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ABANDONED FLOODPLAIN PLANT COMMUNITIES ALONG A REGULATED DRYLAND RIVER

L. V. REYNOLDS[a,b]*, P. B. SHAFROTH[b] AND P. K. HOUSE[c]
[a] *Biology Department, Colorado State University, Fort Collins, Colorado, USA*
[b] *U. S. Geological Survey, Fort Collins Science Center, Fort Collins, Colorado, USA*
[c] *Geology, Minerals, Energy, and Geophysics Program, U. S. Geological Survey, Flagstaff, Arizona, USA*

ABSTRACT

Rivers and their floodplains worldwide have changed dramatically over the last century because of regulation by dams, flow diversions and channel stabilization. Floodplains no longer inundated by river flows following dam-induced flood reduction comprise large areas of bottomland habitat, but the effects of abandonment on plant communities are not well understood. Using a hydraulic flow model, geomorphic mapping and field surveys, we addressed the following questions along the Bill Williams River, Arizona: (i) What per cent of the bottomland do abandoned floodplains comprise? and (ii) Are abandoned floodplains quantitatively different from adjacent xeric and riparian surfaces in terms of vegetation composition and surface sediment? We found that nearly 70% of active channel and floodplain area was abandoned following dam installation. Abandoned floodplains along the Bill Williams River tend to be similar to each other yet distinct from neighbouring habitats: they have been altered physically from their historic state, leading to distinct combinations of surface sediments, hydrology and plant communities. Abandoned floodplains may transition to xeric communities over time but are likely to retain some riparian qualities as long as there is access to relatively shallow ground water. With expected increases in water demand and drying climatic conditions in many regions, these surfaces and associated vegetation will continue to be extensive in riparian landscapes worldwide. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS: riparian vegetation; relict floodplains; fluvial terraces; flow regulation; Bill Williams River

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INTRODUCTION

The natural dynamics of many ecosystems worldwide are changing because of human activities, exotic species invasions and climate change (Pressey *et al*., 2007; Hobbs *et al*., 2009). Often, these three large-scale processes interact to influence ecosystem structure and dynamism (Brook *et al*., 2008), and in some cases, new and different ecosystems are developing where historic habitat is disappearing (Johnson, 2002; Hobbs *et al*., 2009; Catford *et al*., 2013). Understanding the dynamics and importance of these ecosystems on the landscape is crucial to understanding community and biodiversity persistence (Pressey *et al*., 2007).

Rivers and riparian ecosystems worldwide have changed dramatically over the last century because of flow regulation by dams, flow diversions and channel structures (Nilsson *et al*., 2005). Dams can have substantial effects on river hydrology, geomorphology and ecology (Bunn and Arthington, 2002; Graf, 2006; Poff and Zimmerman, 2010). Dams often alter river flows by increasing base flows and homogenizing flood hydrographs and flow regimes (Graf, 2006). Changes in flow regime can, in turn, cause dramatic changes in geomorphology, and aquatic and riparian community composition (Bunn and Arthington, 2002; Nilsson and Svedmark, 2002). In general, regulated rivers have less dynamic and narrower active floodplains than free-flowing rivers (Friedman *et al*., 1998; Graf, 2006).

Floodplain abandonment is a common consequence of upstream dam installation and operation (Graf, 2006). Although floodplains can be abandoned by natural processes such as climate change and incision (Graf, 1988), floodplain abandonment due to flow regulation is a ubiquitous, global phenomenon (Williams and Wolman, 1984; Deiller *et al*., 2001; Start and Handasyde, 2002). Given the vast extent of dam-regulated river segments worldwide (Nilsson *et al*., 2005), abandoned floodplains likely comprise a significant proportion of total bottomland habitat, yet few studies have focused specifically on these fluvial surfaces.

Some studies have suggested that riparian areas abandoned by regulated flow regimes are 'relict ecosystems' that are being invaded by upland, xeric species (Merritt and Cooper, 2000; Johnson, 2002; Dixon *et al*., 2012). They may also be different than pre-dam plant communities, having appeared after flow regulation of a dam and potentially sharing characteristics with both neighbouring upland and riparian habitats (Start and Handasyde, 2002; Cooper and Andersen, 2012). Abandoned floodplains are likely to share riparian characteristics such as alluvial substrates and access to

*Correspondence to: L. V. Reynolds, Department of Biology, Colorado State University, Fort Collins, Colorado 80523, USA.
E-mail: reynoldsl@usgs.gov

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relatively shallow ground water tables. However, they are also likely to resemble adjacent upland habitat in other ways such as an absence of flood disturbance and abundance of upland species (Merritt and Cooper, 2000; Deiller *et al*., 2001; Boudell and Stromberg, 2008).

