






RESEARCH ARTICLE

# The long-term legacy of geomorphic and riparian vegetation feedbacks on the dammed Bill Williams River, Arizona, USA

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## Abstract

On alluvial rivers, fluvial landforms and riparian vegetation communities codevelop as a result of feedbacks between plants and abiotic processes. The influence of vegetation on river channel and floodplain geomorphology can be particularly strong on dammed rivers with altered hydrology and reduced flood disturbance. We used a 56-year series of aerial photos on the dammed Bill Williams River (Arizona, USA) to investigate how (a) different woody riparian vegetation types influence river channel planform and (b) how different fluvial landforms drive the composition of riparian plant communities over time. We mapped vegetation types and geomorphic surfaces and quantified how relations between fluvial and biotic processes covaried over time using linear mixed models. In the decades after the dam was built, woody plant cover within the river's bottomland nearly doubled, narrowing the active channel by 60% and transforming its planform from wide and braided to a single thread and more sinuous channel. Compared with native cottonwood–willow vegetation, nonnative tamarisk locally induced a twofold greater reduction in channel braiding. Vegetation expanded at different rates depending on the type of landform, with tamarisk cover on former high-flow channels increasing 17% faster than cottonwood–willow. Former low-flow channels with frequent inundation supported a greater increase in cottonwood–willow relative to tamarisk. These findings give insight into how feedbacks between abiotic and biotic processes in river channels accelerate and fortify changes triggered by dam construction, creating river systems increasingly distinct from predam ecological communities and landforms, and progressively more resistant to restoration of predam forms and processes.

## KEYWORDS

biogeomorphic feedbacks, dam effects, ecosystem engineer, *Populus*, riparian vegetation encroachment, *Tamarix*

## 1 | INTRODUCTION

Riparian plants interact with fluvial processes at short and long timeframes to drive the codevelopment of river morphodynamics and vegetation communities. Floods and the fluvial environment strongly affect riparian vegetation, providing the necessary dispersal mechanisms, moisture, and mineral substrates for germination and establishment (Mahoney & Rood, 1998; Stella & Battles, 2010). Floods also remove or kill plants through bank erosion, bed scour, and sediment burial (Bendix & Stella, 2013; Bywater-Reyes, Wilcox, Stella, & Lightbody, 2015;

Kui, Stella, Lightbody, & Wilcox, 2014; Wilcox & Shafroth, 2013). Once established, riparian communities respond to abiotic drivers such as distance to the groundwater, channel migration and floodplain accretion (Cooper, Andersen, & Chimner, 2003; Stella et al., 2011), and biotic factors such as competition (Corenblit, Tabacchi, Steiger, & Gurnell, 2007).

The reciprocal role of biotic communities in shaping geomorphic processes and landforms has gained increased focus and prominence (Dean & Schmidt, 2011; Dietrich & Perron, 2006; Gurnell, 2014; Manners, Schmidt, & Scott, 2014). Woody riparian plants along river channels stabilize substrates, reduce scour, and enhance sediment deposition by locally increasing drag (Yager & Schmeckle, 2013). The effects of plants as ecosystem engineers (*sensu* Jones, Lawton, & Shachak, 1994) are evident even for individual seedlings and plant

patches that shape scour and deposition patterns during small floods (Kui et al., 2014; Manners et al., 2015). Vegetation influences on channel and floodplain morphology magnify as riparian plants, particularly woody species, increase in area, size, and density in the decades following large floods (Corenblit et al., 2007). These effects can drive processes such as island formation, channel narrowing, and conversion of braided to single-thread channels (Birken & Cooper, 2006; Braudrick, Dietrich, Leverich, & Sklar, 2009; Crosato & Saleh, 2011; Perucca, Camporeale, & Ridolfi, 2007; Tal, Gran, Murray, Paola, & Hicks, 2004), though the strength of these effects is scale-dependent (Anderson, Bledsoe, & Hession, 2004). As river ecosystem engineers, woody plants generally increase heterogeneity in topography, soil texture, trapped organic material (including seeds and plant fragments), and hydraulic refugia (Gurnell, 2014). For example, riparian plants modify flow fields to induce fine sediment deposition around plant patches at scales ranging from a few square centimeters to entire point bars (Manners, Schmidt, & Wheaton, 2013). In turn, these features influence riparian ecosystem development through effects on life history processes (e.g., dispersal and germination), demographic rates, and species performance (Corenblit et al., 2015; Pickett, Cadenasso, & Meiners, 2013).

Interactions between fluvial forces and riparian plants are often mediated through human alterations to river systems such as dams, which are constructed for multiple purposes including hydropower, flood control, and water supply. Dams commonly reduce peak-flow magnitude, flood duration and sediment loads downstream of reservoirs (Williams & Wolman, 1984). As a consequence of fewer high-magnitude, channel-scouring floods, the influence of existing vegetation on river hydraulics and sediment dynamics is often magnified relative to undammed systems (Manners et al., 2015). At the same time, more stable and often elevated low flows promote better growth conditions and mitigate water stress for obligate riparian plants, particularly during the growing season in water-limited regions (Sankey, Ralston, Grams, Schmidt, & Cagney, 2015; Shafroth, Stromberg, & Patten, 2002). As a result, pioneer plant species that thrive with disturbance are less favored within the riparian community, allowing the expansion of species (including nonnatives) that are adapted to more stable conditions. Over time, co-occurring shifts in the river's geomorphic environment and its dependent riparian communities can give rise to novel ecosystems (Scheffer, Carpenter, Foley, Folke, & Walker, 2001), particularly where hydrogeomorphic alteration, land use, and species invasions interact (Merritt & Poff, 2010).

