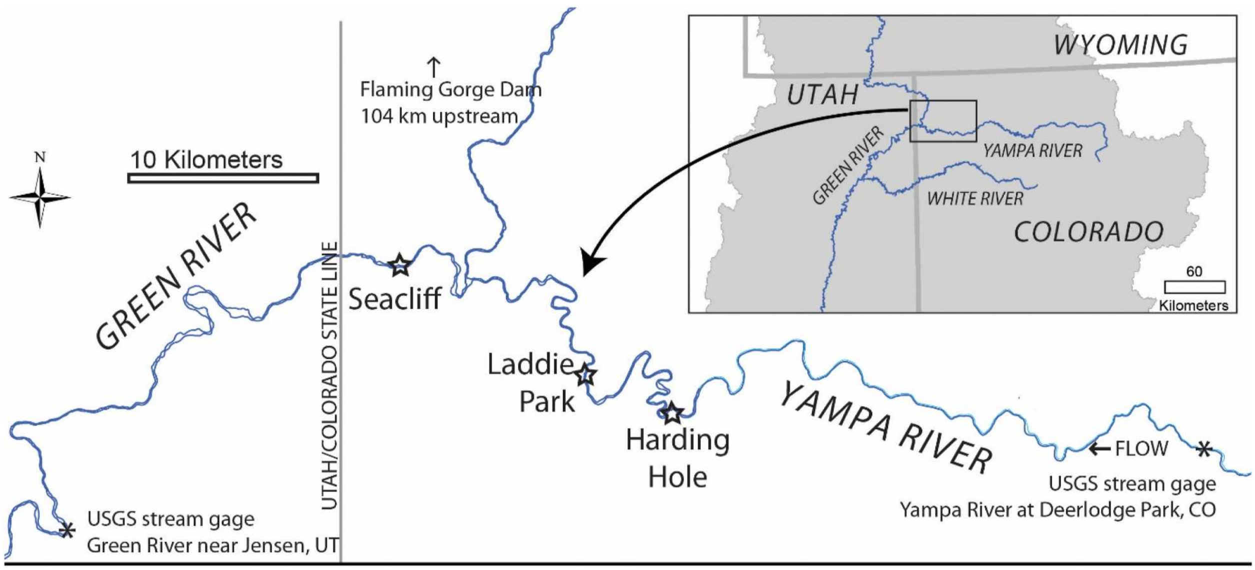

Fig. 1. Location of three study sites used in the development and application of the ecogeomorphic model (adapted from Diehl et al., 2018). Inset shows position of study area within the UCRB.

Yampa/White/Green BIP Phase 3, 2018), and as a result, the future flow scenarios are also likely to change.

3. Methods

To predict how riparian ecosystems will change in response to altered hydrologic regimes, we used an ecogeomorphic model that includes hydrologic, geomorphic and biotic elements (Diehl et al., 2018). We provide background on the ecogeomorphic model in section 3.1 and in Supplementary Information. In sections 3.2 and 3.3 we describe two different approaches used in this study to identify the response of riparian ecosystem attributes to changes in flow regimes. First, to evaluate a spectrum of riparian-ecosystem changes to hydrologic alterations, we applied synthetic flow-duration curves, based on continuous changes from baseline flow conditions, to develop plant response functions (i.e., 'flow-response curves') for total cover and for relative importance of various plant guilds at three sites on the Yampa and Green Rivers (section 3.2). Second, we applied future flow scenarios identified for the Yampa River within Dinosaur National Monument to the entire ecogeomorphic model for a single site (section 3.3). This approach illustrates the potential co-adjustments of the riparian community and event-scale erosion and deposition of sediment.

3.1. Ecogeomorphic model description and application

The ecogeomorphic model applied here (Diehl et al. 2018) consists of flow response curves that collectively predict riparian ecosystem change resulting from a shift in hydrologic properties. Flow response curves are modeled relationships of ecosystem properties to flow regime drivers, and they are typically fit to empirical data using generalized linear models. The flow response curves used in this study were developed from a three-year dataset (Table S1, Supplementary Information) collected at two sites on the Yampa River and one site on Green River, Colorado (Fig. 1). The theoretical approach and development of this ecogeomorphic model are described in Diehl et al. (2017) and Diehl et al. (2018), respectively. Fig. S1 illustrates the structure and process flow of the ecogeomorphic model (Supplementary Information).

Diehl et al. (2018) developed three categories of flow response curves (Table S2). The first class of curves relates the presence of plant guilds to the availability of water (i.e., a limiting resource) and disturbance strength (i.e., a critical stressor), parameterized with the number of days a plot is inundated during the growing season (April 26 to October 10, a total of 168 days per year) and the maximum velocity of a given flood event, respectively. The model is based on data for six unique plant guilds that represent a range of ecologic and morphologic traits, from hydric to xeric and from short herbaceous to tall woody plants (Diehl et al., 2017 and Table S3). The April 26 to October 10 growing season encompasses both the typical freeze-free period and the temporal range of peak flows. The second set of curves predicts the distribution of plants, including presence/absence of plants in general and proportion of cover, both of which depend on water availability and disturbance strength. The proportion of cover is also dependent on the types of guilds present. The third set of curves predicts the occurrence and direction of topographic change (i.e., erosion versus deposition) from individual floods, as a function of the sediment transport rate (i.e., maximum event velocity), sediment supply (i.e., represented by proxy as flow distance from main channel), and vegetation cover.

Diehl et al. (2018) tested the predictive power of the ecogeomorphic model using an independent set of observations from randomly located plots at the same sites used to develop the model; these data represent observations from a fourth field survey in 2015 (Table S1). Based on this validation approach, the model had average classification rates (i.e., proportion of correctly classified plots) of 69% for plant-guild presence and 66% for plant distribution (Diehl et al., 2018). Predictions were stronger of plant guild absence (74%) than they were of presence (54%) (Table S2). Because our model testing indicated higher classification rates for riparian vegetation responses (i.e., the first two classes of curves described above) than for topographic responses (i.e., the third set of curves in the ecogeomorphic model; additional information in Supplementary Information and Diehl et al. (2018)), we have greater confidence in the riparian-vegetation response elements of the ecogeomorphic model and focus on those in this paper.