Abandoned floodplains also tend to occur in areas that are targets of riparian restoration, such as along rivers where flood flows have been reduced by water management or where woody plant encroachment has stabilized banks (Williams and Wolman, 1984; Johnson, 2002; Beauchamp and Shafroth, 2011). A global survey found that floodplains on five continents are threatened by human alteration (Tockner and Stanford, 2002), and in both North America and Europe, floodplains have been targeted as critical habitat in need of restoration (Hughes and Rood, 2003; Arizpe *et al*., 2008). However, because they have been abandoned by the river, abandoned floodplain characteristics are different from active floodplain areas (Deiller *et al*., 2001; Johnson, 2002). It is important for managers to understand how these surfaces are unique in order to plan effective restoration and management (Beauchamp and Shafroth, 2011).

In this study, we examined plant community composition on abandoned floodplains along the Bill Williams River, Arizona, USA, a highly flow-regulated river with geomorphic surfaces that were active channel or floodplain under the natural flow regime but that have not flooded since installation of a large dam in 1968. We addressed the following questions: (i) What per cent of the bottomland do abandoned floodplains comprise? and (ii) Are abandoned floodplains quantitatively different from adjacent uplands, tributaries and active floodplains in terms of vegetation composition and structure, and surface sediment?

METHODS

Study area

Our study was conducted along the Bill Williams River in the basin and range physiographic province and the transition zone between the Sonoran and Mojave deserts in western Arizona. Average annual precipitation along the river ranges from 21.7 cm near Alamo Dam (elevation of 393 m, http://www.wrcc.dri.edu, Coop Station Number 020100) to 12.2 cm near the river mouth in Parker, Arizona (elevation of 128 m, Coop Station Number 026250), whereas annual temperatures along the river are more consistent, averaging 21.6 °C. Leading up to our April 2010 sampling effort, January through March 2010 precipitation (11.94 cm) was above average (7.92 cm). Precipitation patterns in the months immediately before the growing season can significantly affect herbaceous community composition (Stromberg *et al*., 2012).

The Bill Williams River begins at the confluence of the Santa Maria and the Big Sandy Rivers and flows ~58 km before emptying into Lake Havasu, a reservoir on the Colorado River (Figure 1). The flow regime is altered by