In riparian zones of the southwestern USA, invasive tamarisk (*Tamarix*) shrubs, which established region-wide in the early 20th century, expanded rapidly on many rivers after flow regulation (Merritt & Poff, 2010; Nagler, Glenn, Jarnevich, & Shafroth, 2011; Stromberg, Beauchamp, Dixon, Lite, & Paradzick, 2007a). Tamarisk has similar disturbance requirements as native pioneer shrubs and trees, but it is more tolerant of low soil moisture and high soil salinity, and it has a longer seed dispersal window than the native species. All of these characteristics contribute to tamarisk's expansion on floodplains throughout the region, particularly along regulated rivers (Busch & Smith, 1995; Glenn & Nagler, 2005; Merritt & Poff, 2010; Stromberg, Lite, et al., 2007b). Although many studies

document the effect of dams on vegetation expansion in river corridors with reduced disturbance regimes (e.g., Choi, Yoon, & Woo, 2005; Johnson, 1994), relatively few have quantified the long-term effects of fluvial geomorphic change on riparian vegetation composition and development (but see Kalliola, Salo, Puhakka, & Rajasilta, 1991). To restore the habitat and ecosystem functions that native riparian communities provide, we find that it is critical to know specifically how channel and floodplain dynamics influences the composition of riparian communities (Pataki, Bush, Gardner, Solomon, & Ehleringer, 2005; Stella, Rodríguez-Gonzalez, Dufour, & Bendix, 2013).

In this context, we set out to quantify the mutual influences of fluvial processes and riparian vegetation within an entire river corridor, and over a timeframe that captures these interactions and their feedbacks within the fluvial system. Specifically, we investigated (a) how different woody riparian vegetation types influence the evolution of river channel planform and floodplain development and (b) how fluvial landforms with different morphologies resulting from the river's modified hydrology drive the distribution, composition, and density of riparian vegetation over time. We studied the Bill Williams River (BWR) in the southwestern USA, which has been dammed since 1968 and supports a mix of native and nonnative riparian woodlands. Previous research in this system has examined patterns of change in channel width and vegetation cover in response to flow regulation (Shafroth et al., 2002), as well as reach-scale seedling and geomorphic response to individual floods (Shafroth, Auble, Stromberg, & Patten, 1998; Wilcox & Shafroth, 2013). However, the interactions and feedbacks of these processes with changes in channel morphology have not been studied to date. We accomplished this by interpreting and analyzing vegetation and geomorphic landform change, interactions, and feedbacks on a 56-year time series of aerial photographs. Using linear mixed models, we analyzed change in vegetation development and channel-floodplain morphology at two spatial scales, corridor-wide trends and local river-segment shifts in planform that were associated with different plant communities.

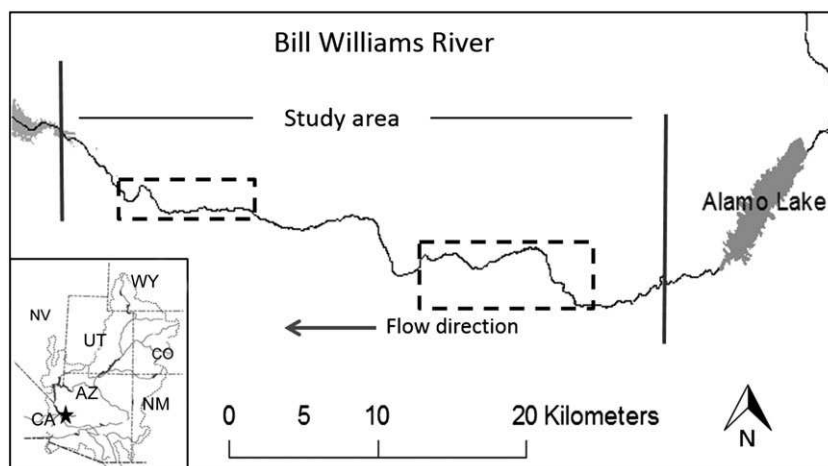
## 2 | METHODS

### 2.1 | Study area

The study was conducted on the BWR, a predominantly sand-bedded river with a catchment area of 13,800 km<sup>2</sup> in the semiarid southwestern U.S (Figure 1). The river begins at the confluence of the Santa Maria and Big Sandy rivers and flows through alternating canyon and alluvial reaches into the Colorado River at Lake Havasu. The 30-year monthly mean temperatures at Alamo Dam, Arizona, are 10.2 °C and 33.7 °C for December and July, respectively, and mean annual precipitation is 230 mm (Western Regional Climate Center, 2015). Precipitation rates are higher in the upper basin, from which most of the BWR's flow originates.

The river's hydrology and geomorphology have been dramatically influenced by Alamo Dam, which was built in 1968 for flood-control purposes (House, Shafroth, & Beauchamp, 2006). There are no

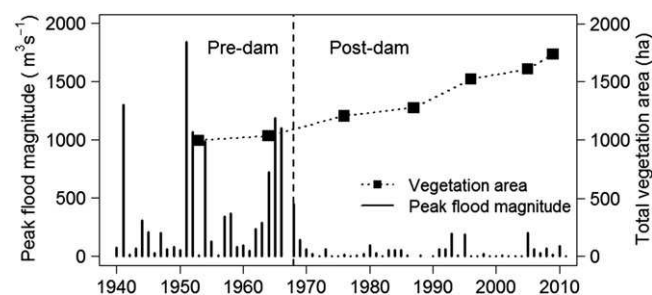
**FIGURE 1** Bill Williams River, western Arizona, USA. The study area is delineated between the two vertical lines in the main panel. This reach was used to analyze the postdam vegetation change responding to the geomorphic evolution of the channel and floodplains. The areas bounded by dashed boxes are the perennial reaches of the river that were used to analyze local effects of vegetation on channel planform change



perennial tributaries downstream of the dam, and its outlet capacity limits controlled outflows to a maximum of approximately  $200 \text{ m}^3 \text{ s}^{-1}$ , which is  $<11\%$  of the predam 10-year flood (House et al., 2006). Since the construction of the dam, peak discharges downstream (USGS gauge #09426000) have been drastically reduced in magnitude and frequency (Figure 2; House et al., 2006, Wilcox & Shafroth, 2013), and sediment from 80% of the river's watershed is trapped in Alamo Lake (Dekker, 2012; House et al., 2006). Our field observations indicate that the channel has incised immediately downstream of Alamo Dam, but the downstream study reaches examined here (described below) do not show evidence of incision. Low flows have increased, particularly since the 1990's (Shafroth et al., 2010). Shafroth et al. (2002) tracked riparian vegetation and channel width dynamics over a 45-year period using historical aerial photos. They found that vegetation cover increased sharply as channel width decreased (width reduced by 71%) and that these changes were related to flow regulation, specifically lower peak-flow magnitudes and higher low flows during the growing season.

