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LEGACIES OF FLOOD REDUCTION ON A DRYLAND RIVER

J. C. STROMBERG,[a]* P. B. SHAFROTH[b] and A. F. HAZELTON[a]
[a] *School of Life Sciences, Arizona State University, Tempe, Arizona, USA*
[b] *United States Geological Survey, Fort Collins Science Center, Fort Collins, Colorado, USA*

ABSTRACT

The Bill Williams (Arizona) is a regulated dryland river that is being managed, in part, for biodiversity via flow management. To inform management, we contrasted riparian plant communities between the Bill Williams and an upstream free-flowing tributary (Santa Maria). Goals of a first study (1996–1997) were to identify environmental controls on herbaceous species richness and compare richness among forest types. Analyses revealed that herbaceous species richness was negatively related to woody stem density, basal area and litter cover and positively related to light levels. Introduced *Tamarix* spp. was more frequent at the Bill Williams, but all three main forest types (*Tamarix*, *Salix/Populus*, *Prosopis*) had low understory richness, as well as high stem density and low light, on the Bill Williams as compared to the Santa Maria. The few edaphic differences between rivers (higher salinity at Bill Williams) had only weak connections with richness. A second study (2006–2007) focused on floristic richness at larger spatial scales. It revealed that during spring, and for the study cumulatively (spring and fall samplings combined), the riparian zone of the unregulated river had considerably more plant species. Annuals (vs. herbaceous perennials and woody species) showed the largest between-river difference. Relative richness of exotic (vs. native) species did not differ. We conclude that: (1) The legacy of reduced scouring frequency and extent at the Bill Williams has reduced the open space available for colonization by annuals; and (2) Change in forest biomass structure, more so than change in forest composition, is the major driver of changes in plant species richness along this flow-altered river. Our study informs dryland river management options by revealing trade-offs that exist between forest biomass structure and plant species richness. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS: dryland river; flood disturbance; flow management; plant species richness; riparian vegetation; *Salix*; *Populus*; *Tamarix*

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INTRODUCTION

The majority of the world's rivers have been dammed and flow-regulated to supply water, power, flood control and/or recreational opportunities (Nilsson *et al.*, 2005). River damming and flow-regulation alter many of the factors that influence riparian plant species richness, including flood disturbance, spatio-temporal heterogeneity and resource levels (Naiman *et al.*, 1993; Sait *et al.*, 2005). Thus, one commonly reported effect of regulation is reduced levels of downstream plant species richness along river channels and in floodplains (Nilsson and Jansson, 1995; Baattrup-Pedersen and Riis, 1999; Jansson *et al.*, 2000). In semiarid Colorado, for example, plant species richness in the riparian zone was 40% lower on a flow-regulated river than on a free-flowing counterpart (Uowolo *et al.*, 2005). In semiarid Arizona, plant species richness in a below-dam reach was less than half that in the above-dam reach during dry seasons, with differences less pronounced during wetter seasons (Beauchamp and Stromberg, 2008). In some cases, however, richness either does not differ or is higher at sites below dams (Jansson *et al.*, 2000; Bernez *et al.*, 2004). These multiple ecological outcomes arise because of the variety of riverine environmental contexts and the variation in dam management practices.

One hydrologic change common in below-dam reaches is a reduction in the frequency and magnitude of flooding (Graf, 2006). Where pre-dam flood intensities are high, reduction in flood scour can lead to increased plant species richness as predicted by the intermediate disturbance hypothesis (Azami *et al.*, 2004). In other contexts, reduced flood disturbance may decrease species richness by reducing the ability of colonizers to co-exist with competitors and by reducing spatial and temporal heterogeneity in the riparian landscape (Merritt and Cooper, 2000; Capon, 2005; Parsons *et al.* 2005; Wintle and Kirkpatrick, 2007). Flood reduction and river damming also can contribute to declines in richness by disrupting hydrochory at the dam-reservoir barrier and by restricting water-borne seed dispersal (Jansson *et al.*, 2005; Merritt and Wohl, 2006; Brown and Chenoweth, 2008).

Another common change in the riparian zones of dammed rivers is altered resource availability. On dryland regulated rivers, dry-season base flows sometimes increase in conjunction with dampening of flow extremes, and this reduction in water stress could lead to increased richness

*Correspondence to: J. C. Stromberg, School of Life Sciences, Arizona State University, Tempe, Arizona 85287-450, USA.
E-mail: jstrom@asu.edu

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along stream channels (Tabacchi *et al.*, 1996; Stromberg *et al.*, 2007). Countering this, streamside and floodplain sediments often become coarser downstream of a storage reservoir (Williams and Wolman, 1984), and this edaphic change can reduce plant richness by decreasing retention of water and nutrients (Jansson *et al.*, 2000; Beauchamp and Stromberg, 2008). Further, riparian soils can become drier or saltier as a result of reduced frequency of seasonal flooding, thereby reducing plant species diversity (Doupe *et al.*, 2006).

Overstory and understory species within riparian plant communities are influenced by different suites of environmental variables. Shifts in forest tree species composition often accompany river regulation (Merritt and Poff, 2010; Mortenson and Weisberg, 2010), and these overstory changes may further alter environmental conditions for understory species. The nature and extent of change will vary depending on functional traits of the new overstory dominants. In western USA, *Tamarix* spp. has increased in abundance along many rivers (Friedman *et al.*, 2005). Some have hypothesized that this halophyte can cause salts to concentrate in the upper soil layers and thus reduce understory richness. Although studies on free-flowing rivers have shown differences in soil traits and plant species richness to be relatively small between *Tamarix* and other woody vegetation types, such differences may be magnified on regulated rivers where the frequency of flushing floods is reduced (Stromberg, 1998; Bagstad *et al.*, 2006; Ladenburger *et al.*, 2006).

Increasingly, flows are being released to below-dam ecosystems as part of river restoration efforts (Richter and Postel, 2004). These 'environmental flows' often target one or a few aspects of an ecosystem about which flow–ecology relationships are well-understood. Of note, winter/spring flood pulses have been released into various rivers in western North America, informed by studies that have revealed strong linkages between flooding patterns and recruitment dynamics of pioneer trees including *Populus* spp. (Mahoney and Rood, 1998; Shafroth *et al.*, 1998). Significant gaps remain in our knowledge of other flow-biota linkages, however, including those between flow regimes and plant species richness.

Plant species richness is of management concern for several reasons. Floristic richness can influence ecosystem functioning, in part by influencing trophic interactions (Lecerf *et al.*, 2005). Due to this influence, floristic richness also can be used as an indicator of underlying ecosystem processes—where plant species are diverse, for example, there often also are high numbers of butterflies and other invertebrates that form the food base for many riparian birds and mammals (Hawkins and Porter, 2003). Further, plant species richness is related to ecosystem resilience (Chapin *et al.*, 1997) in that the number and types of species present influence how a plant community responds to press disturbance such as drought and pulse disturbance such as flooding.

Understanding the suite of vegetation changes that have occurred below a dam and determining causal mechanisms are crucial steps towards informing management plans. We conducted a case study of a regulated dryland river and its above-dam unregulated tributary to test the following predictions: (1) Species richness would be higher (a) where there is more light and less overstory vegetation (owing to reduced competitive exclusion) and (b) where soils have finer texture and lower salinity (relating to resource availability controls); (2) forests would be denser and soils coarser and more saline on the regulated river; and thus (3) richness of plant species (and colonizers in particular) would be lower on the regulated river. Additionally, we investigated understory richness by forest type, to see if patterns differed between rivers.

METHODS

Study design

We conducted two studies, both of which involved spatial contrasts of plant species richness and environmental variables between the Bill Williams River, located below Alamo Dam, and the Santa Maria River, located upstream of Alamo Dam in arid western Arizona (Figure 1). The first study (1996–1997) focused on differences in herbaceous species richness among woody vegetation types and on relationships between richness and environmental factors. The second study (2006–2007) focused on site-level differences in floristic richness (herbaceous and woody), with data collected at sites matched for hydrology and geomorphology between rivers. For both studies, richness data were collected following the winter and summer rainy seasons over a one and a half to two year period to capture inter- and intra-annual variability.

Study area

The Santa Maria River presents a close match to the Bill Williams River in terms of climate, geomorphology, land use and dominant vegetation, although there are some differences. Both are within the Basin and Range Physiographic Province, in an area transitional between the Sonoran and Mojave deserts. The region is hot and arid with mean annual temperature of 21.6°C and mean annual precipitation of 22.6 cm at Alamo Dam (#020100, 393 m, 1975–2007; http://www.wrcc.dri.edu).