The ecogeomorphic model relies on hydrologic metrics identified from flow duration and flood frequency curves. The model was developed using hydrologic data from the USGS Yampa River at Deerlodge Park, CO stream gage for the two Yampa River sites and the USGS Green River near Jensen, Utah gage for the Green River site (Fig. 1). Output from two-dimensional (2D) hydraulic models developed for each of the three sites was used to define a plot's inundation discharge and discharge-velocity rating curve. Hydraulic models were built in iRIC's FaSTMECH (Nelson et al., 2016) and are described in Diehl et al. (2018). To represent the typical inundation conditions for woody and herbaceous plants during the growing season, Diehl et al. (2018) constructed flow duration curves (i.e., the proportion of time any given flow is exceeded during a typical year) for the growing season period as defined above. They used a 5-year time series to model herbaceous plant responses and a 20-year time series to model woody plants, which have longer life spans. Flood frequency curves were constructed for the hydrologic record (1923–2015), and maximum velocity during a 3-year and 20-year return period flood were used for herbaceous and woody plants, respectively (Diehl et al., 2018).

For both approaches outlined below (sections 3.2 and 3.3), we used the ecogeomorphic model to evaluate the impact of a flow regime on riparian ecosystem change at the plot scale. For the flow regime scenarios considered, we updated the number of days each plot was inundated during the growing season (i.e., water availability) and the maximum velocity associated with the 3-year or 20-year flood (i.e., disturbance strength) using our 2D hydraulic models. These updates depended on the hydrologic attributes of the scenario and the inundation discharge and discharge-velocity rating curve, specific to a single plot.

3.2. Modeling hydrologic alteration along a continuum

We modeled future ecosystem responses along a continuum of hydrologic change using synthetic flow duration curves that represent a range of potential future conditions. These synthetic curves were generated by adjusting elements of the baseline flow duration distributions, which were compiled using a recent 20-year period (1996–2015) of mean daily discharge records for the growing season, recorded at the two USGS stream gages (Fig. 1). From these baseline curves, we identified the flows with 1% and 75% daily exceedance probabilities (EP) and herein refer to them as "high" and "low" flows, respectively. The high flow (1% EP) is equaled or exceeded ~1–2 days during the growing season. It is representative of flows that are important for physical processes (e.g., sediment transport, channel migration and floodplain development) and also punctuated biotic responses related to dispersal, colonization, and mortality from scour. The low flow (75% EP) is equaled or exceeded 124 days, on average, during the growing season. It is representative of discharge levels that frequently inundate or provide moisture to channel edges that correspond to water-table levels in many rivers and that influence key plant traits tied to stable water supply (e.g., growth, hydric stress, inundation tolerance). As a way to evaluate the full spectrum of potential shifts to ecosystem attributes, we analyzed 81 distinct combinations of bivariate shifts in high and low flows, with reductions of up to 99% and increases of up to 100% of the baseline values (Fig. 2). Future flood peak magnitudes for floods with a 3-year and 20-year return period were also simulated using the same proportional change as the high flow for a given scenario.

We applied the range of these synthetic curves to the three study sites (Fig. 1) and compiled the combined results as change surfaces for each response variable. These change surfaces depict how long-term shifts in flow attributes (e.g., 1% EP high flows and 75% EP low flows) translate to shifts in vegetation cover and composition as expressed through riparian plant guilds, relative to baseline conditions. Because plant communities evolve over time, we note that by projecting the baseline hydrology out 20 years, similar to the other scenarios, the presence, composition, and cover of riparian plant guilds in the baseline hydrologic scenario differ from those we documented in our field surveys.

To evaluate how the hydrologic shifts simulated here alter functional diversity, or the representation of plant traits, we quantified Simpson's diversity index, D $(1/\sum_i^s p_i^2)$, where p_i is the proportional representation of each riparian plant guild and s is the total number of guilds. We use D to summarize the relative abundance of each of the six guilds modeled. Thus, the index is a measure of functional diversity, and more specifically, functional evenness. Larger D values indicate a more equal representation of plant guilds, and therefore, of functional traits.

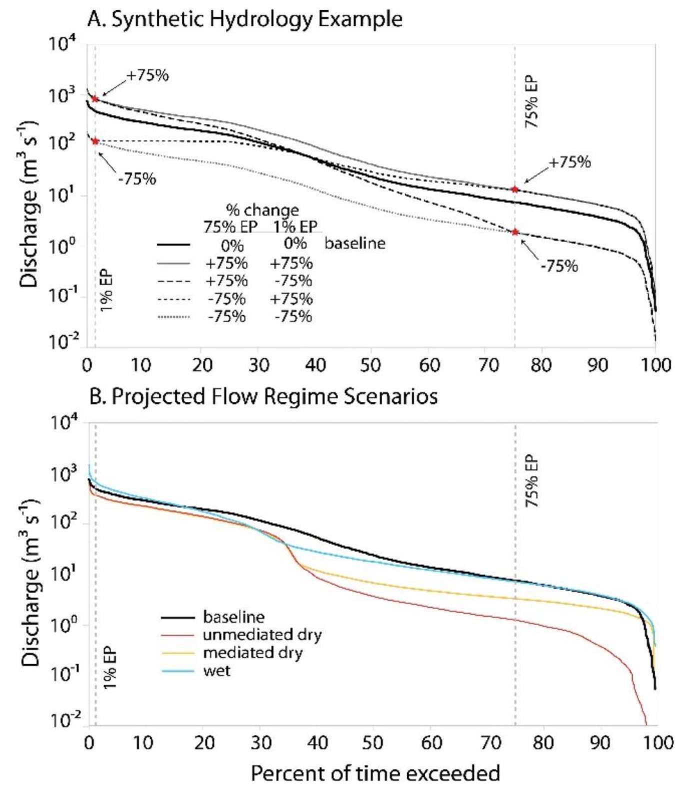

Fig. 2. Growing-season flow-duration curves used in application of the ecogeomorphic model: (A) Yampa baseline (black line) and four example synthetic exceedance probability (flow duration) curves that differ from the baseline by ±75%; these were created by adjusting the 1% and 75% exceedance probabilities (EPs) relative to the baseline condition; (B) Flow-duration curves for three projected flow regime scenarios identified by the Yampa/White/Green BIP and the baseline condition for the Yampa River (black line).