## 2.2 | Aerial photo series and vegetation cover interpretation

We analyzed seven sequential sets of aerial photos, taken at roughly decadal intervals between 1953 and 2009 at similar low river-discharge levels, in order to quantify changes in vegetation cover and



**FIGURE 2** Annual peak flood data (left axis) downstream of Alamo dam (USGS gauge #09426000), and dense vegetation cover change over time (right axis). The peak flood values are the largest instantaneous discharge in a given water year (Oct. 1 to Sept. 30). Total vegetation area is the summed areas of dense and sparse patches delineated in the vegetation analysis

geomorphic unit boundaries since dam construction (Table S1). The photo analysis was performed along 45 river kilometers downstream of the dam, excluding a bedrock canyon reach and the lowermost portion of the river, which is influenced by backwater effects from Lake Havasu (Figure 1). From these photos, we delineated vegetation cover types on mylar overlays of all the aerial photograph series prior to 2009. Overlays were scanned to create digital images, georeferenced, and transferred to ArcGIS (v 10.1, Environmental Systems Research Institute, Redlands, California, USA; Shafroth et al. 2002). The 2009 photo series was digitized directly within ArcGIS.

From these aerial photos, we identified nine cover types, including six plant community types and three nonvegetation cover types. Nonvegetation types included channels, bare surfaces, and cultivated areas (Appendix S2). Vegetation cover types included sparse ( $<50\%$  plant cover) and dense ( $\geq 50\%$  plant cover) modes of three plant assemblages dominated respectively by (a) nonnative tamarisk (*Tamarix* spp.); (b) native cottonwood (*Populus fremontii*) and willow (*Salix gooddingii*); and (c) other native species consisting primarily of *Prosopis glandulosa*, *Hymenoclea monogyra*, *Tessaria sericea*, *Atriplex* spp., and *Lycium* spp. All vegetation types typically contained lesser proportions of other, nondominant species. The cottonwood–willow and tamarisk signatures were indistinguishable on the coarser-resolution 1953 and 1964 photos; therefore, these vegetation types were combined for those photo sets, with only sparse and dense modes identified as separate cover classes. The vegetation cover types were ground-truthed in 1996, 2004, and 2005. In addition, stand age was determined at 67 locations along the river corridor (Shafroth et al., 2002).

## 2.3 | Geomorphic landform interpretation and channel planform analysis

In parallel to the vegetation cover interpretation, we analyzed channel and floodplain geomorphic changes using the same aerial photograph series. Contemporaneous geomorphic units in each photo year were delineated within the BWR bottomland, including (a) “low-flow channels,” which constituted the low-flow, perennial river; (b) “high-flow channels,” which were floodplain features that had evidence of periodic activation in higher magnitude floods (Appendix S2); and (c) landforms labeled “terrace,” which represented areas with no evidence of

inundation or geomorphic change since 1953. Terraces surfaces remained unchanged in subsequent years, and thus were excluded from the analysis of geomorphic change and floodplain development (active and abandoned channels) within the river bottomland.

As the river moved laterally over time, two types of floodplain developed. We used the designation “former low-flow channel” (former LFC) to indicate areas that had been the perennial river channel in prior years and were later abandoned; whereas, we used “former high-flow channel” (former HFC) to indicate areas that had been dry, high-flow channels in prior years. The earliest photo series was delineated first, and the associated line work copied and modified based on geomorphic change in the next series. This process was propagated through the entire photo set to develop a sequence of polygon coverages with landforms consistently labeled to depict decadal-scale change in the river's floodplain since 1953 (Appendix S2). Floodplain units that were not reworked subsequently by the river retained their original label (e.g., 1953 former HFC); whereas, reworked areas were relabeled accordingly (e.g., 1976 former LFC). This process resulted in 12 geomorphic units, reflecting each combination of age class and landform type, which were subsequently included as random factors in linear models predicting change in riparian vegetation area over time (section 2.4).

To check our assumptions about environmental differences between floodplain areas designated former LFC versus former HFC, we modeled river hydraulics using HEC-RAS (v5.0, U.S. Army Corps of Engineers), a one-dimensional flow model that simulates water surface profiles and the extent of inundation at various flow levels along a river corridor. We ran HEC-RAS for three flows:  $55 \text{ m}^3 \text{ s}^{-1}$  (a 2- to 5-year recurrence interval flood under the postdam hydrologic regime),  $110 \text{ m}^3 \text{ s}^{-1}$  (a postdam 10-year flood), and  $200 \text{ m}^3 \text{ s}^{-1}$ , which is both the maximum flood flow possible from Alamo Dam's spillway and the postdam flood of record (Appendix S3). The HEC-RAS model was calibrated using high water marks measured at 20 locations during a 2005 flood, and roughness values were based on U.S. Geological Survey vegetation maps (Fields, 2009). Topography and bathymetry input data for the modeling were derived from 2006 LiDAR imagery (Fields, 2009; Reynolds, Shafroth and House, 2014). At the time of the February 2006 LiDAR surveys, river flows were  $<1 \text{ m}^3 \text{ s}^{-1}$ , such that inundation depth and extent was minimal. Field surveys of selected reaches during that period showed that water depths were generally ca. 10 cm. We therefore consider that, even though the LiDAR surveys did not penetrate subaqueous portions of the channel, they provided a sufficiently accurate representation of channel topography for flood modeling purposes. From the HEC-RAS results and using the geomorphic unit coverage from the 2005 photo year, we then calculated the percentage of each floodplain type within each of the inundation zones generated by HEC-RAS. Considering the 2–5 year flood ( $55 \text{ m}^3 \text{ s}^{-1}$ ), former LFC areas were inundated to a greater extent (57% of its land area) than former HFC zones (33%). A  $200 \text{ m}^3 \text{ s}^{-1}$  event would exclude only 12% of former LFC areas, versus 31% of former HFC surfaces, which would remain significantly drier during large floods. Therefore, our vegetation analyses proceeded with the assumption of a wetter and more fluvially active environment in the former LFC zones (Appendix S4).