The Bill Williams and Santa Maria both have alternating segments of perennial and intermittent stream flow. Because regulation has increased low flows on the Bill Williams,

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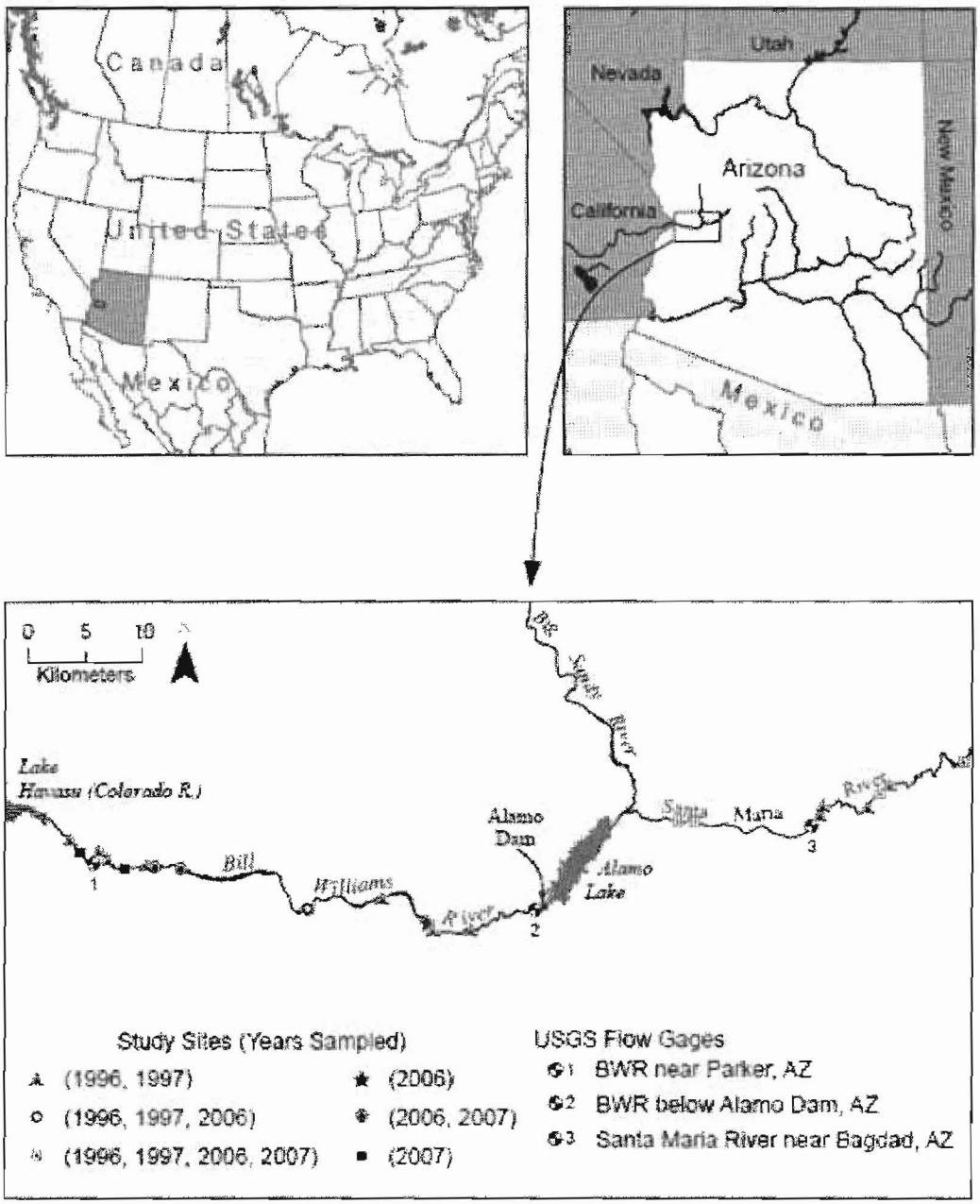

Figure 1. Loeation of sites for the 1996–1997 and 2006–2007 studies. Note that some sites overlapped between the two study periods. Also shown are locations of stream gages.

more of the Bill Williams is now perennial than it was formerly (Shafroth *et al.*, 2002). These perennial reaches are characterized by shallower and more stable alluvial water tables than are intermittent reaches, which are more common along the Santa Maria River (Shafroth, 1999; Shafroth *et al.*, 2000). The Santa Maria is a smaller river, with average annual stream flow rate of $1.62\,m^3\,s^{-1}$ at the Bagdad gaging station (USGS #09424900; 415 m above sea level; 1969–1985 and 1989–2007). The Bill Williams had an average annual flow rate of $3.89\,m^3\,s^{-1}$ for that same period (Alamo Dam station #09426000; 295 m).

Alamo Dam, completed in 1968, is primarily managed for flood control to minimize water fluctuations in the Colorado River arising from Bill Williams' inflows. Water flows also are managed to provide reservoir recreation and to maintain and restore riparian and aquatic ecosystems in the below-dam reach. Although operation of the dam has substantially reduced flood magnitude and frequency, several small

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experimental floods have been released in recent decades as part of restoration efforts (Shafroth *et al.*, 2010; Figure 2). The Santa Maria has an unmodified flow regime, characterized by episodic occurrence of large floods. Seasonally, precipitation and flow peaks are greatest in winter (December–March) and late summer (August–September).

Both rivers have reaches with wide, unconstrained floodplains and other reaches that flow through relatively narrow canyons. The Santa Maria generally has a narrower riparian corridor. Average stream gradient on both rivers is similar (0.003 at Bill Williams, 0.004 at Santa Maria). Since completion of Alamo Dam, channels have narrowed considerably and floodplain vegetation has concomitantly expanded along the Bill Williams River (Shafroth *et al.*, 2002). Although some geomorphic adjustments are ongoing, major changes to bottomland geomorphology occurred within approximately 20 years of dam closure, an adjustment timeframe similar to that observed along other sand-bed streams in western USA (Williams and Wolman, 1984; Andrews, 1986; Johnson, 1997). Dynamics of bottomland geomorphology for the Santa Maria River have not changed notably during this period and are generally characterized by channel widening events associated with large floods, followed by periods of narrowing between floods (Shafroth *et al.*, 2002).

The riparian zones and watersheds of both have a long history of use as ranch lands. The Bill Williams has had portions of its riparian zone converted to crop fields. Currently, a mix of federal, state and private entities own and manage the land along both rivers. Much of the riparian land at Bill Williams is managed for biodiversity conservation