3.3. Evaluating integrated ecosystem response to future flow scenarios for Laddie Park, Yampa River

We complemented predictions of vegetation response for the three sites with a case study to evaluate potential changes to the riparian ecosystem for specific flow-regime scenarios at one of the sites, Laddie Park in Dinosaur National Monument (Figs. 1 and 3). Similar to the other two study sites, Laddie Park has multiple channels separated by a mid-channel bar, a type of setting that provides critical habitat for endangered fish (Tyus and Karp, 1990) and has been the focus of other ecogeomorphic studies (Manners et al., 2014, 2013). At this site we applied the integrated ecogeomorphic model to three future flow scenarios (Table 1; Yampa/White/Green BIP, 2015). These scenarios represent flow regimes under (1) a dry climate, with high consumptive demands, and without implementation of water-resource projects ("unmediated dry"); (2) a dry climate, with high consumptive demands, and with implementation of water-resource projects ("mediated dry"); and (3) a wet climate, with existing consumptive demands, and with implementation of water-resource projects ("wet") (Table 1). The three scenarios were chosen, out of the six total evaluated in the BIP, because they represent the maximum and minimum changes from the baseline condition. We also applied the ecogeomorphic model to the 1996–2015 baseline flow condition (described in section 3.2) as a point of reference (Fig. 2).

The three future flow scenarios were provided to us in monthly flow volumes for a 56-year period, based on adjustments to flow volumes measured from 1950 to 2005. We disaggregated the total volume of water predicted to pass the Yampa River at Deerlodge Park, CO USGS stream gage into average daily discharge values. To do this, we scaled

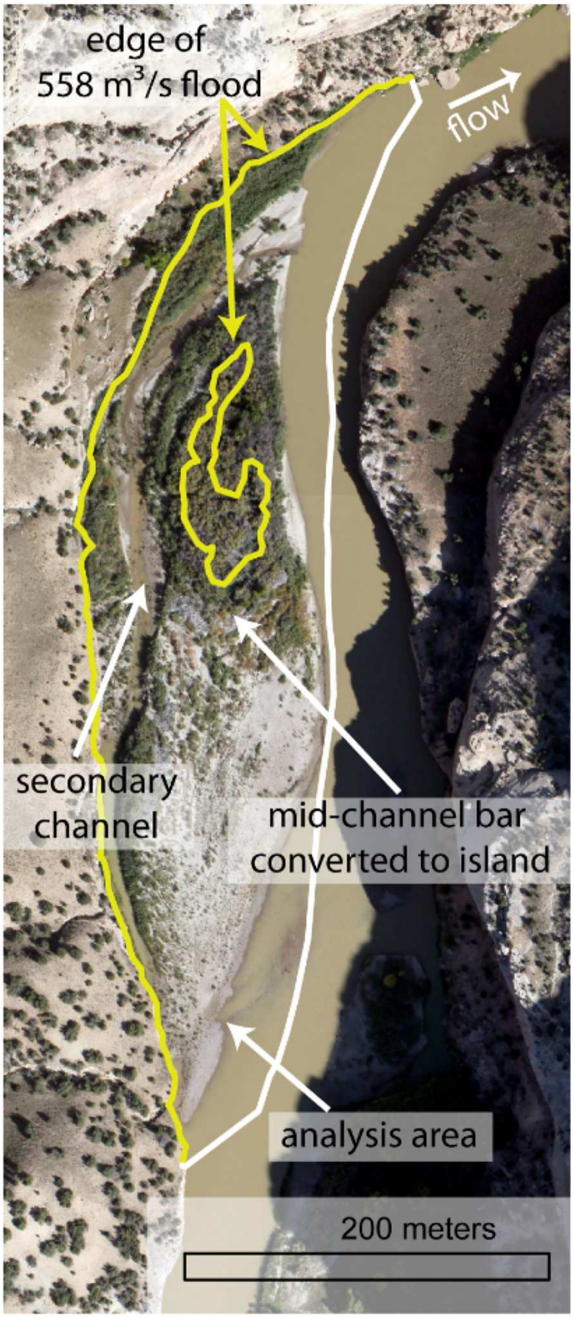

Fig. 3. Laddie Park study site on the Yampa River; larger study area shown in Fig. 1. Area of analysis is shown, defined on river left by the edge of the 100-year flood for the mediated dry scenario (558 m^3 s^{-1}). The Laddie Park site is characteristic of systems with bedrock-controlled, deeply incised meanders and, more specifically, of subreaches in such settings that have multiple channels separated by mid-channel bars. During the past century, an increase in the clustering of wet and dry years led to the vegetation establishment on the Laddie Park mid-channel bar, promoting both sediment accumulation in the form of inset floodplains and vertical accretion on the existing bar (Manners et al., 2014).

daily historical data, for the years 1950–2005, to match the predicted monthly volumes for each year. The resulting time series represents the variability in monthly flow volume within and between each year in the predicted 56-year time series, while at the same time reflecting the Yampa River's annual and decadal variability (Manners et al., 2014; Murphy and Ellis, 2014). Next, we developed flow duration and flood frequency curves for the three future flow change scenarios, for the

Table 1
Projected future flow scenarios identified by the State of Colorado in the Yampa/White/Green River BIP (2015). Changes to hydrology, including with respect to exceedance probability (EP) of low (75% EP) and high (1% EP) flows and recurrence interval of moderate (3-year) and large (20-year) floods, are relative to a baseline condition based on 1996–2015 flows. Exceedance probabilities are based on flow duration curves constructed using mean daily discharge for the growing season, and recurrence intervals are determined from annual maximum mean daily discharge. The baseline condition served as a fourth set of flows evaluated in our ecogeomorphic modeling.

Scenario		Change in Hydrology from Baseline Condition			
		75% EP (low flows)	1% EP (high flows)	3-yr Flood	20-yr Flood
1. High Demand, Dry Hydrology, No Projects[a]	"Unmediated Dry"	−83%	−28%	−33%	−28%
2. High Demand, Dry Hydrology, All Projects[b]	"Mediated Dry"	−56%	−29%	−35%	−29%
3. Existing Demand, Wet Hydrology, All Projects[c]	"Wet"	−5%	35%	33%	55%

[a] Corresponds to Yampa/White/Green BIP model scenario #6.
[b] Corresponds to Yampa/White/Green BIP model scenario #1.
[c] Corresponds to Yampa/White/Green BIP model scenario #5.

56-year record, for use in the ecogeomorphic model (Fig. 2). We then calculated the 1% and 75% EP flows, as we did for the synthetic hydrograph analysis (section 3.2), as well as the 3-year and 20-year flood magnitudes (based on the daily mean discharges), for the three future flow scenarios. We compared the predicted riparian-vegetation conditions in response to the three future flow scenarios to those expected under the baseline condition (i.e., no change in hydrology). We also quantified *D* for each of these scenarios, to measure their effect on functional diversity, as for the flow simulations described in section 3.2.