We characterized river planform change in terms of channel width, sinuosity, and braiding index, computing metrics at a local (reach) scale,

and also averaging the reach-scale measures for the entire river corridor. For this analysis, we studied two perennially flowing segments comprising 21 river kilometers, or 40% of the river's total length (Figure 1) because these metrics were difficult to distinguish for intermittently flowing river segments. We analyzed local planform change within 21, 500-m-long perennial reaches, each at least 500 m from another reach. This reach length represents approximately 15 times the average channel width and was sufficiently long to quantify planform metrics. We tested for spatial autocorrelation among the 21 reaches for each geomorphic index using Moran's  $I$  and determined that these reaches were independent of each other (Legendre & Legendre, 1998). Each reach extended laterally to encompass the entire bottomland width; therefore, reach area varied. Within each sample reach and photo series, we generated a channel centerline, and where there were multiple channels, the centerline for the widest channel was used (also called the main channel centerline). Channel width within each reach was calculated as the area of river channel divided by the length of the main channel centerline (Shafroth et al., 2002) and sinuosity was calculated as the length of the main channel centerline divided by the corresponding valley length. The braiding index was calculated as the number of channels intersecting a central transect perpendicular to the center line of each reach (Friend & Sinha, 1997).

## 2.4 | Quantitative and statistical analyses

We analyzed vegetation and geomorphic trends from 1953–2009 by first calculating summary statistics of vegetation cover in each photo series, as well as time-series averages of the channel width, sinuosity, and braiding index metrics. Using a linear mixed model, riparian vegetation area (in  $\text{m}^2$ ) was modeled as a function of the three predictors: vegetation type (cottonwood–willow versus tamarisk), floodplain origin (former HFC versus LFC), and time, represented by the photo year (Shafroth et al., 2002). We included all two- and three-factor interaction terms to account for nonlinear effects on vegetation area, the response variable, which was quantified as the sum of both sparse and dense patches for a single vegetation type. We also specified a random factor for geomorphic unit ( $n = 12$ , representing two floodplain types, LFC and HFC, in the six photo series. See section 2.3), to control for repeated measurement on the same landform across multiple photo series. Vegetation area was log transformed to meet the normal distribution assumption of the residuals. Statistical code for the model (using SAS software) is included in Appendix S5.

Next, we quantified at a local scale (i.e., the 500 m reaches) the effects of vegetation cover, tamarisk versus cottonwood–willow, on three metrics of river channel planform: width, braiding index, and sinuosity. Aerial photo data for these statistical models were limited to the period between 1976 and 2009, because the 1953 and 1964 images were too coarse to distinguish the two vegetation types (see section 2.2). For each response metric, there was a total of 105 observations, representing 21 transects  $\times$  5 postdam photo series. For all responses, the predictors were the proportion cover of each vegetation type (cottonwood–willow or tamarisk) within the river reach, with sparse and dense modes combined. We ensured independence of the sampling units and controlled

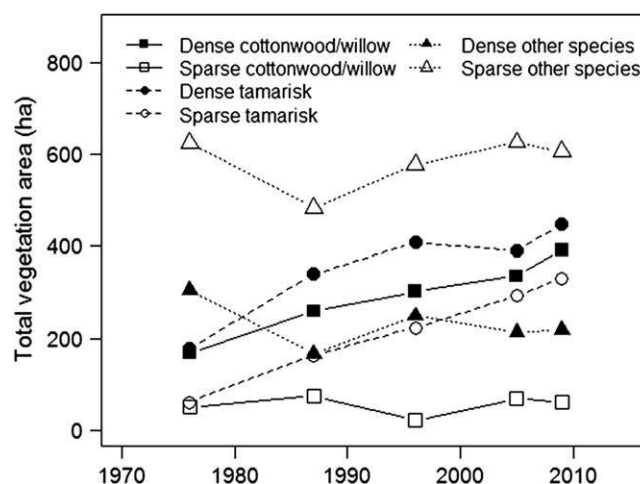
for potential pseudoreplication (*sensu*, Hurlbert, 1984) in a number of ways. The two predictor variables, proportion tamarisk and proportion cottonwood–willow, were not correlated due to the presence of other vegetation and nonvegetation types; therefore, both were retained as separate factors in the models. For all three morphological indices, “transect” was treated as a random factor in the models, to control for differences in topography and hydraulics among the 21 reaches. Individual photo years were treated as a repeated-measure variable that accounted for variation in hydrology (e.g., flood magnitude and frequency) and differences in sediment dynamics between consecutive photo dates, and we added a first-order autoregressive term to ensure that the sequential correlation of planform metrics in each river reach did not influence the model results (Lindsey & Lambert, 1995). For the braiding index model, which had count response data, we fit a generalized linear mixed model using the Poisson distribution (log link) for residuals. In the models predicting channel width and sinuosity, we log transformed those response variables to meet the normal distribution assumption of the residuals. All data analyses were performed in SAS (v9.3, SAS Institute Inc. Cary, NC); see Appendix S5 for the statistical language code.

### 3 | RESULTS

#### 3.1 | Vegetation change over time

Between 1953 and 2009, overall vegetation cover increased from 994 to 1,740 ha, or from 42% to 73% of total bottomland area (Figure 2). This increase in vegetated area was first evident in comparison of the 1953 and 1964 photo sets, before the dam was built; the initial (1953) photo series followed two large, channel-resetting flood events in 1951 (Figure 2). Vegetation expansion continued after the 1968 construction of Alamo Dam, which resulted in a profound reduction in the magnitude and frequency of downstream flooding. Aerial photograph analysis indicates that the postdam expansion largely reflects new plant recruitment on previously unvegetated surfaces. Dense vegetation followed a similar trend as for overall vegetation cover, increasing from 24% to 44% of the total river corridor area. The proportion of bottomland covered with dense vegetation was relatively steady at 24–32% from 1953–1987, and increased to 40% between 1987 and 2005. Increases in density reflect a combination of growth of existing vegetation in sparsely vegetated patches, and new plant recruitment. Variability in the vegetation expansion among inter-photo periods likely reflects (a) the consequence of the high summer flow and low flood frequency, particularly the large changes in the initial postdam period; (b) postdam land use and management changes such as agricultural abandonment along some reaches between 1987 and 1996; and (c) environmental flow releases from Alamo Dam, including increases in baseflow, in recent decades (Figure 2; Shafroth et al., 2002, Shafroth et al., 2010).