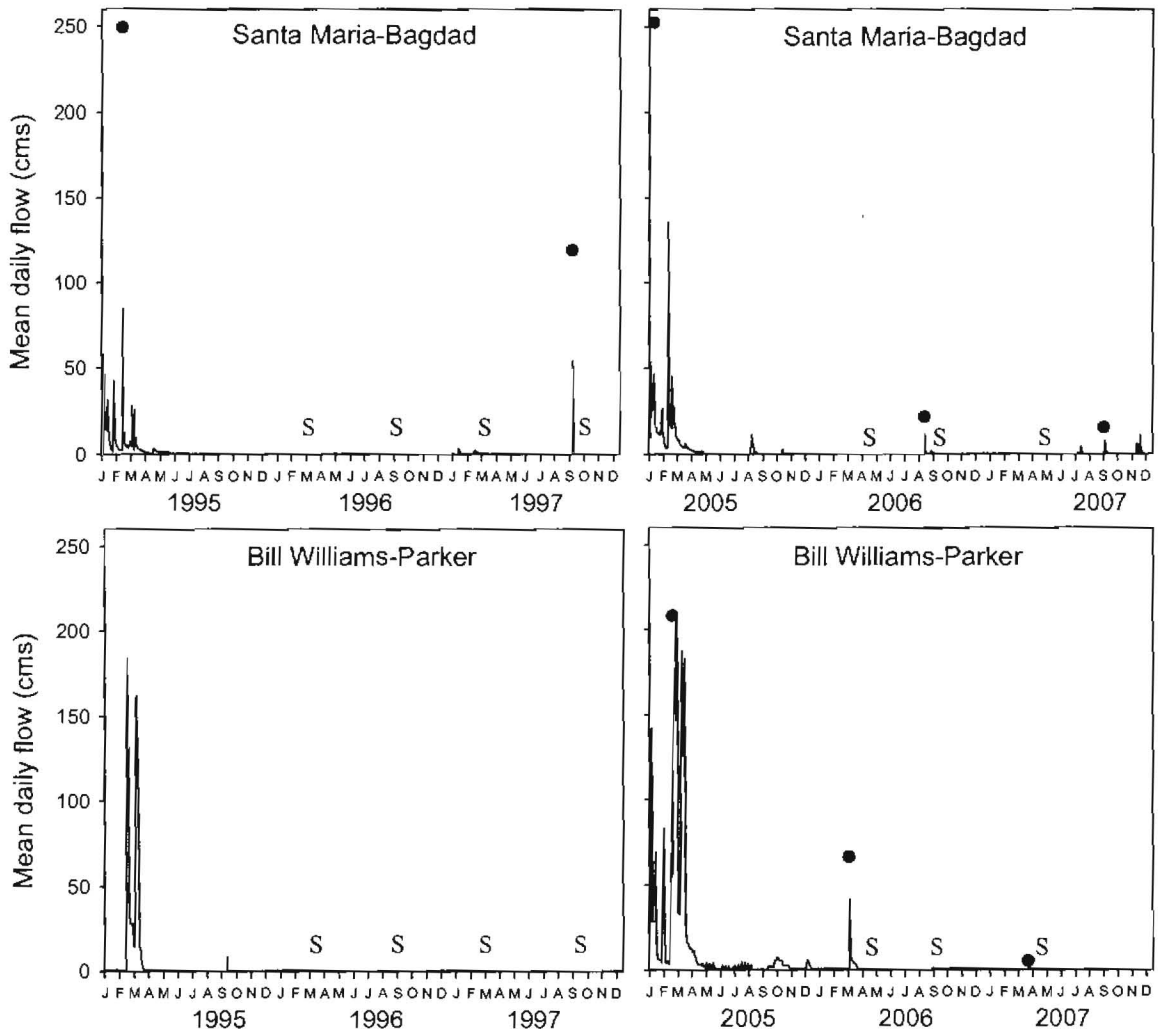

Figure 2. Stream flows in the Santa Maria and Bill Williams rivers prior to and during the study. The continuous black line indicates mean daily flow; '●' indicates annual peak flow; 'S' indicates vegetation sampling times (Peak flow data not available for 1995 at Bill Williams).

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(with a large National Wildlife Refuge in its lower reaches), whereas the Santa Maria has reaches influenced by livestock grazing and off-road vehicle use.

Floodplains of both rivers are vegetated by pioneer riparian trees and shrubs including *Populus fremontii*, *Salix gooddingii*, *Tamarix* spp. (*T. chinensis*, *T. ramosissima*, and/or hybrids), *Pluchea sericea* and *Hymenoclea monogyra*. The highest portions of the river floodplains and the terraces are vegetated primarily by *Prosopis* (*P. velutina* and *P. glandulosa*), late successional taxa. Because much of this hydrogeomorphic zone at Bill Williams has been converted to irrigated or fallowed farmland, high floodplains and terraces at both rivers were excluded from the 2006–2007 sampling.

Field data collection

1996–1997 study. In 1996 and 1997, vegetation was sampled in a manner to emphasize herbaceous species richness and understory comparisons among woody vegetation types. Data were collected at eight sites along each the Bill Williams and Santa Maria (Shafroth *et al.*, 2002; Figure 1). Sites were selected to represent typical geomorphic, hydrologic and vegetative conditions present along each river. Six of the sites on the Bill Williams were perennial and two had intermittent stream flow; on the Santa Maria two were perennial and six were intermittent. Site valley width ranged from 159 to 555 m at Bill Williams and from 131 to 765 m at Santa Maria. Elevation ranged from 152 to 271 m (Bill Williams) and 314 to 539 m (Santa Maria).

Data were collected in stratified random fashion within sites. One riparian cross-section was established per site, within which discrete vegetation patches were subjectively delineated. Patches included young to mature stands of trees (with *Tamarix*, *Salix–Populus* and *Prosopis* the three most common), tree seedlings, shrublands (e.g. *H. monogyra*, *P. sericea*), herbaceous areas and unvegetated areas. Woody stem density (live and dead) and basal area were measured, by species, in one randomly placed quadrat (100 m^2) per patch. A second quadrat was randomly placed within a patch if the patch extended for >50 m along the cross-section.

Herbaceous cover, by species, was recorded in one 2-m^2 (1 m × 2 m) plot nested in each quadrat. Plants were identified to species using Kearney and Peebles (1960) and recent taxonomic treatments published as part of the Vascular Plants of Arizona project (http://nhc.asu.edu/vpherbarium/vpap.html). Data were collected four times (March and September of 1996, and March and October of 1997). A total of 117 (Bill Williams) and 110 (Santa Maria) 2-m^2 plots were sampled per river. 52% of the 2-m^2 plots (both rivers combined) were within patches dominated by young to mature trees of *Tamarix*, *Salix–Populus* or *Prosopis*, using basal area as the measure of dominance. These forest types were the subject of subsequent statistical comparison. Young forest stands were more prevalent on the Santa Maria and older stands were common on the Bill Williams (Shafroth *et al.*, 2002), but forest size classes were collapsed for analysis in this study.

Several environmental variables were measured at each 2-m^2 plot. Plot distance from active channel edge and elevation above channel bed were determined from cross-sectional topographic surveys. Per cent cover of litter (e.g. leaves, stems) within each plot was visually estimated in March 1996. Solar radiation (PAR) above ground surface was recorded in plots in June 1997 (after forest leaf-out) using a LICOR quantum sensor and values were converted to a percentage of full sunlight. One soil sample (upper 30 cm) was collected adjacent to each study plot in 1996. The percentage of coarse sediments (>2 mm) in the soil was determined by sieving, and percentages of sand, silt and clay were determined using the hydrometer method (Day, 1965). The pH of a suspension of a 1:1 soil/water slurry was measured with an Orion combination electrode. Electrical conductivity of the filtered 1:1 solution was measured with a Beckman Instruments conductivity probe.

2006–2007 study. In 2006 and 2007, plant species richness was sampled to assess floristic richness at site and river scales. Vascular plant species (woody and herbaceous) richness was sampled in plots systematically distributed across the floodplain/stream bank zone of four sites at Bill Williams and four sites at Santa Maria (Figure 1). The sites were selected to provide between-river matches with respect to stream hydrology and valley geomorphology. The four sites per river included two moderately confined canyon reaches (average floodplain width of 74 m for Santa Maria and 93 m for Bill Williams) and two wide, unconfined reaches (respective floodplain widths of 547 and 857 m). For safety reasons, canyon reaches of the Bill Williams were substituted with another less remote canyon pair in 2007. One of each valley form type was selected to have perennial flow and the other to have intermittent flow, based on long-term field observations. Site elevation ranged from 143 to 259 m (Bill Williams) and from 363 to 512 m (Santa Maria).

At each site, data were collected at three riparian cross-sections located 100 m apart. The first cross-section at each site was located randomly. Each riparian cross-section was divided into 10 segments, with the segment lengths scaled to the width of each individual floodplain. Two of the 10 segments were anchored along the low-flow channel (one on each side of the stream). In April and September of 2006 and May of 2007, one 10-m^2 plot (2 m × 5 m; long axis perpendicular to stream) was sampled per segment for vascular plant presence/absence (total of 30 plots per site). Site-level richness was calculated as the cumulative number

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of species sampled in the 30 plots. River-wide richness was calculated as the total number of species sampled at all four sites (120 plots).

Data on soil variables were calculated at the site scale. Soil samples (upper 5 cm) were collected in May 2007 from each of 10 segments of one transect per site. After sieving to remove coarse sediments, soils were analysed for particle size and organic matter content by MotZZ Laboratory, Tempe, Arizona, and the percentages were averaged to produce site-level values.

Weather and hydrology

During both study periods, precipitation was below average to average (Table I). In the year prior to each study, winter rains were abundant and both rivers had large spring floods (Figure 2). In spring of 2006, a moderate experimental flood release inundated about 40% of the Bill Williams' bottomland (Shafroth *et al.*, 2010) and our vegetation sampling occurred 6 weeks after peak discharge. The Bill Williams River had a smaller experimental flood release in April, 2007, inundating about 14% of the bottomland; vegetation sampling occurred 4 weeks after the peak flow. A flood occurred in the Santa Maria on 26 September 1997, with vegetation sampled within 15 days after the peak. The Santa Maria also flooded on 25 August 2006 with a smaller peak on 8 September 2006, 2 days prior to vegetation sampling. Correlations and regressions (see next section) are not presented for October 1997 because soil conditions may have been altered by the late summer flood.

Analysis

Plant–environment relationships. Pearson correlation analysis was used to examine relationships, by season, of plot-level herbaceous species richness (1996–1997 data) with environmental variables. Four (stem density, electrical conductivity, per cent full sunlight and distance from channel) of 10 environmental variables were log-transformed to achieve a normal distribution. For these same seasonal data sets, forward-stepping multiple regressions were used to predict herbaceous species richness from environmental variables. To reduce multicollinearity, the environmental data sets were first analysed with hierarchical cluster analysis; this provided a basis for selecting subsets of independent variables. Independent variables included in the regression models were plot elevation above channel bed, stand basal area, per cent of full sunlight, litter cover, coarse soil content, silt content and electrical conductivity. Probability values for variable entry and removal from the models were set at $p = 0.15$ (default settings of SYSTAT v. 12). For these and other tests, values were considered significantly different at $p \leq 0.05$.