To apply the ecogeomorphic model, we first iteratively updated the hydraulic model, accounting for the feedback between plot-level hydrologic conditions and the likely presence and cover of plants. A change in vegetation cover influences flow velocities and inundation stage, in turn altering the likelihood that a given guild will be present in a plot and how densely the plot is vegetated. Once the predicted guild presence and cover from the flow response curves reached an equilibrium with flow variables (i.e., <5% cover change with further iteration), we then use the updated model to predict the topographic response of the site to floods (Supplementary Information).

To compare the plant response to the three scenarios and baseline condition, we summarize the presence, cover, and guild composition at the Laddie Park site for the area (41,000 m^2) inundated by the mediated dry scenario's 100-year flood elevation, corresponding to a 558 m^3 s^{-1} flood. Over time, areas above the 100-year flood are likely to be colonized by upland plants. Because these types of guilds were not included in our model, we chose to only compare areas where riparian plants were projected to dominate across all four scenarios. To simplify our discussion, we summarized some of the results based on dominant habitat type (i.e., mesic, hydric, xeric). Because of the governing influence of hydrology on these habitat types, we anticipated that guilds within each group would have a relatively similar response to hydrologic shifts. Maps of probable habitat distributions were created for the dominant habitat types by separating predictions into presence and absence, based on thresholds from logistic regressions used to describe flow response curves (Table S2 and Diehl et al., 2018). We normalized values that exceeded the presence threshold to range between 0 and 100%.

4. Results

4.1. Plant cover and guild response to synthetic hydrographs

Plant response predicted by the ecogeomorphic model was sensitive to changes in both low (i.e., 75% EP) and high (i.e., 1% EP) flows, with vegetation presence (Fig. 4A) and cover (Fig. 4B) anticipated to increase the most with decreases in both the high and low flows. In other words, drier conditions were predicted to result in expansion and encroachment of vegetated surfaces and increased plant cover.

The two hydric guilds are sensitive to changes in both low and high flows (Fig. 5A–B). Declines in low flow magnitude were projected to decrease cover of hydric guilds, most substantially with a concurrent decrease in high flow magnitudes. Conversely, hydric guild cover was projected to increase moderately with large increases to both low and high flows. The response of the three mesic guilds varies (Fig. 5C–E), though all three are more sensitive (i.e., a greater rate of change) to alterations in high flows compared to low flows. For both decreased high and low flows, mesic short herb presence was projected to increase at the expense of mesic tall herbs, shrubs and trees, all of which were projected to decrease. Of all the guilds, the xeric late-seral shrubs is the most sensitive to changes in high flows (Fig. 5F). Small changes to high flows were projected to result in large (relative to the response of the other guilds) changes in the presence of xeric plants. Xeric plant cover decreases with an increase in high flows, and conversely, increase in response to a decrease in high flows.

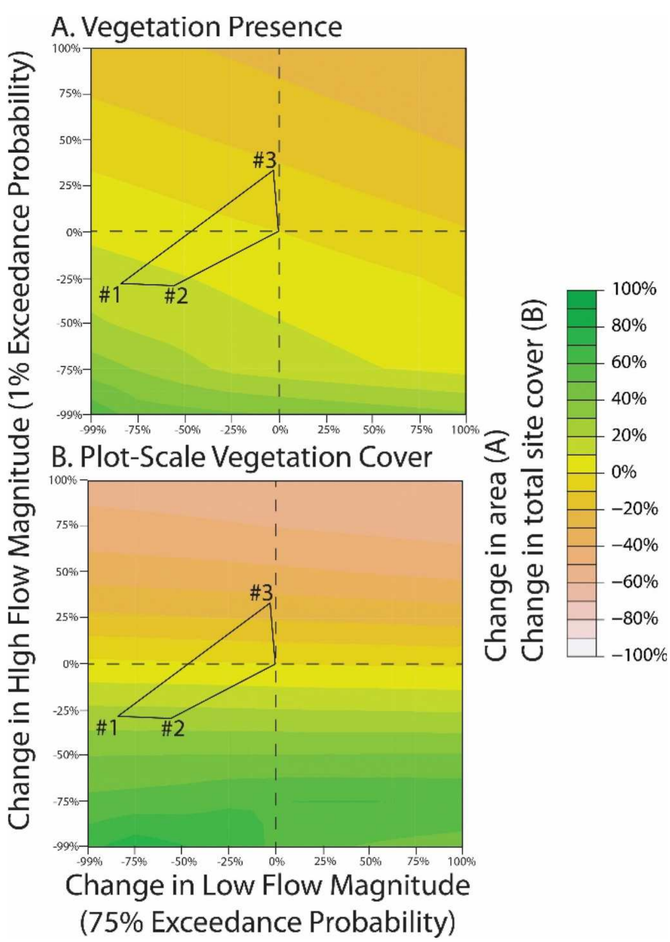

Fig. 4. Change surfaces depicting shifts in vegetation properties on the Yampa and Green Rivers with altered hydrologic regimes relative to baseline conditions (represented by the plot origin), including percent changes in (A) probability of riparian vegetation presence and (B) proportion of vegetation cover, measured at a plot scale. Surfaces represent average of 1 m^2 plot-scale changes at three study sites. The polygon circumscribes the range of Yampa River flows projected across the three modeled scenarios: (1) unmediated dry; (2) mediated dry, and (3) wet (Table 1).

Plant guild evenness (i.e., Simpson's D) showed little sensitivity to moderate changes in either high or low flows (Fig. 6). As the magnitude of changes in high and low flows increases, changes in plant guild evenness increases. Decreases to low flows were projected to reduce guild evenness and conversely, increasing baseflow discharge would proportionately diversify the distribution of guilds (Fig. 6).

The overall range of hydrologic modifications projected by the three Yampa River future flow scenarios (described in section 3.3), as bounded by the polygons in Figs. 4–6 corresponds to a −10 to +20% change in the likely presence of plants in general (Fig. 4A) and a −30 to +30% change in plant cover (Fig. 4B). Under the dry and mediated dry scenarios, hydric guild distributions were projected to contract 10–30%, while the mesic and xeric guilds expanded or contracted by as much as 40% (Fig. 5). As a result, plant guild composition on the Yampa River was predicted to homogenize, decreasing evenness by 10–20% (Fig. 6).