The rate of expansion varied greatly among the vegetation types (Figure 3). Overall, the area of bottomland covered in dense vegetation of all plant community types increased 25% more than areas with sparse cover. Tamarisk patches increased the greatest



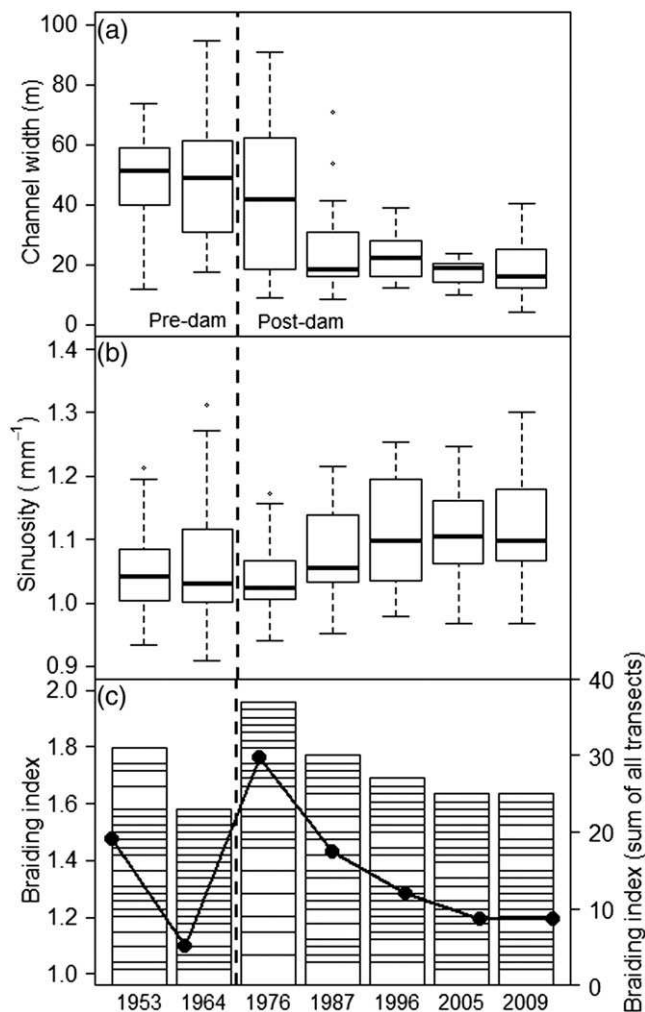
**FIGURE 3** Vegetation area change over time for the three vegetation types along the Bill Williams River. The total area of both tamarisk vegetation types, sparse and dense, increased in the postdam period, as well as dense patches of native cottonwood–willow vegetation. All other vegetation types remained roughly constant over four decades, including sparse cottonwood–willow, which occupied the smallest area

amount from 1976 through 2009, adding 270 ha of dense woodland (a 154% increase), and an equal area of sparse shrubs (a 442% increase). Dense patches of native cottonwood and willow increased 224 ha (133% over 1976 totals); whereas, sparse patch area remained constant at low proportions of total area (Figure 3). Both sparse and dense patches of other species (primarily mesquite and burro-brush) remained relatively constant over time.

#### 3.2 | Channel geomorphic evolution

The channel planform metrics all showed a strong trend of channel narrowing and simplification between 1976 and 1996, with more stable values since 1996 (Figure 4). The active channel narrowed from ca. 50 m in the predam period to ca. 20 m in 2009 (Table 1; Figure 4 a). The rate of narrowing was highest ( $1.6 \text{ m year}^{-1}$ ) from 1976 to 1996 and remained relatively constant after 1996. Channel sinuosity increased slightly, from 1.04 to 1.12 (an approximately 8% increase) between 1976 and 1996 (Figure 4b), after which it did not change. The channel braiding index decreased 32% from its maximum in 1976, with 75% of multi-thread reaches evolving into single-thread channels by 2009 (Figure 4c). As with the narrowing and sinuosity, the decrease in channel braiding occurred between 1976 and 1996, and primarily in upstream segments (Figure 4c where the vertical boxes become narrower over time).

The rate of newly created floodplain also showed a diminishing trend after dam construction (Figure 5). Between 1953 and 1964, a total of 1,281 ha of new land was created by river movement and channel abandonment, comprising an average rate of  $116 \text{ ha year}^{-1}$ . Floodplain reworking and creation of new surfaces declined through 1987, was briefly higher in the 1996 photo series (881 ha total new land, comprising  $98 \text{ ha year}^{-1}$ ) following  $\sim 200 \text{ m}^3/\text{s}$  flow releases in 1993 and 1995, and then declined precipitously in the current period to the lowest rate overall ( $89 \text{ ha year}^{-1}$  from 2005–2009). By 2009, the distributions of floodplain ages were still skewed toward predam



**FIGURE 4** Changes in river channel (a) width, (b) sinuosity, and (c) braiding index. The vertical dashed line separates predam measurements from postdam ones. In panel c, the mean braiding index (filled circles, left axis) was the average across 21 study reaches. The right axis is the sum of the braiding index of all reaches. Each rectangle represents one reach, and the stack from bottom to top represents the sample of reaches moving from upstream to downstream

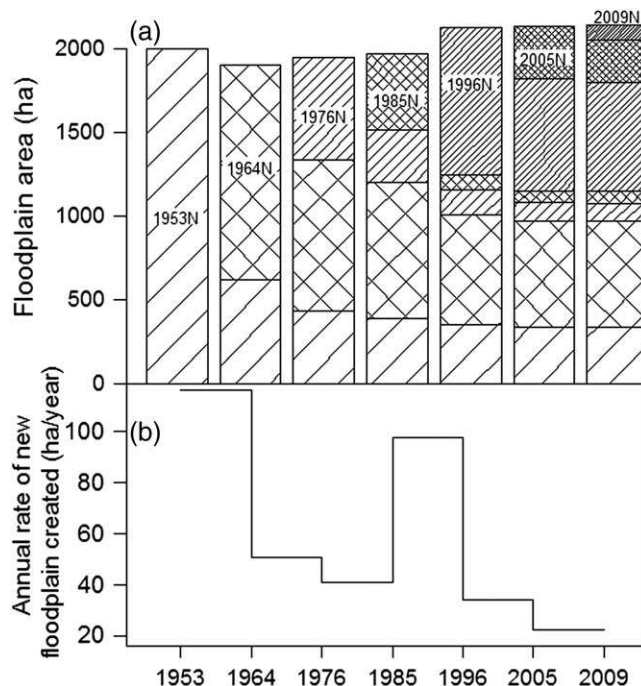
**TABLE 1** Corridor-wide changes in channel planform metrics and vegetation cover

	1953	1964	1976	1986	1996	2005	2009
Visible river length <sup>a</sup> (km)	33.3	27.3	34.0	38.0	39.0	46.3	40.5
Channel width (m)	49.1	51.9	44.0	26.0	22.7	17.6	19.2
Sinuosity (m m <sup>-1</sup> )	1.84	1.50	1.87	2.09	2.15	2.55	2.23
Braiding index	1.35	1.09	1.64	1.57	1.29	1.31	1.28
Proportion of dense vegetation cover <sup>b</sup>	0.24	0.23	0.30	0.32	0.40	0.40	0.45

<sup>a</sup>Visible river length was the length of the channel that had flowing water on the aerial photo.