Between-river differences. Student's *t*-tests were used to test for differences in plot-level environmental variables and understory species richness (1996–1997 data) between rivers, for each forest type (*Tamarix*, *Salix–Populus*, *Prosopis*). To account for potential effects of stand age (Stromberg 1998; Uowolo *et al.*, 2005), data were also analysed with analysis of covariance (ANCOVA) using basal area as covariate and proxy for stand age. The ANCOVAs were conducted for species richness and for three environmental variables (sunlight, litter and electrical conductivity) strongly correlated with stand basal area.

At the site level, between-river differences in environmental variables (soil measured in 2007) and site-level richness (2006 and 2007 data) were assessed with Wilcoxon matched pairs test. For this analysis, the four sites per river were matched with respect to flow status and valley form. The non-parametric test was used because of small sample size. To further examine richness patterns, species accumulation curves for the 2006–2007 data sets were generated using sample-based rarefaction (Colwell, 2005). To assess patterns of dominance and diversity, rank–abundance curves were calculated for the 2006–2007 data sets using frequency as the measure of abundance.

To examine richness patterns by plant group, species were classified by life span and growth habit (annuals and biennials, herbaceous perennials and woody species), geographic origin (native or introduced to USA), and wetland status (non-wetland vs. wetland, which encompassed obligate wetland, facultative wetland, facultative and facultative upland groups). In lieu of extensive trait analysis, annuals were used as our proxy for ruderal, colonizing species (Grime, 1979). Classifications were based on information provided in USDA PLANTS database (http://plants.usda.gov) and SEInet database (http://swbiodiversity.org/seinet), as modified, in some cases, by professional judgment. For specimens that could be identified only to genus, professional judgment was used to assign plants to categories.

Table I. Total precipitation and mean temperature during 4-month blocks preceding vegetation samplings. Weather data are from Alamo Dam Station. Long-term precipitation averages (1961–1990) are 9 cm for January–April and 8 cm for June–September

Sampling time	Precipitation (cm)	Temperature (°C)
March 1996	3.3	14
September 1996	2.1	31
March 1997	6.1	14
October 1997	10.0	30
April 2006	1.5	15
September 2006	5.4	33
May 2007	1.9	15

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Table II. Correlation coefficients (Pearson 'r' values) between plot-level values for richness of herbaceous plant species and environmental variables at Bill Williams ($n = 117$ plots) and Santa Maria ($n = 110$ plots) Rivers, for three sampling periods. Variables are listed in order from highest to lowest average correlation as calculated at Bill Williams

	Bill Williams River			Santa Maria River		
Richness vs.	March 1996	Sept. 1996	Mar. 1997	March 1996	Sept. 1996	March 1997
Elevation above channel	−0.57*	−0.51*	−0.35*	−0.41*	−0.05	0.44*
Woody stem density	−0.45*	−0.37*	−0.43*	−0.25*	−0.02	−0.03
Distance from channel	−0.40*	−0.37*	−0.28*	−0.24*	−0.13	0.16
Sunlight	0.17	0.25*	0.49*	0.24*	−0.01	0.03
Litter	−0.33*	−0.34*	−0.24*	−0.23*	−0.05	0.16
Basal area	−0.28*	−0.24*	−0.37*	−0.19*	−0.02	0.02
Coarse particles	0.17	0.29*	0.36*	0.05	−0.06	−0.25*
Silt	−0.22*	−0.20*	−0.28*	−0.22*	0.00	0.15
Sand	0.21*	0.18	0.28*	0.23*	0.02	−0.13
Clay	−0.13	−0.11	−0.20	−0.20*	−0.06	0.02
EC	−0.12	−0.11	−0.21*	0.19*	0.15	0.09

*$p \leq 0.05$.

RESULTS

Environmental correlates of herbaceous species richness

Plot-level herbaceous species richness at Bill Williams increased significantly with several factors—proximity to the channel (lateral and vertical distance), decreasing density and basal area of woody stems, increasing light and decreasing litter cover (Table II). Richness was correlated negatively with soil silt content, presumably an indirect effect of the association of fine sediments with densely wooded stands (data not shown). Correlations of richness with electrical conductivity were negative, but weak. Multiple regression analysis confirmed key roles for elevation above channel bed and degree of stand openness (e.g. per cent of full sunlight, basal area) as factors related to understory richness at Bill Williams, although the total variance explained was low (Table III).

Correlations at Santa Maria were variable among sampling periods but were similar to those at the Bill Williams for March 1996 (Table II). Multiple regression models for Santa Maria included the same variables as for Bill Williams (i.e. plot elevation above channel bed, basal area, light availability) but also included soil variables (Table III). Interestingly, in moderately wet 1997, plot

Table III. Results of forward-stepping multiple regression analysis predicting plot-level herbaceous species richness from environmental variables at the Bill Williams (BW) and Santa Maria (SM) Rivers, for three sampling periods

River and date	Variables in model and direction of influence	p-value of regressor	F ratio of model	Variance explained
BW, March 1996	Elevation above thalweg (−)	<0.01	$6.8_{2,110}$	$r^2 = 0.11$
	Basal area (−)	0.02		
BW, Sept. 1996	Elevation above thalweg (−)	<0.01	$5.9_{2,114}$	$r^2 = 0.08$
	Per cent full sunlight (+)	0.02		
BW, March 1997	Elevation above thalweg (−)	<0.01	$5.9_{2,114}$	$r^2 = 0.10$
	Per cent full sunlight (+)	<0.01		
SM, March 1996	Elevation above thalweg (−)	<0.00	$8.9_{5,100}$	$r^2 = 0.31$
	Basal area (−)	0.06		
	Coarse soil particles (−)	0.13		
	Silt (−)	0.01		
	Electrical conductivity (+)	<0.01		
SM, Sept. 1996	No significant model			
SM, March 1997	Elevation above thalweg (+)	<0.00	$9.24_{4,101}$	$r^2 = 0.27$
	Per cent full sunlight (+)	<0.00		
	Coarse soil particles(−)	0.10		
	Electrical conductivity (+)	0.10		

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elevation showed a positive relationship with richness, in contrast to the negative relation shown at Bill Williams.

Differences in environmental factors: stand-level and site-level

Tamarix and *Salix–Populus* stands had significantly greater basal area at Bill Williams than at Santa Maria (Table IV). All three forest types (*Tamarix*, *Salix–Populus*, *Prosopis*) had significantly greater woody stem density at Bill Williams. Contributing to the high stem density at Bill Williams were stems of shrubs (e.g. *P. sericea*) as well as shrubby trees (i.e. *Tamarix*).

Other significant between-river differences included less light in *Tamarix* and *Salix/Populus* understories, greater litter cover in *Tamarix* and greater electrical conductivity in *Tamarix* and *Prosopis* at Bill Williams. Many forest stands at Santa Maria were young (with correspondingly low basal area) (Figure 3), and between-river differences in many of these variables were related to differences in basal area (Table V).

Soil texture differed little between rivers at the stand-level (Table IV). At the site level, as well, there were similar percentages of sand (78 ± 5 vs. 79 ± 7; mean $\pm$ 1SE), silt (16 ± 3 vs. 15 ± 5) and clay (6 ± 1 vs. 6 ± 2) at Santa Maria and Bill Williams respectively ($p > 0.05$). Organic matter also did not differ between rivers (1.1 ± 0.4 vs. 1.0 ± 0.5).

Differences in species richness: stand-level and site-level

At the stand level, herbaceous understories were less species-rich at Bill Williams than at Santa Maria (Figure 4). Between-river differences were particularly large in March 1997, with significantly more species at Santa Maria across forest types. For *Salix-Populus*, species richness was significantly greater at Santa Maria than at Bill Williams for the other three sampling times, as well.

At the site level, plant species richness was significantly greater at Santa Maria than Bill Williams during spring of 2006 and 2007 (Table VI; Figure 5). Site-level richness during September 2006, however, did not differ significantly between rivers. River-wide patterns paralleled site-level patterns, with richness higher in spring than in fall, and higher at Santa Maria.

Rank–abundance curves (Figure 5), as well as patterns of absolute frequency (Table VII), indicated that a smaller number of species dominated the spring plant communities at Bill Williams. Another between-river difference was the presence of large numbers of rare (infrequent) species at Santa Maria during spring. During September, in contrast, the shapes of the rank–abundance curves were nearly identical among rivers.