4.2. Integrated ecosystem response to projected changes in the flow regime: Laddie Park, Yampa River

In the Laddie Park analysis, the proportion of the site area within the 100-year flood zone (corresponding to 558 $m^3 s^{-1}$) that is vegetated is projected to increase in the dry scenarios and decrease in the wet one, relative to the baseline (Table 2; Fig. 7). In the dry scenarios, both vegetation presence and average cover increases as estimated on a plot basis. In the wet scenario, the number of plots predicted to have vegetation increases, but the average plot cover decreases. In all scenarios vegetation cover is greatest (>75%) on the island and on the upper elevations along the left bank, and lowest (0–25%) through the secondary channel.

Hydric guild habitat occupies ~10% of modeled vegetated areas for the baseline hydrologic condition. Slight changes at Laddie Park were predicted to occur in response to shifts to both high and low flows, predominately through the secondary channel and at the head of the mid-channel bar (Table 2; Fig. 7). In the dry scenarios, hydric habitat expands into the middle of the secondary channel as a result of decreased peak flood velocities. Differences in the changes to low flows in the dry scenarios determine the contraction (unmediated dry) or expansion (mediated dry) at the head of the mid-channel bar. Low-lying areas here are close to the inundation threshold set for hydric plants (i.e., >126 days inundated, creates unsuitable habitat). In the wet scenario, habitat contracts because prolonged inundation crosses the threshold for hydric plant tolerance, suppressing plant growth.

Mesic guild habitat occupies ~50% of modeled vegetated areas for the baseline hydrologic condition. Although short mesic guild habitat was anticipated to increase substantially for the dry scenarios, most notably within the secondary channel, tall mesic herbs and mesic shrub/tree guild distributions were expected to contract, disappearing from higher elevation surfaces (Table 2; Fig. 7C). As a result there is a general reduction in mesic guild habitat. In the wet scenario, mesic habitat increases to 60% of future vegetated areas, expanding to higher elevations. Although the spatial distribution of potential mesic guild habitat is broad, the probability of occurrence for these guilds is relatively low, generally less than 25%. The exception is for the mediated dry scenario, where there is a higher probability that mesic plants (specifically, short mesic herbs) will establish in the secondary channel.

Xeric guild habitat occupies 38% of future vegetated areas for the baseline hydrologic condition; this was projected to decrease slightly for the wet scenario but to increase substantially under both dry scenarios. These projected shifts in guild presence will collectively result in a decrease of Simpson's diversity index from the baseline case ($D = 2.4$; Table 2) for all three scenarios, by between 6% and 17%.

The combination of altered flood characteristics with shifts in the cover, composition, and spatial distribution of plant guilds also

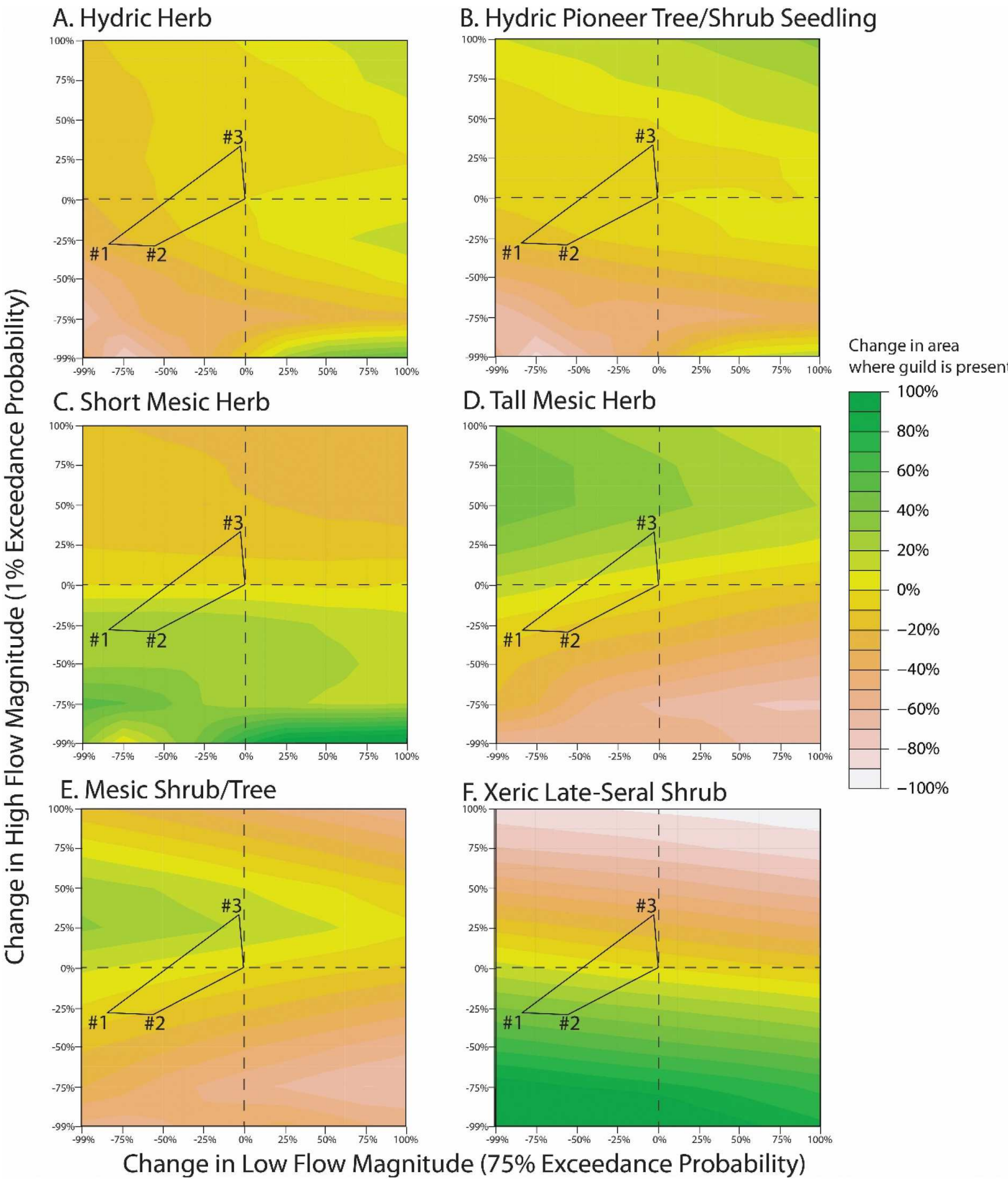

Fig. 5. Change surfaces depicting shifts in the probability of individual plant guild presence predicted by the ecogeomorphic model with altered hydrologic regimes, relative to baseline conditions (represented by the plot origin), on the Yampa and Green Rivers. Surfaces represent average of 1 m^2 plot-scale changes at three study sites. The polygon circumscribes the range of Yampa River flows projected across the three modeled scenarios: (1) unmediated dry; (2) mediated dry, and (3) wet (Table 1).

influenced channel geomorphic effects of individual floods. Results from the topographic response curves for Laddie Park are summarized in Supplement Fig. S2. These results generally showed that, compared to the baseline condition, depositional areas increase under all scenarios. Erosional areas decrease slightly during the dry scenarios and increase as a result of moderate floods under the wet scenario. There is a more significant decrease in erosional areas as a result of large floods.