<sup>b</sup>Proportion of dense vegetation cover was measured relative to the total area of river bottomland delineated in the vegetation analysis.

surfaces that had escaped reworking in the postdam period. In contrast, most of the floodplain area created after dam closure had been reworked subsequently. This suggests that currently, only a small



**FIGURE 5** Change in floodplain creation over time. Except for the 1985–1996 period, the absolute amount and rate of floodplain creation has decreased steadily since dam construction. Panel a, time-series change in new floodplain area evident in each photo year. Total floodplain area was ca. 2000 ha with the variation due to changes in river area. Each series indicates the area of new floodplain land created (bar marked N) in a given year, and the same shading scheme in subsequent series indicates changes in surface area for that landform. Panel b, the annual rate of new floodplain creation between photo dates. The horizontal lines linking consecutive photo years indicate the average rate of floodplain creation, calculated as the total new floodplain created between photo dates divided by the number of intervening years

portion of the historic floodplain is active and the majority of the bottomland is functionally disconnected from surface flows (Figure 5).

### 3.3 | Corridor-wide influence of landforms on vegetation development

In the postdam period, almost all vegetation types increased or remained constant on all floodplain surfaces. However, there were large differences in the expansion rate among vegetation types, and these were mediated by interactions with the origins of the landform, alternatively as former low-flow or high-flow channels. These differences were significant, as indicated by the year  $\times$  species  $\times$  landform origin interaction in the linear mixed model predicting vegetation expansion (Table 2). On former LFC surfaces, cottonwood–willow cover, with both sparse and dense patches combined, increased 12% over the past 40 years; whereas, cover of tamarisk-dominated patches decreased 4% (Table 2; Appendix S6). On former HFC areas, cottonwood-dominated patches decreased 24% over four decades. In contrast, tamarisk patches increased 40% over the past 40 years, about three times as fast as the cottonwood on the former LFC areas (Appendix S6).

**TABLE 2** Linear mixed model predicting vegetation area (ha) as a function of vegetation composition (tamarisk vs. cottonwood–willow), landform origin (former low-flow channel, LFC, versus former high-flow channel, HFC), and time (photo year), with geomorphic unit (12 units) as a random effect. Vegetation area was log transformed to satisfy residual assumptions

Effect	Estimate	Standard error	DF	F value	Pr > F
Year	0.01	0.004	70	0.02	0.898
Species <sup>a</sup>	31.93	10.10	70	2.09	0.153
Landform origin <sup>a</sup>	22.08	11.37	70	0.02	0.887
Year × species	−0.016	0.005	70	2.22	0.141
Year × landform origin	−0.011	0.006	70	0.02	0.880
Species × landform origin	−41.76	15.29	70	7.46	0.008
Year × species × landform origin	0.02	0.008	70	7.58	0.008

<sup>a</sup>Estimated coefficient value for “species” is cottonwood–willow, and “landform origin” is the LFC.

### 3.4 | Local influence of vegetation type on river morphology

The effects of tamarisk on river morphological indices (channel width, sinuosity, and braiding index) were significant in the linear models that quantified the influence of local vegetation type on the adjacent channel planform (Table 3). River channels bordered by more tamarisk-dominated vegetation tended to be less braided and more sinuous compared to those with proportionally more cover of native species (Table 3). In contrast, the amount of cottonwood–willow cover in a reach did not show a significant relationship with either sinuosity or degree of braiding; however, the trends (i.e., the signs of estimated coefficient values) were similar to tamarisk. River channel narrowing was equally sensitive to higher vegetation cover by cottonwood–willow and tamarisk vegetation types (Table 3).

## 4 | DISCUSSION

Interactions among flow regimes, vegetation, and geomorphic processes commonly drive the codevelopment of plant communities and channel morphology. In this study, we found two notable dynamics related to how native versus tamarisk-dominated plant communities interact with flow regulation. First, the extent to which tamarisk would become dominant on a floodplain surface was strongly linked to its landform origin and hydrologic connectivity (i.e., greater expansion on less frequently inundated surfaces). Second, the degree of local planform change for a channel segment in the postdam era was strongly linked to the vegetation type lining its banks, with tamarisk acting as an ecological engineer (*sensu* Corenblit et al., 2015) that exerted a significantly greater influence on simplifying channel form

than the native willow–cottonwood community. Taken together, these findings provide insight into how feedbacks between abiotic and biotic processes in alluvial river channels accelerate and fortify changes following dam construction compared to historical conditions (Merritt & Poff, 2010). The strength of these feedbacks in turn highlights the challenges inherent in attempting to reverse the ecological changes resulting from the combination of dams and species invasions.

### 4.1 | Planform change over time

The changes in channel planform we documented throughout the river corridor following dam construction are consistent with other studies showing long-term river adjustments in the reaches below dams, including channel narrowing (Williams & Wolman, 1984), minor sinuosity increases (Tiegs & Pohl, 2005), and reductions in braiding index and planform complexity to a single-thread channel (e.g., Gendaszek, Magirl, & Czuba, 2012). Our study revealed a distinct temporal sequence to the channel's development; the rate of morphological change peaked within 10–30 years of the onset of flow regulation, then subsequently diminished. Comparative diachronic studies with decadal-scale timesteps are not common, but studies in a larger river system in California show a more lagged channel response to dam construction and a less variable rate over time compared to the Bill Williams system (Michalková, Piégay, Kondolf, & Greco, 2011). Concurrent with channel planform changes, much of the Bill Williams bottomland area transitioned from active channel to drier, less fluvially active surfaces (Reynolds et al., 2014). Less bottomland turnover occurred with each photo time series until by the mid-1990s; the dynamic portion of the active channel was confined within a small proportion of its historical footprint. This “scaling-down” of the formerly