Differences in species composition: site level analysis

Between-river differences in species richness were primarily due to patterns of annuals (Tables VI and VIII). During April 2006, for example, there were twice as many annual species at Santa Maria than at Bill Williams whereas numbers of herbaceous perennials and woody species did not differ greatly. Relative frequency of annuals also was greater at Santa Maria (e.g. 0.68 vs. 0.46, respectively, for April 2006).

Wetland and non-wetland groups both were significantly more species-rich at Santa Maria than Bill Williams during May 2007 (Table VI). In April 2006, only the non-wetland group was more species-rich at Santa Maria. Neither group differed significantly in September 2006. For the 2006–2007 study as a whole, a total of 51 wetland species

Table IV. Environmental differences between the free-flowing Santa Maria (SM) River and the flow-regulated BillWilliams (BW) River, by forest type, as measured in 1996 or 1997. Values are means $\pm$ 1SE

	Tamarix		*Salix-Populus*		*Prosopis*	
	SM	BW	SM	BW	SM	BW
Woody stem density (live and dead; no. $100\,m^{-2}$)	208 ± 34	$501 \pm 86^*$	126 ± 26	$351 \pm 96^*$	70 ± 16	$798 \pm 239^*$
Basal area (live; $m^2\,ha^{-1}$)	7 ± 2	$24 \pm 4^*$	24 ± 6	$45 \pm 7^*$	17 ± 3	14 ± 4
Sunlight (% of full)	$84 \pm 7^*$	30 ± 6	$67 \pm 7^*$	32 ± 10	47 ± 8	33 ± 11
Litter cover (%)	32 ± 8	$56 \pm 5^*$	48 ± 6	53 ± 9	55 ± 7	54 ± 12
Particles >2 mm (%)	$45 \pm 8^*$	6 ± 3	17 ± 4	10 ± 6	5 ± 2	3 ± 3
Sand (%)	82 ± 6	78 ± 4	76 ± 4	75 ± 8	67 ± 3	66 ± 7
Silt (%)	9 ± 4	16 ± 4	18 ± 4	17 ± 6	25 ± 3	26 ± 6
Clay (%)	5 ± 1	6 ± 1	6 ± 1	9 ± 2	7 ± 1	8 ± 1
Soil electrical conductivity ($ds\,m^{-1}$)	0.4 ± 0.1	$1.3 \pm 0.3^*$	0.7 ± 0.1	1.0 ± 0.3	0.5 ± 0.1	$1.6 \pm 0.6^*$
pH	7.8 ± 0.2	7.9 ± 0.0	8.0 ± 0.1	7.9 ± 0.1	7.8 ± 0.1	8.0 ± 0.2
# of plots	16	3	28	13	22	7

*Significant difference between rivers at $p \leq 0.05$ (t-test)

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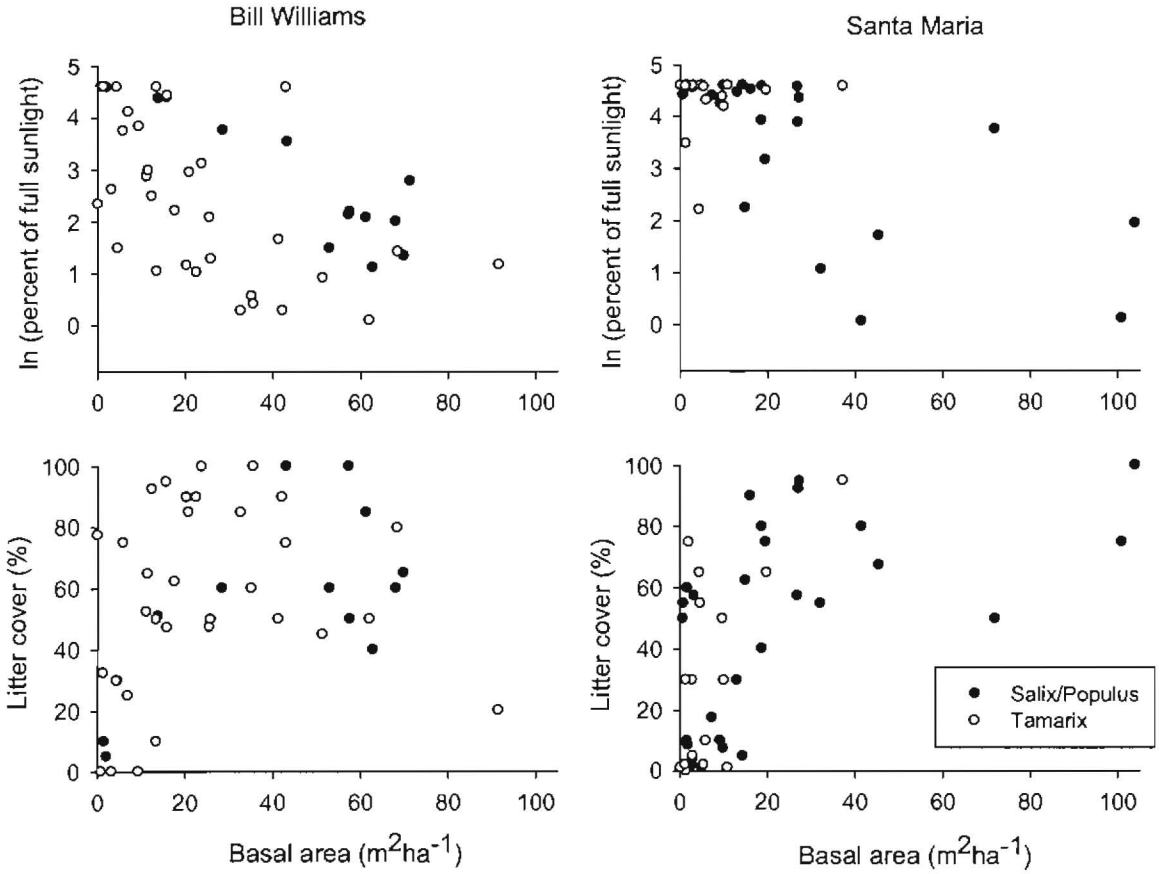

Figure 3. Per cent of full sunlight (natural log transformed) and ground-layer litter cover as a function of stand basal area for patches dominated by *Salix–Populus* and for those dominated by *Tamarix*. Left panel shows the regulated Bill Williams River; right panel shows the free-flowing Santa Maria. Each data point represents a forest stand.

and 59 non-wetland species were recorded at Santa Maria compared to 40 and 28 respectively at Bill Williams (Table VIII). However, although numbers of wetland species differed, wetland plants had greater relative frequency of occurrence at Bill Williams than at Santa Maria for all sampling times (Table VI, bottom rows).

Both rivers had similar percentages and frequencies of native and exotic species (Tables VI and VIII). The number of exotics was greater at Santa Maria than at Bill Williams during spring but so too was the number of natives, thus the percentage of exotics was similar at both rivers (e.g. 30% exotic at Santa Maria and 28% exotic at Bill Williams in April, 2006). Assessments based on frequency show similar trends, with, for example, 46 and 50% of all plant occurrences in April 2006 at Santa Maria and Bill Williams, respectively, being exotics.

Table V. Environmental differences between rivers within *Tamarix* dominated stands and *Salix* or *Populus* dominated stands, based on analysis of covariance with basal area as covariate

	Sunlight[a]		Litter		Electrical conductivity[a]		
	F value	*p* value	*F* value	*p* value	*F* value	*p* value	df
Tamarix dominated stands							
River effect	11.8	<0.01	<1	0.86	8.2	<0.01	48
Basal area	15.8	<0.01	15.8	<0.01	0.6	0.5	48
Salix–Populus dominated stands							
River effect	0.45	0.57	0.4	0.55	0.6	0.45	40
Basal area	39.1	<0.01	11.6	<0.01	3.9	0.06	40

[a]Natural log transformed.