5. Discussion

5.1. Variable response of different riparian plant guilds to future shifts in low and high flows

Our results illustrate the variable impact of likely, near-future changes in high and low-flow attributes of the flow regime on different properties of the riparian ecosystem along semiarid rivers in the UCRB. Our model shows strong sensitivity of riparian plants to

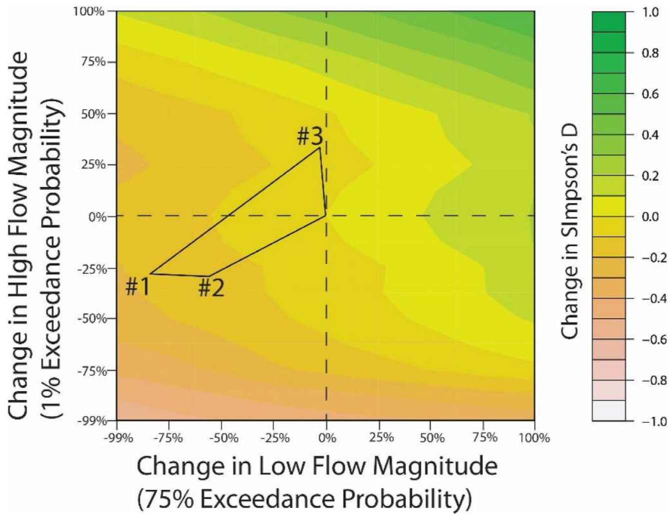

Fig. 6. Change surface depicting modeled shifts in guild evenness with altered hydrologic regimes, relative to baseline conditions (represented by the plot origin), on the Yampa and Green Rivers. Surface represents average of 1 m^2 plot-scale changes at three study sites. The polygon circumscribes the range of Yampa River flows projected across the three modeled scenarios: (1) unmediated dry; (2) mediated dry, and (3) wet (Table 1).

changes in high flows, especially with respect to the presence of xeric plant guilds and plant cover. We also found that changes to low flows were important, especially for determining the magnitude and direction of changes to hydric and mesic plants, and for overall riparian plant functional diversity.

Whereas future flow projections in the Yampa River basin consistently predict decreases in low flows, projections for high-flows are more variable; most projections indicate that high flows will decrease, but under some scenarios high flows are predicted to increase (e.g., the wet scenario in Table 1). Changes in high-flow magnitude and timing would alter the spatial and temporal patterns of fluvial disturbance along channel margins and floodplains, and therefore the area available for plant recruitment and establishment, seed dispersal patterns (Merritt and Wohl, 2002; Stella et al., 2006; Stromberg et al., 2010), growing conditions, and flood vulnerability of native versus nonnative plants (Kui et al., 2019; Shafroth et al., 1998).

In dry climates, such as the semiarid southwestern US, warming-induced increases in evapotranspiration rates and decreases in soil moisture (Barnett et al., 2005) will increase the importance of water availability to riparian plants late in the growing season. The importance of low flows can be discerned by comparison of the two Yampa River dry scenarios. As shown in Table 1, water-resource projects could lessen, but not eliminate, the magnitude of climate-change-induced reductions to low flows. Our modeling shows that compared to the unmediated dry scenario (83% reduction in low flows), the mediated dry scenario (56% reduction in low flows) results in greater expansion of hydric and short mesic guild habitats, greater contraction of tall mesic herb and mesic shrub guild habitat and, in turn, greater reductions in functional diversity.

Anticipated changes to hydrologic attributes with a drying climate are likely to increase plant cover and vegetation encroachment onto low-elevation surfaces, as well as favor drought-tolerant guilds such as xeric late-seral shrubs. These model predictions are consistent with observed shifts in plant-community distribution on dryland rivers and particularly within the CRB (Friedman et al., 2005; Kui et al., 2017; Merritt and Cooper, 2000; Reynolds and Shafroth, 2017). The expansion of xeric plants will be at the expense of mesic and hydric plants, including early-seral tree species, such as the mesic shrub/tree guild. This is consistent with other predictions of native riparian-plant declines with climate change (Perry et al., 2012; Stromberg et al., 2010).

Table 2
Results for the application of the baseline condition and three projected flow scenarios to the ecogeomorphic model at Laddie Park.

Scenario	Iteration Error		Presence and Cover[c]			Hydric		Mesic			Xeric	
	Guild[a]	Presence[b]	Vegetation Presence[d]	Plot-Scale Vegetation Cover[e]	Site Vegetation Cover[f]	Herb[g]	Pioneer Tree/Shrub Seedling[g]	Short Herb[g]	Tall Herb[g]	Shrub[g]	Late-Seral Shrub[g]	Simpson's D
Baseline	0.7%	1.7%	69%	54%	37%	7%	10%	6%	34%	36%	38%	2.44
1. Unmediated Dry	0.3%	0.1%	75%	69%	52%	8%	10%	16%	26%	26%	52%	2.28
2. Mediated Dry	4.4%	1.7%	76%	72%	55%	12%	12%	25%	19%	28%	52%	2.11
3. Wet	3.1%	2.7%	71%	44%	31%	4%	10%	6%	42%	43%	34%	2.02

[a] Percent difference between final and previous model iteration for all guild predictions, based on the iteration approach described in Section 3.3.
[b] Percent difference between final and previous model iteration for the predicted presence of plants, based on the iteration approach described in Section 3.3.
[c] All scenarios are analyzed for area below 558 $m^3 s^{-1}$, corresponding to 100-yr flood under "unmediated dry" scenario (Fig. 7).
[d] Percent of plots where plants are likely to be present.
[e] Average plant cover within those plots where plants are likely to be present.
[f] Total plant cover for site, accounting for plant presence and cover.
[g] Percent of modeled area with habitat suitable for given guild.