**TABLE 3** Linear mixed model results quantifying the influence of local vegetation cover on adjacent channel morphological changes (width, sinuosity, and braiding index)

Response	Vegetation type <sup>a</sup>	Estimated value	Standard error	F value	P value
Channel width (m)	Cottonwood–willow	−0.627	0.161	15.18	<.001
	Tamarisk	−0.501	0.137	13.37	<.001
Sinuosity (m m <sup>−1</sup> )	Cottonwood–willow	0.021	0.022	0.89	.35
	Tamarisk	0.036	0.018	3.92	.05
Braiding Index	Cottonwood–willow	−0.441	0.328	1.8	.18
	Tamarisk	−0.632	0.276	5.25	.03

<sup>a</sup>For each vegetation type, proportion cover (0–1) was calculated based on the sum of sparse and dense patch area relative to its corresponding reach area.

active zone is a common pattern observed in heavily regulated rivers (del Tanago, Bejarano, de Jalon, & Schmidt, 2015; Trush, McBain, & Leopold, 2000).

## 4.2 | Vegetation change over time

The rate and composition of riparian vegetation change over time were strongly linked to floodplain geomorphology (Table 2), which in turn was influenced by changes to the river's hydrologic regime following dam construction (Figure 2). Although the temporal scale and spatial resolution of data available did not allow for direct comparison of hydrologic change to the vegetation response, the distinction in floodplain surfaces, HFC versus LFC, provided a good proxy for the hydrogeomorphic drivers (Appendix S3). The great postdam expansion in vegetation occurred principally for tamarisk on floodplains that developed on former high-flow channels. This suggests that the reduced inundation frequency associated with flow regulation favored tamarisk's life history requirements and disfavored native pioneer trees, both in terms of new recruitment and in growth of existing plants (Auerbach, Merritt, & Shafroth, 2013; Glenn & Nagler, 2005; Shafroth et al., 2002; Stromberg, Beauchamp, et al., 2007a). Although bare and moist sediments are required for germination of willow, cottonwood, and tamarisk (Cooper, Merritt, Andersen, & Chimner, 1999; Stella, Battles, McBride, & Orr, 2010; Stella, Battles, Orr, & McBride, 2006), tamarisk has a longer seed dispersal window than the natives (Shafroth et al., 1998) and is better adapted to more xeric floodplain environments, with higher tolerance to drought and saline soils (Busch & Smith, 1995; Cleverly, Smith, Sala, & Devitt, 1997; Merritt & Shafroth, 2012).

Concurrent with tamarisk's spread on drier floodplains, cottonwood–willow increased in area and coexisted with tamarisk in more flood-prone areas. These former low flow channels also were likely moister during the seedling establishment phase, which can provide cottonwood–willow an advantage over tamarisk (Sher, Marshall, & Taylor, 2002). Most studies in the southwestern USA have found declines in native riparian trees and shrubs following damming (Busch & Smith, 1995; Merritt & Poff, 2010). Sankey et al. (2015), however, found that new vegetation encroachment into the formerly active channel of the Colorado River in Grand Canyon after construction of Glen Canyon Dam comprised a mix of tamarisk and native woody species, primarily seep willow and arrowweed. Due to their hydrologic connectivity with river channels, lower floodplain areas (e.g., former LFC) likely retain conditions that promote cottonwood–willow establishment and growth, such as shallow water tables, fine-grained alluvial substrates, and organic matter after floods (Räpple et al. in press; Shafroth et al., 1998; Shafroth et al., 2002; Singer et al., 2012). These conditions also sustained tamarisk; however, studies comparing the different taxa show that native plants have equal or faster growth rates in mesic environments (Glenn & Nagler, 2005), and increases in native tree density can limit tamarisk density (Sher et al., 2002). Thus, although tamarisk was able to maintain its community presence in the wetter, frequently flooded zones, its ability to expand was likely limited by the success of neighboring cottonwood and willow (Stromberg, Lite, et al., 2007b).

## 4.3 | Vegetation effects on local river morphology

The relative influences of tamarisk and flow regime on channel change have been the subject of some debate (Auerbach et al., 2013; Birken & Cooper, 2006), and our results suggest that the composition of riparian vegetation, not only its presence, influences local channel morphology. In a prior study on the BWR, flood and low flow magnitudes explained ca. 60% of the variation in channel width change along the entire corridor (Shafroth et al., 2002). Here, we found that the type of vegetation is a secondary driver that explains local differences in the rate of channel narrowing in perennial reaches. Our finding that tamarisk was more strongly associated with planform changes than native vegetation likely reflects cumulative and long-term feedbacks between plant traits such as stem architecture and root strength, and geomorphic processes such as bank erosion and sediment deposition over many flood events (Griffin, Kean, Vincent, Smith, & Friedman, 2005; Kui et al., 2014; Langendoen, Lowrance, & Simon, 2009; Manners et al., 2014). By studying plant–river dynamics at the local river segment scale, rather than at the coarser whole-corridor scale, we gained understanding of the local influence of different vegetation types on geomorphic change, which has been observed in other riparian contexts (Everitt, 1998; Graf, 1978; Micheli, Kirchner, & Larsen, 2004).

Vegetation encroachment also influenced river morphological change by facilitating the transformation of a braided channel into a single-thread, more sinuous channel. Abandonment of braided channels often reflects the combined effects of dam-induced changes in transport capacity and sediment supply, and an increase in vegetation density and associated sediment trapping (Gran & Paola, 2001). Tamarisk had a stronger and uniquely significant association with changes in sinuosity and braiding compared to native woodlands. These results are consistent with other studies that show increased bank strength by nonnative tamarisk and Russian olive compared to native trees (Cadot, Rathburn, & Cooper, 2011), and flume studies that measured greater sedimentation around tamarisk individuals and patches compared with cottonwood of equivalent height and density (Kui et al., 2014; Manners et al., 2015). Because the bottomland areal coverage of tamarisk was about twice that of cottonwood–willow, tamarisk's overall influence on river morphology within the BWR corridor is substantial.