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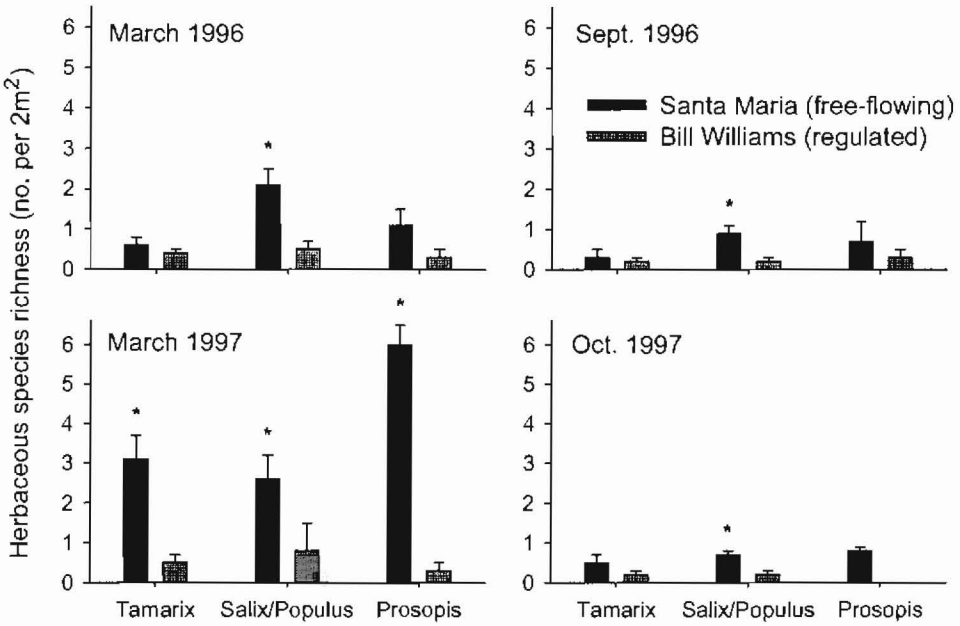

Figure 4. Herbaceous species richness (per 2-m^2) at the free-flowing Santa Maria and flow-regulated Bill Williams River, in three forest types during four sampling periods. Values are means ± 1SE. Sample sizes at Santa Maria and Bill Williams, respectively, are 16 and 33 (*Tamarix*), 28 and 13 (*Salix–Populus*) and 22 and 7 (*Prosopis*). '*' indicates significant difference between rivers ($p \leq 0.05$; *t*-test).

Table VI. Vascular plant species richness, in total and by plant group, along the free-flowing Santa Maria (SM) River and flow-regulated Bill Williams (BW) River during 2006 and 2007. Values shown are site means ± 1SE (cumulative species in 30, 10-m^2 plots per site). Also shown are river-wide richness values (cumulative species in 120, 10-m^2 plots) and proportional abundances based on frequency measurements

	April 2006		September 2006		May 2007	
	SM	BW	SM	BW	SM	BW
Cumulative richness per site	54 ± 4*	32 ± 2	16 ± 3	23 ± 2	33 ± 4*	14 ± 2
-Annuals	36 ± 5*	17 ± 2	5 ± 2	9 ± 1	16 ± 3*	3 ± 1
-Herb. Perennials	10 ± 2	8 ± 1	4 ± 2	7 ± 1	8 ± 1	5 ± 1
-Trees and shrubs	8 ± 1	7 ± 1	7 ± 1	7 ± 1	8 ± 1	5 ± 1
-Wetland species	27 ± 3	21 ± 1	13 ± 3	19 ± 4	20 ± 3*	13 ± 2
-Non-wetland species	27 ± 5*	11 ± 2	3 ± 1	2 ± 1	12 ± 1*	1 ± 1
-Native species	37 ± 4*	22 ± 2	11 ± 3	19 ± 2	21 ± 3*	9 ± 2
-Exotic species	16 ± 1*	9 ± 1	5 ± 1	4 ± 1	11 ± 2*	5 ± 1
River-wide richness	98	57	34	43	62	25
Proportional freq. annuals[a]	0.68	0.46	0.13	0.20	0.42	0.11
Proportional freq. wetland[b]	0.63	0.78	0.88	0.94	0.79	0.98
Proportional freq. exotics[c]	0.46	0.50	0.38	0.41	0.47	0.44

*Significant between-river difference at $p \leq 0.05$, within sampling times (Wilcoxon rank sum).
[a]Frequency of annuals and biennials relative to that of all taxa.
[b]Frequency of wetland plants (obligate wetland, facultative wetland, facultative and facultative upland) relative to that of all taxa.
[c]Frequency of exotic plants relative to that of all taxa.

DISCUSSION

Based on a spatial contrast with an unregulated river, the riparian ecosystem of the dammed and flow-regulated Bill Williams River is characterized by low plant species richness and presence of few rare (infrequent) species, with the extent of between-river differences varying by season and by plant group. Low plant species richness has been documented on other regulated rivers of the American West, with causes attributed to edaphic differences (Beauchamp and Stromberg, 2008) or to altered river flooding processes that exacerbate effects of forest aging processes on species richness (Uowolo *et al.*, 2005). Our analysis suggests that one contributor to low richness at the Bill Williams is post-

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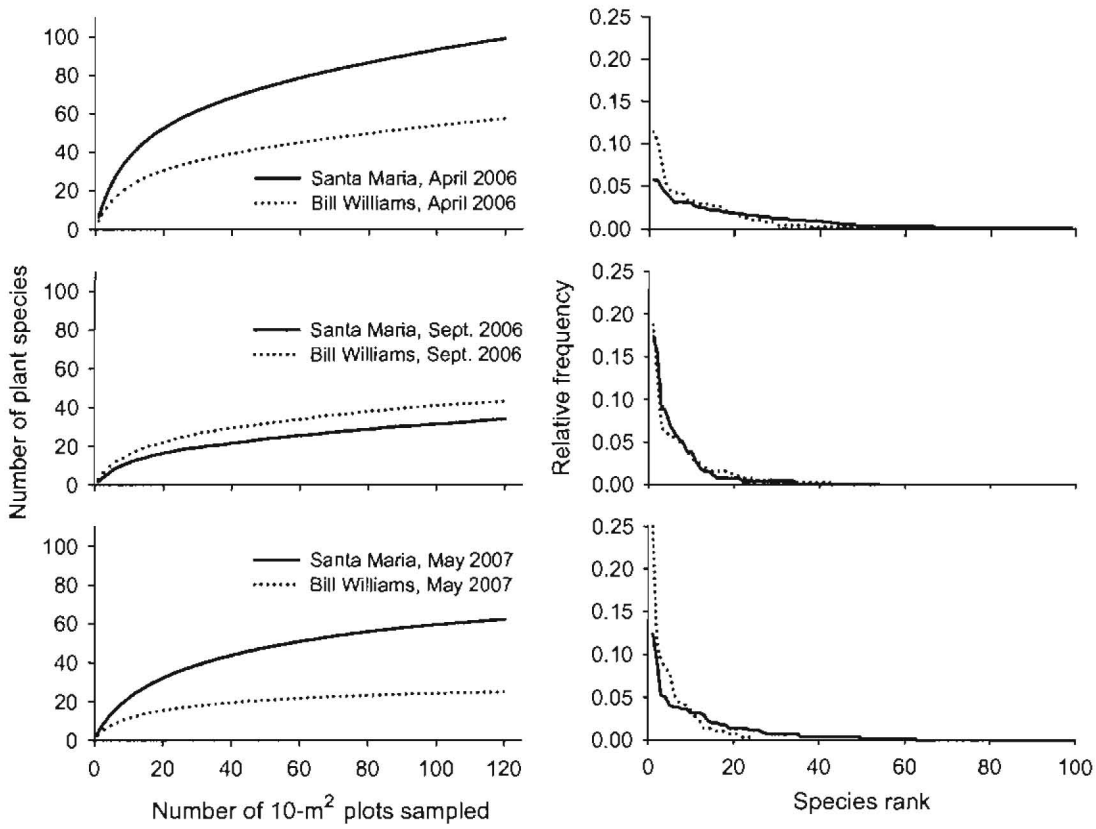

Figure 5. Left panel: Vascular plant species accumulation curves based on sampling of 120, 10-m^2, non-nested, floodplain plots at the Santa Maria River and the flow-regulated Bill Williams River. Right panel: Rank–abundance curves for the same three sampling times. Relative frequency is the number of occurrences of a species divided by the total number of plant occurrences.