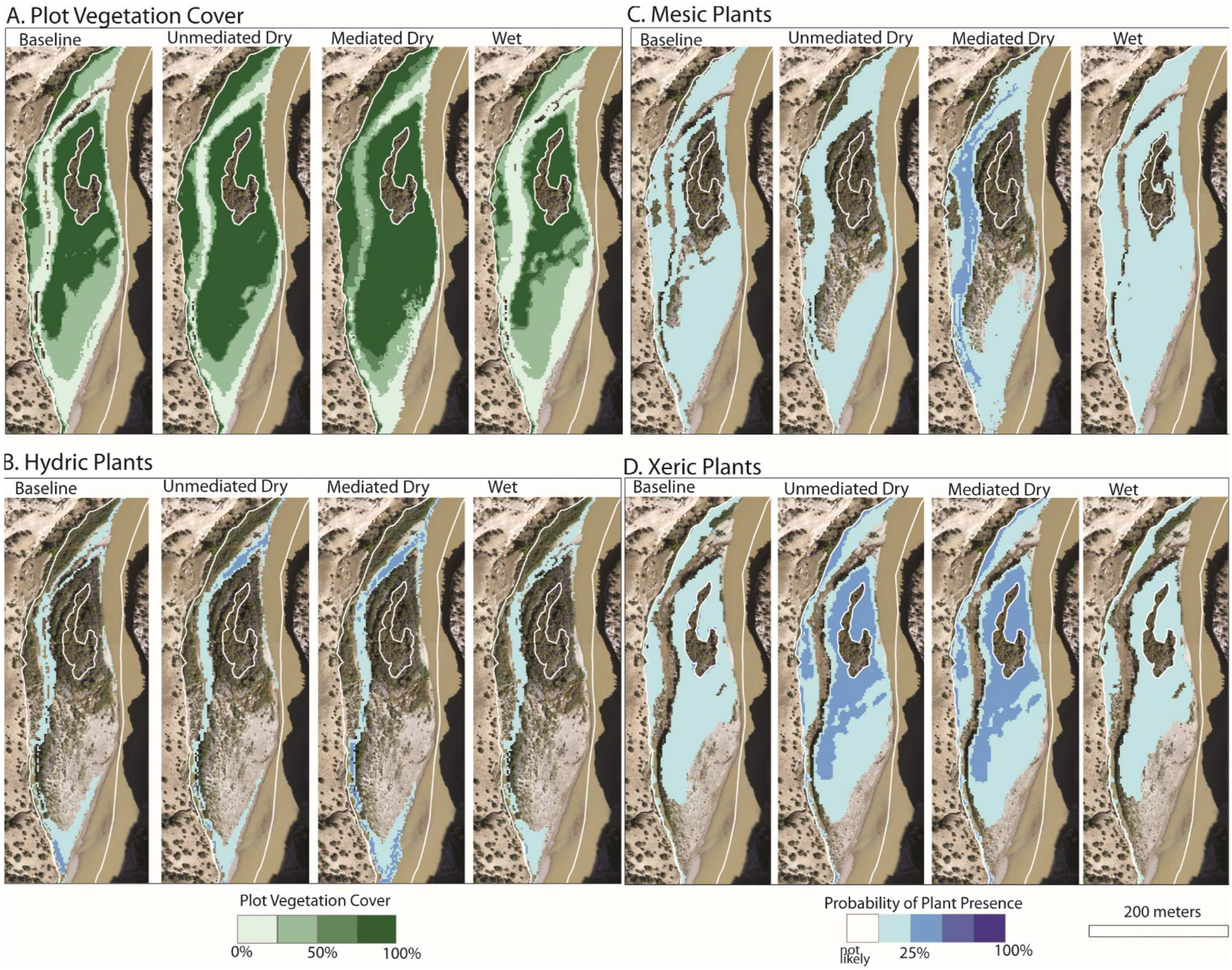

Fig. 7. Ecogeomorphic model results for Laddie Park, including prediction of future plot vegetation cover (A) and likely presence of hydric (B), mesic (C), and xeric (D) habitat types, given one of four flow scenarios (Table 1). All shaded areas are above the threshold for likely plant presence and are normalized to be between 0 and 100%; the darker the color, the greater the likelihood of plant presence. The white line indicates the extent of the area of analysis (see Fig. 3). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Concentration of plants lower in the channel will likely be countered by decreases in vegetation biomass on higher-elevation floodplain surfaces (Reynolds and Shafroth, 2017), beyond those we modeled, as these areas desiccate under a drier climate.

Because dominant guild members are morphologically different with respect to their effects on hydraulics and sediment transport, predicted shifts in the plant community may produce additional ecogeomorphic feedbacks. The major xeric guild plants in this region (i.e., tamarisk species) have multiple, woody stems that are more rigid than the mesic and hydric plants that currently occupy these settings, such as small tree seedlings and obligate riparian herbaceous plants (Diehl et al., 2017). Flume studies show that multiple-stemmed plants alter hydraulics and sediment transport to a greater extent than single-stemmed plants (Manners et al., 2015). Expansion of plants such as tamarisk would thus be expected to contribute to greater sediment deposition under drier conditions and reduced flood erosion, as represented in our modeling of the Yampa River at Laddie Park.

Results from the coupled ecogeomorphic model highlight sensitivities that would otherwise be overlooked in a singularly focused ecological or physical model. A coupled model, for example, may predict vegetation-mediated changes to channel form. Close to the channel, where commonly occurring floods are typically erosional and maintain unvegetated surfaces, the increases in plant presence and cover predicted by our model under future-flow dry scenarios would increase flow resistance, mediated by the guild-based differences in plant morphology (e.g., stem size and rigidity, shrub versus tree habit). Coupled with a reduction in the magnitude of common floods, these changes would reduce the magnitude and frequency of erosional events (Martínez-Fernández et al., 2018; Räpple et al., 2017) as suggested by our results, and potentially cause channel narrowing. The geomorphic effectiveness of high flows for transporting sediment and shaping channel morphology is well established (Wolman and Miller, 1960). Yet in semiarid rivers, such as the Yampa and Green, shifts to low flows have a significant impact on the composition, structure, and distribution of the riparian vegetation community, which in turn influence flow hydraulics, sediment transport, and channel geometry (Bywater-Reyes et al., 2018; Dean and Schmidt, 2011; Manners et al., 2015). Thus, low flows with high exceedance probabilities may be effective discharges from an ecogeomorphic perspective.