Because the relationship between vegetation type and channel change relies on correlation between these variables, multiple working hypotheses can be considered to explain the patterns observed. For example, the shifts in channel planform may have caused the observed differences in local vegetation type (rather than vice versa), or other physical factors (e.g., hydrogeology and substrate characteristics) may have driven both phenomena. However, local patterns of vegetation dominance (tamarisk versus native cottonwood–willow) existed prior to the local shifts in channel form. Moreover, we have conducted detailed mapping of substrate sizes relative to vegetation distribution in two study reaches and found no difference in species composition with grain size. Overall, compelling mechanisms are lacking that would explain either a causal chain of planform change influencing vegetation distribution, or of a separate physical or ecological process that would favor both increased channel simplification and increased tamarisk dominance in the same locales.

#### 4.4 | Conceptual model of plant-river development

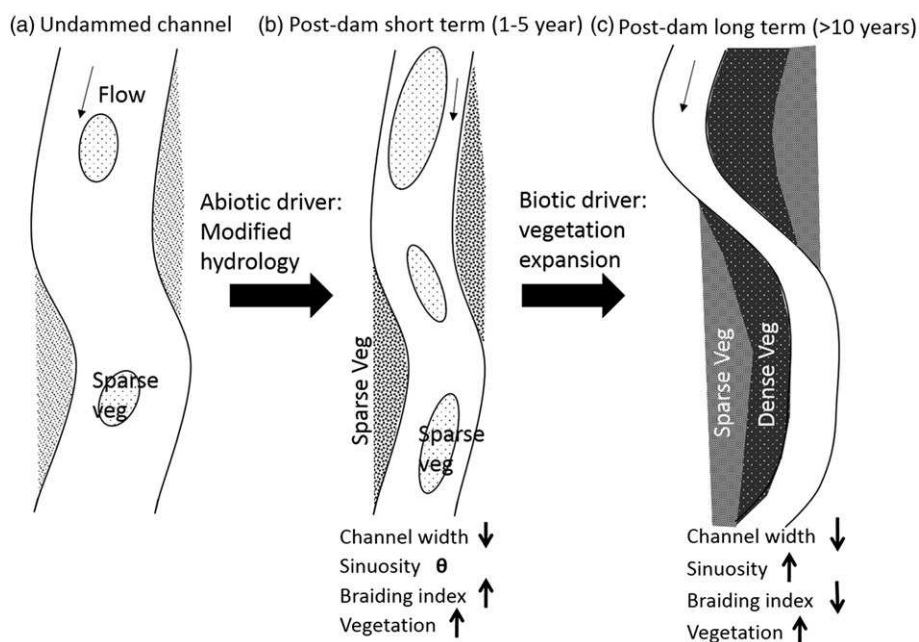
On the basis of our understanding of geomorphic evolution and plant community development on the BWR, we propose a conceptual framework to characterize how sand-bed, dryland alluvial channels evolve in several stages following flow regulation (Figure 6). In an undammed, free-flowing state, channel shape reflects the balance of sediment supply and transport capacity; bottomlands have sparse woody vegetation, and vegetation effects on hydraulics and sediment transport are modest, particularly following channel-resetting floods (Corenblit et al., 2007). In this state, wide, braided active channels are maintained by floods, high sediment supply, and low baseflows (Figure 6a; Parker, 1976; Knighton, 1998). Following dam closure, a short-term increase in braiding may occur as floods are reduced, minor reworking of the channel occurs at lower flow levels, and point bars and islands become exposed and immobilized (Figure 6b). Those bare surfaces are suitable sites for woody pioneer plant establishment, initiating a phase where biotic forces exert increasing influence on channel morphology. The reduction in disturbance regime and increases in low flows would support extensive establishment, growth, and persistence of vegetation on both high and low floodplains. Because many woody pioneer species possess fast growth and vigorous clonal traits, this transition can occur relatively quickly, within 5–10 years after flow regulation. Similar changes have been observed following channel cutoff and abandonment (Stella et al., 2011).

In the decades following dam construction, persistent changes to the flow and sediment regime allow plants to colonize islands and abandoned channels, precluding reactivation of secondary channels by small-magnitude floods (Braudrick et al., 2009). Eventually, flow is routed through a deeper channel, and the braided channel form

simplifies to single thread. In contrast to the initial channel response following dam closure, the longer term evolution is mediated largely by the biotic processes of vegetation establishment and woodland development (Figure 6c). This transition (from B to C in Figure 6) can be a multidecade process, with reduced flood disturbance playing an important primary control on river morphology, and with secondary impacts and positive feedbacks from the vegetation (Auerbach et al., 2013; Shafroth et al., 2002).

#### 4.5 | Management implications

Arresting and reversing the trends of channel simplification and tamarisk expansion on the Bill Williams and other rivers present considerable challenges (Sankey et al., 2015). Efforts to provide environmental flows to favor native species have been underway since the mid-1990's on the BWR (Shafroth et al., 2010), and high-flow releases have had some success in increasing the relative density of native willow over tamarisk in the wettest areas of the river bottomland (Shafroth et al., 1998; Wilcox & Shafroth, 2013). However, tamarisk's expansion on drier, less fluvially active floodplains also continued during this period. The strength of positive feedbacks between river morphology and riparian vegetation often makes initial changes resilient to attempts to reverse them (Suding & Gross, 2006), and this may be the case for tamarisk. Environmental flow prescriptions, supplemented with active tamarisk control methods (e.g., mechanical removal or biological control agents) may begin to slow or reverse its spread. In this case, it is an open question whether geomorphic changes will reverse in similar fashion, for example, by inducing local bar and bank erosion and redistribution of bottomland sediment within the river corridor. Whatever the outcome of these approaches,



**FIGURE 6** Conceptual model applicable to sand-bed, dryland alluvial rivers showing the two-stage suite of geomorphologic and riparian vegetation feedbacks triggered by flow regulation that shift the river ecosystem away from a predam state. The shift from a to b occurs in a relatively short time frame (5–10 years) after dam closure and is triggered primarily by large changes in abiotic drivers (reduced peak flows and sediment supply, and increased baseflows). The shift from b to c happens over a longer (decadal) timeframe, when the channel becomes progressively narrower and more single thread. This response phase is mediated by colonization of woody plants in the former active channel (dark grey) and increased vegetation cover and density on drier, less frequently inundated floodplains (light grey)

acknowledging the “underfit” condition of the modern-day active stream within its much larger historical setting is a necessary first step to restoring natural processes to severely altered rivers (House et al., 2006; Mueller et al. In Press; Trush et al., 2000).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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