Table VII. Frequency of occurrence of vascular plant species along the Santa Maria (SM) and Bill Williams (BW) Rivers in April 2006. Frequency is calculated as the fraction of 120, 10-m^2 plots in which a plant species was recorded. Species are listed in descending order of abundance, based on average frequency at both rivers

Species name	Family	Freq. at SM	Freq. at BW	Nativity[a]	Habit/life span[b]	Wetland indicator class[c]
Tamarix spp.	Tamaricaceae	0.37	0.49	E	T/S	Fac
Cynodon dactylon	Poaceae	0.31	0.44	E	HP	Fac
Polypogon monspeliensis	Poaceae	0.27	0.33	E	A	FacWet
Melilotus indicus	Fabaceae	0.37	0.07	E	A	FacUp
Cryptantha barbigera	Boraginaceae	0.17	0.19	N	A	–
Pluchea sericea	Asteraceae	0.13	0.23	N	S	FacWet
Schismus sp.	Poaceae	0.20	0.14	E	A	–
Salix gooddingii	Salicaceae	0.16	0.18	N	T	ObWet
Bromus rubens	Poaceae	0.23	0.09	E	A	FacUp
Sonchus oleraceus	Asteraceae	0.20	0.13	E	A	FacUp
Amsinckia menziesii var. intermedia	Boraginaceae	0.16	0.12	N	A	–
Pseudognaphalium luteoallbum	Asteraceae	0.08	0.18	E	A	FacWet
Schoenoplectus americanus	Cyperaceae	0.14	0.12	N	HP	ObWet
Erodium cicutarium	Geraniaceae	0.19	0.06	E	A	–
Populus fremontii	Salicaceae	0.12	0.13	N	T	FacWet
Sisymbrium irio	Brassicaceae	0.10	0.13	E	A	–
Lepidium virginicum var. medium	Brassicaceae	0.20	0.01	N	A	FacUp
Typha domingensis	Typhaceae	0.03	0.18	N	HP	ObWet

(*Continues*)

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Table VII. (Continued)

Species name	Family	Freq. at SM	Freq. at BW	Nativity[a]	Habit/life span[b]	Wetland indicator class[c]
Hordeum murinum var. glaucum	Poaceae	0.20	0.00	E	A	FacUp
Baccharis salicifolia	Asteraceae	0.08	0.11	N	S	FacWet
Mimulus guttatus	Scrophulariaceae	0.14	0.03	N	A	ObWet
Conyza canadensis	Asteraceae	0.08	0.08	N	A/B	FacUp
Nicotiana obtusifolia var. obtusifolia	Solanaceae	0.11	0.04	N	HP	FacUp
Xanthium strumarium	Asteraceae	0.14	0.01	N	A	Fac
Brassica tournefortii	Brassicaceae	0.09	0.05	E	A	–
Pluchea odorata	Asteraceae	0.00	0.14	N	HP	FacWet
Hymenoclea monogyra	Asteraceae	0.12	0.02	N	S	–
Bromus diandrus	Poaceae	0.13	0.00	E	A	–
Polygonum lapathifolium	Polygonaceae	0.00	0.13	N	A	ObWet
Juncus bufonius	Juncaceae	0.12	0.00	N	A	ObWet
Castilleja exserta ssp. exserta	Scrophulariaceae	0.10	0.01	N	A	–
Veronica anagallis-aquatica	Scrophulariaceae	0.07	0.04	N	HP	ObWet
Calibrachoa parviflora	Solanaceae	0.07	0.03	N	A	FacWet
Daucus pusillus	Apiaceae	0.10	0.00	N	A	–
Heliotropium curassavicum	Boraginaceae	0.01	0.09	N	HP	FacWet
Prosopis velutina	Fabaceae	0.09	0.01	N	T/S	FacUp
Herniaria hirsuta ssp. cinerea	Caryophyllaceae	0.09	0.00	E	A	–
Pectocarya recurvata	Boraginaceae	0.08	0.02	N	A	–
Bromus marginatus	Poaceae	0.07	0.01	N	HP	–
Eriogonum thomasii	Polygonaceae	0.04	0.04	N	A	–
Astragalus nuttallianus	Fabaceae	0.07	0.00	N	A	–
Lactuca serriola	Asteraceae	0.06	0.01	E	A/B	FacUp
Eriogonum thomasii	Polygonaceae	0.02	0.04	N	A	–
Lupinus sparsiflorus	Fabaceae	0.06	0.00	N	A	–
Plantago patagonica	Plantaginaceae	0.06	0.00	N	A	–
Silene antirrhina	Caryophyllaceae	0.06	0.00	N	A	–
Bowlesia incana	Apiaceae	0.05	0.00	N	A	FacUp
Datura wrightii	Solanaceae	0.05	0.00	N	HP	–
Eriastrum diffusum	Polemoniaceae	0.04	0.00	N	A	–
Erigeron divergens	Asteraceae	0.04	0.00	N	B	–
Cryptantha micrantha	Boraginaceae	0.03	0.00	N	A	–
Polanisia dodecandra ssp. trachysperma	Capparaceae	0.03	0.00	N	A	FacUp
Vulpia octoflora	Poaceae	0.03	0.00	N	A	FacUp
Nama hispidum	Hydrophyllaceae	0.00	0.03	N	A	–
Unknown	Unknown	0.03	0.00	Unk	Unk	Unk
Ambrosia psilostachya	Asteraceae	0.03	0.00	N	HP	Fac
Centaurium calycosum	Gentianaceae	0.03	0.00	N	A	FacWet
Cyperus odoratus	Cyperaceae	0.01	0.02	N	P	FacWet
Heterotheca subaxillaris	Asteraceae	0.03	0.00	N	A	FacUp
Phacelia distans	Hydrophyllaceae	0.03	0.00	N	A	–
Phalaris minor	Poaceae	0.03	0.00	E	A	–
Polypogon viridis	Poaceae	0.01	0.02	E	HP	FacWet
Stylocline micropoides	Asteraceae	0.03	0.00	N	A	–
Ambrosia ambrosioides	Asteraceae	0.02	0.00	N	SS	–
Baccharis sarothroides	Asteraceae	0.00	0.02	N	S	Fac
Bromus catharticus	Poaceae	0.02	0.00	E	A	–
Bromus tectorum	Poaceae	0.02	0.00	E	A	–
Chloracantha spinosa	Asteraceae	0.02	0.00	N	HP	Fac
Chloris virgata	Poaceae	0.00	0.02	N	A	–
Cirsium neomexicanum	Asteraceae	0.02	0.00	N	HP	–
Eleocharis macrostachya	Cyperaceae	0.02	0.00	N	HP	ObWet
Gilia scopulorum	Polemoniaceae	0.02	0.00	N	A	–
Juncus ensifolius	Juncaceae	0.02	0.00	N	HP	FacWet
Leptochloa fusca ssp. uninervia	Poaceae	0.01	0.01	N	A	FacWet

(*Continues*)

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Table VII. (Continued)

Species name	Family	Freq. at SM	Freq. at BW	Nativity[a]	Habit/life span[b]	Wetland indicator class[c]
Logfia arizonica	Asteraceae	0.02	0.00	N	A	–
Lycium parishii	Solanaceae	0.01	0.01	N	S	–
Malacathrix glabrata	Asteraceae	0.00	0.02	N	A	–
Mentzelia pumila	Loasaccae	0.00	0.02	N	A/B	Unk.
Nasturtium officinale	Brassicaceae	0.02	0.00	E	HP	ObWet
Salvia columbariae	Lamiaceae	0.01	0.01	N	A	–
Sporobolus cryptandrus	Poaceae	0.01	0.01	N	HP	FacUp
Acacia constricta	Fabaceae	0.00	0.01	N	T/S	–
Acacia greggii	Fabaceae	0.01	0.00	N	T/S	FacUp
Allionia incarnata	Nyctaginaceae	0.01	0.00	N	HP	–
Astragalus sp.	Fabaceae	0.01	0.00	N	Unk	–
Avena fatua	Poaceae	0.01	0.00	E	A	–
Bebbia juncea	Asteraceae	0.00	0.01	N	SS	–
Calycoseris wrightii	Asteraceae	0.01	0.00	N	A	–
Castilleja minor	Scrophulariaceae	0.01	0.00	N	A	ObWet
Centaurea melitensis	Asteraceae	0.01	0.00	E	A/B	–
Chamaesyce albomarginata	Euphorbiaceae	0.00	0.01	N	HP	–
Centrostegia thurberi	Polygonaceae	0.01	0.00	N	A	–
Descurainia pinnata	Brassicaceae	0.01	0.00	N	A	–
Dicoria canescens	Asteraceae	0.00	0.01	N	A	–
Draba cuneifolia	Brassicaceae	0.01	0.00	N	A	–
Encelia farinosa	Asteraceae	0.01	0.00	N	S	–
Evax verna var. verna	Asteraceae	0.01	0.00	N	A	–
Glandularia bipinnatifida	Verbenaceae	0.01	0.00	N	HP	–
Gutierrezia sarothrae	Asteraceae	0.01	0.00	N	S	–
Juncus articulatus	Juncaceae	0.00	0.01	N	HP	ObWet
Lesquerella gordonii	Brassicaceae	0.01	0.00	N	A	–
Linanthus demissus	Polemoniaceae	0.01	0.00	N	A	–
Malva parviflora	Malvaceae	0.01	0.00	E	A	–
Marrubium vulgare	Lamiaceae	0.01	0.00	E	HP	Fac
Monoptilon bellioides	Asteraceae	0.01	0.00	N	A	–
Myosurus cupulatus	Ranunculaceae	0.01	0.00	N	A	FacWet
Parietaria hespera	Urticaceae	0.00	0.01	N	A	–
Perityle emoryi	Asteraceae	0.00	0.01	N	A	–
Poa bigelovii	Poaceae	0.01	0.00	N	A	–
Polygonum argyrocoleon	Polygonaceae	0.00	0.01	E	A	ObWet
Salix exigua	Salicaceae	0.00	0.01	N	S	ObWet
Senecio flaccidus var. monoensis	Asteraceae	0.01	0.00	N	SS	–
Sphaeralcea sp.	Malvaceae	0.01	0.00	N	Unk.	–
Stephanomeria pauciflora	Asteraceae	0.00	0.01	N	SS	–
Verbascum thapsus	Scrophulariaceae	0.01	0.00	E	B	–
Veronica peregrina	Scrophulariaceae	0.01	0.00	N	A	ObWet

[a]N = native, E = introduced to USA.
[b]A = annual, B = biennial, HP = herbaceous perennial, SS = subshrub, S = shrub, T = tree.
[c]ObWet = Obligate wetland, FacWet = facultative wetland, Fac = facultative, FacUp = facultative upland, '–' = non-wetland.

dam expansion of woody cover and development of extensive stands of dense, mature forests. These structural changes are a product of long-term flood reduction, and influence understory richness, in part, by increasing competition for space and light.