Details of the shape of the flow duration curve are also important, especially as they interact with an individual site's characteristics. In some cases, predictions made using synthetic hydrographs (section 3.2) versus those based on the Yampa River scenarios (section 3.3, Table 2) show inconsistencies as a result of differences in flows other than those with a 1% or 75% EP. For example, from the synthetic hydrographs, our model predicts that hydric guild habitat will contract under the range of projected Yampa flow regimes. However, we found that at the Laddie Park site, hydric guilds expanded under dry scenarios. Dips in the dry-scenario flow duration curves alter inundation properties most dramatically in the secondary channel and at the head of the island at of the Laddie Park site, where hydric guild habitat is optimal.

5.2. Strengths and limitations of ecogeomorphic model predictions

The ecogeomorphic model used in this study aims to account for the complex and dynamic nature of riparian ecosystems by incorporating some of the important feedbacks between ecological and physical processes. Although models cannot fully account for these feedbacks, our flow-response curve approach provides insight into the general magnitude and direction of change and highlights the most sensitive components of riparian ecosystems in the study region. The model relies on a range of plant guilds that represent groupings of species with similar life-history strategies and morphological traits, which can strongly influence physical processes such as flood stage, scour intensity and sediment deposition (Bywater-Reyes et al., 2018; Gurnell, 2014; Lightbody et al., 2019), although the specific influence of morphological traits on physical processes may depend on the geomorphic setting (Butterfield et al., 2020). In turn, plant guild presence depends on inundation properties and disturbance intensity, which strongly influence life history processes including dispersal, germination, establishment and mortality (Kui et al., 2019; Mahoney and Rood, 1998; Scott et al., 1997). Physical processes and the dynamics of plant guilds are thus coupled, and our predictions capture the nature of major co-adjustments in riparian ecosystems.

Our results are most applicable to confined, dryland rivers with geomorphic settings analogous to the field sites on the Yampa and Green Rivers used to build the flow response curves that serve as the foundation of the ecogeomorphic model (Diehl et al., 2018). Confined, canyon-bound rivers with alternate-bar morphology, such as at our sites, provide important habitat for endemic fish populations (Tyus and Karp, 1989) and are highly sensitive to shifts in environmental variables (Manners et al., 2014; Van Steeter and Pitlick, 1998). Our finding that hydric plants are only moderately sensitive to shifts in hydrologic attributes, especially at the site on the Yampa, may be less applicable to lower-gradient, unconfined settings, where we might expect hydric plants to expand and contract more dramatically than along canyon-bound reaches (e.g., Räpple et al., 2017).

The ecogeomorphic model described here was developed using three years of plot-scale data (Diehl et al., 2018), and predictions in this paper represent the adjustment of the riparian vegetation community over multiple decades. Over that time period other factors are anticipated to change such as atmospheric CO_2 concentrations, air temperature, and the length of the growing season (Dettinger et al., 2015). These factors will have ecological effects including increased heat and water stress (Morgan et al., 2004), altered phenology (Menzel et al., 2006), and regional changes in species geographic distributions (Walther et al., 2002), independent of the response curves used in our predictions.

5.3. Biodiversity and management implications of altered riparian ecosystem functions under future scenarios

Predicted decreases in functional diversity under future hydrologic regimes indicate an increasingly uneven representation of guilds, and potentially reduced resilience to stresses from further hydrologic changes and other disturbances (Stella and Bendix, 2019). Reductions in biodiversity, and particularly functional diversity, are often correlated with diminished ecosystem services, although a mechanistic understanding of relationships between biodiversity metrics and services is limited (Hooper et al., 2005). In the southwestern US, replacement of native cottonwood/willow forests with monospecific tamarisk stands has decreased the structural diversity of the canopy and impacted riparian fauna (Nelson and Wydoski, 2008; Sogge et al., 2008), channel morphology, aquatic habitat for invertebrates and native endemic fish species (Pitlick and Van Steeter, 1998; Rinne and Miller, 2006), and recreation (Zavaleta, 2000).

Although riparian ecosystems are likely to be less functionally diverse under future flow regimes, water managers may have opportunities to sustain desirable ecosystem characteristics (Beechie et al., 2010). Linking attributes of the flow regime to specific shifts in riparian plant presence, cover, and erosion and deposition provides management guidance by identifying discharge components that may be most consequential for maintaining critical ecosystem processes and for river management. High flows associated with spring snowmelt floods are a critical part of water-resource development planning (Scott and Friedman, 2018) and environmental flow prescriptions in the region, especially in dammed rivers (e.g., Hazel et al., 2010; Shafroth et al., 2010). Low flows are also amenable to manipulation by river managers. Reducing consumptive demands (e.g., by limiting irrigation withdrawals), efficient operation of existing reservoirs, and coupled surface water-groundwater management could mitigate climate-induced decreases in baseflows. Our work demonstrated the importance of multiple components of flow regimes, from spring snowmelt floods to low flows that predominate late in the growing season, for supporting a full suite of habitat types. These results highlight a management need and opportunity to sustain functionally diverse riparian ecosystems by managing for flow variability.

6. Conclusion

Evaluating different flow regimes using an ecogeomorphic model indicates that plant community characteristics are highly sensitive to shifts in high flows and show secondary sensitivity to shifts in low flows. Future streamflow projections for the rivers of the UCRB generally predict reductions of multiple flow attributes spanning high flows associated with snowmelt floods to groundwater-fed baseflows. With such likely changes to the flow regime, reductions in functional diversity, mostly via loss of mesic tall herbs and shrubs, and increases in presence and cover of drought-tolerant, non-native plant species are likely. During the past century, the riparian community in the region has been homogenizing in response to multiple stressors including river regulation and 20th century climatic changes, which have degraded habitat quality and ecosystem services. River managers tasked with balancing human water demands with ecological needs should aim to retain natural variability in river flows, including maintaining or enhancing high flows during the early part of the growing season and sustaining low flows later in the growing season.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Rebecca M. Diehl: Conceptualization, Data curation, Formal analysis, Funding acquisition, Project administration. **Andrew C. Wilcox:** Supervision, Writing - review & editing. **John C. Stella:** Supervision, Writing - review & editing.

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Appendix A. Supplementary data

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