Flood flow changes

Our study indicated that species richness was low in the dense forest understories of the Bill Williams, perhaps because the reduced light levels and thick litter cover preclude germination and survivorship of small-seeded, colonizing species (Nilsson and Grelsson 1990; Elderd 2003; Xiong *et al.* 2003). Along meandering rivers, flood reduction can lead to reduction in forest canopy by reducing regeneration rates (Friedman *et al.*, 1998; Johnson, 1998). In contrast, on rivers with braided or compound channels and where large floods are a major cause of tree mortality, flow-regulated declines in flood intensity can trigger expansion of forest canopies. This is the case for the Bill Williams, where multi-decade flood

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Table VIII. Vascular plant species recorded in plots (120, 10-m^2 plots per river) along the Santa Maria and the flow-regulated Bill Williams during three sampling times (2006–2007), in total and by plant group. Values in parentheses indicate the fraction of the total species per river within a particular plant group. A total of 136 taxa were sampled for both rivers combined

	Santa Maria	Bill Williams
Total species	110	68
Annuals[a]	69 (0.64)	39 (0.57)
Perennials	39 (0.36)	29 (0.43)
Wetland[b]	51 (0.46)	40 (0.59)
Non-wetland	59 (0.54)	28 (0.41)
Native[c]	83 (0.75)	53 (0.78)
Exotic	27 (0.25)	15 (0.22)

[a]Includes annnals and biennials. Perennials includes herbaccous perennials and woody species.
[b]Includes plants classified as obligate wetland, facultative wetland, facultative and facnltative upland.
[c]Defined as plants recently introduced to the USA (USDA, NRCS 2010).

reduction has resulted in increased woody plant abundance in the floodplain and encroachment of woody vegetation into channels formerly maintained in an open state by scouring during large floods (Shafroth *et al.*, 2002).

The Santa Maria, in contrast, like many other free-flowing desert rivers (Bagstad *et al.*, 2006), experiences frequent large floods that produce wide channels, open patches within the floodplain mosaic, and gaps within the forest canopies. As old forests are scoured or eroded, a portion of the reworked sediments are colonized by stands of young pioneer trees. Typically, some portion of newly reworked patches persist with only sparse wooded cover for multiple years (Friedman and Lee, 2002). Herbaceous plants, including the many annual species that typify dryland river floras, establish on these surfaces in varying abundance from year to year depending on water availability (Bagstad *et al.*, 2005; Capon, 2007). These annuals were the plant group with the largest difference in richness between the riparian zones of our regulated and unregulated study rivers.

Forest composition changes

In conjunction with the increase in forest canopy along the Bill Williams has been an increase in *Tamarix*, an introduced shrubby tree (Shafroth *et al.*, 2002). The presence of the extensive mature stands of *Tamarix* is another key legacy of river damming and flood reduction. *Tamarix* has become abundant along many regulated rivers of the American West, in part because its opportunistic reproductive strategy and its tolerance of relatively low soil moisture and high soil salinity allow it to establish where its competitors (*Populus*, *Salix*) have been excluded by lack of appropriately timed floods or insufficient water (Glenn and Nagler, 2005; Merritt and Poff, 2010).

Some authors have concluded that dense *Tamarix* stands are a cause of low diversity for many taxa (reviewed in Shafroth *et al.*, 2005). Our study, however, showed plant species richness at the Bill Williams to be low in all forest types (*Tamarix*, *Salix–Populus* and *Prosopis*), consistent with each having elevated woody stem densities and reduced light levels than their typically younger counterparts on the unregulated Santa Maria. This suggests that change in forest biomass structure, rather than change in forest composition, is a key driver of changes in plant species richness along this flow-altered dryland river. However, we temper this statement by noting that although forest types differed in dominant species, they all contained *Tamarix* as a component of the community.

Low-flow changes

Another type of hydrologic change that may be influencing floristic patterns is the more constant base flow (and more constant water table depth) of the flow-regulated Bill Williams. Where flood scour is not intense, the presence of constant stream flows allow for development of dense forest canopies. This increase in forest biomass, in turn, can mediate (and dampen) the diversity response to short-term, seasonal water pulses (Stromberg *et al.* 2009). Thus, base flow increase may be contributing to the reduced size of seasonal diversity pulses at the Bill Williams River. Changes in the low-flow conditions also may explain the pattern for wetland plants (vs. non-wetland) to have greater relative frequency at the regulated river.

Edaphic changes

Edaphic differences were minor between our study rivers and were not a major driver of species richness patterns. Soils at the regulated river did have higher electrical conductivity than those at the free-flowing river, but the values were generally too low to negatively affect glycophytes (Busch and Smith, 1995). This pattern may have been influenced, however, by the occurrence of larger winter floods in the year preceding both of our studies.

Our investigation also revealed few between-river differences in soil texture. In contrast, extensive coarsening of soils (and associated declines in plant species richness) has occurred in below-dam reaches of some southwestern rivers owing to sediment capture behind dams combined with release of large erosive floods in years when runoff fills reservoirs to capacity (Beauchamp and Stromberg, 2008). It remains possible that edaphic changes are influencing vegetation patterns on parts of the Bill Williams, particularly

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in reaches nearer to the dam site where soils are coarsest (Shafroth 1999).

Confounding factors

Field studies of river damming are complicated by inherent difficulty in differentiating river regulation effects from underlying differences in climate, hydrogeology, geomorphology and land use between dammed and undammed river pairs. For our study, one confounding factor is climate. Both rivers are in a climatic zone that favours high floristic diversity of cool-season annuals over warm-season annuals (Smith *et al.*, 1997; Bowers, 2005), and richness at both rivers was greatest in spring. This also was the season in which between-river differences were most evident. The slightly higher elevation (and presumably slightly cooler temperatures) of the Santa Maria sites may have contributed to these between-river differences by allowing for greater survivorship of cool-season annuals.

Another confounding factor is river size. River floodplains are populated by plant species that have high fidelity to riparian zones (obligate riparian) and by those that also occur in uplands (facultative riparian). Both groups were well represented on our study rivers, as indicated by the presence of species of wetland affinity and of upland affinity. Both groups differed in richness between study rivers, in at least one season. The between-river differences for the species of upland affinity may have been influenced by river size and setting. The influence of watershed composition on riparian interior floristic richness in general is strong in dryland regions (Tabacchi *et al.*, 1996), and rates of immigration of desert upland species to interior riparian patches may have been particularly high at Santa Maria given its narrower valley setting.

CONCLUSIONS

Our main conclusions are that increased forest abundance is associated with reduced richness of plant species (particularly of annuals) on the Bill Williams River and that change in forest biomass structure, more so than change in forest species composition, is the major driver of changes in plant species richness along this flow-altered dryland river. Past management goals have had the effect of reducing flood intensity, leading to the biological outcome of dense forest cover but low richness of plant species in the riparian zone of this regulated river. This may have consequences for regional biodiversity at the population level. The many infrequent species that occurred in the tail end of rank-abundance curves of the free-flowing Santa Maria River may be abundant elsewhere in their geographic range (Murray *et al.*, 1999), but may differ in genetic structure from populations in other settings.

Within the riparian zone, trade-offs undoubtedly exist for riparian animals between dense forests and low plant species richness vs. sparser forests but high richness. Where floral resources are abundant, richness of insects with taxon-specific host plant affiliations, such as butterflies, typically is high (Nelson and Andersen, 2007). In contrast, where broadleaf forests are dense, habitat is abundant for riparian-obligate birds that rely on shady, multi-layered canopies (Hunter *et al.*, 1987). Decisions are ongoing as to how to release future flows Alamo Dam into the Bill Williams River so as to allow for biodiversity conservation, recreation and flood control. Our study indicates that consideration should be given to trade-offs that exist between forest biomass structure and plant species richness.

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