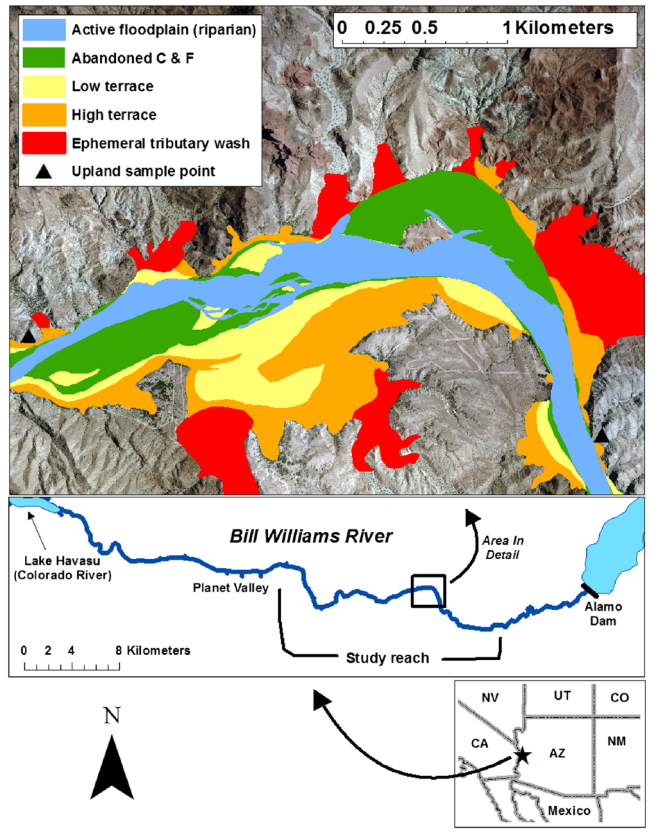

Figure 1. An example stream reach of the Bill Williams River, Arizona, showing currently active floodplain (riparian), abandoned floodplains, terraces and adjacent surfaces including abandoned channel and floodplains (Abandoned C & F, a result of combining abandoned '53 and abandoned '64 surfaces, see Methods section), low terraces (combined terrace 1 and 2 surfaces, see Methods section), high terraces (combined terrace 3 and 4 surfaces, see Methods section), ephemeral tributary washes and upland sample points. Inset map in the lower right shows the location of the Bill Williams River on a regional map, and inset map in the middle indicates the full length of the Bill Williams River with major landmarks and study area. This figure is available in colour online at wileyonlinelibrary.com/journal/rra

Alamo Dam, a flood control structure completed in 1968 and located at the upstream extent of the Bill Williams. Historically, the river was characterized by both perennial and intermittent sections along its length and a flashy hydrograph with annual flow peaks occurring in response to Pacific frontal storms in the winter and early spring and dissipating tropical cyclones in the late summer and fall (House *et al*., 2006). Some intermittent sections still persist below Alamo Dam; however, since dam installation, base flows have increased, flood peaks have greatly decreased and flood durations have increased (Shafroth *et al*., 2000; House *et al*., 2006).

Geomorphic surface mapping

Abandoned floodplain surfaces were identified along the Bill Williams River using hydraulic flow simulation and

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geomorphic mapping based on analysis of a series of historic aerial photographs, LiDAR-based imagery and limited field reconnaissance. First, to identify which surfaces were flooded under the current, dam-regulated flow regime and which surfaces were flooded under the historic flow regime, we utilized a one-dimensional hydraulic model that was developed to simulate flood flows (HEC-RAS; US Army Corps of Engineers, http://www.hec.usace.army.mil/software/hec-ras/) on the basis of 2005 river valley topography (Fields, 2009). Two floods were simulated: (ii) the maximum flow discharge possible from Alamo Dam (200 m^3/s), which has occurred three times since dam installation; and (ii) a pre-dam flood flow with a 10-year recurrence interval under the pre-dam flow regime (August 1951; 1840 m^3/s) and that has not been exceeded since. The 1951 flood simulation inundated nearly all floodplain and terrace surfaces along the river. Abandoned floodplains were defined as surfaces that were inundated by the 1951 flood simulation but that were not inundated by the maximum discharge released by the dam. Surfaces that were inundated by the maximum possible discharge from the dam included currently active channel and active floodplain (hereafter, 'riparian' surfaces). The maximum discharge has been released three times in the past 20 years.

Second, to subcategorize abandoned floodplains into different surface types, orthorectified aerial photos from 1953 and 1964 LiDAR-based imagery from 2005 and field reconnaissance were used to map geomorphic surfaces along the river. Six categories of abandoned floodplain surfaces were identified, on the basis of surface elevation relative to the channel, distance away from the channel and the time since they were active channel or floodplain according to our interpretation of valley bottom geomorphology: active channel surfaces abandoned after 1964 (the lowest surface, hereafter 'abandoned '64'); active channel surfaces abandoned after 1953 ('abandoned '53'); terrace 1; terrace 2; terrace 3; and terrace 4 (the highest surface). Terraces 1–4 were high floodplain surfaces prior to dam installation and are numbered in increasing elevation above the channel. The terraces were likely only inundated by large floods under the pre-dam flow regime, and their absolute ages are not known, whereas abandoned '64 and abandoned '53 surfaces were active channel or low floodplains prior to dam installation in the pre-dam era. The years 1953 and 1964 are useful benchmark years because they occurred before the installation of Alamo Dam in 1968 and after the 10-year flood in1951. In addition to abandoned channel, floodplain and terrace surfaces, three adjacent surfaces were mapped for comparison: riparian (defined earlier), uplands and ephemeral tributary washes (Figure 1).

Surface polygons were mapped using ArcGIS (versions 9 and 10, ESRI Enterprises, GIS systems http://www.esri.com/index.html). With ArcGIS statistical tool box, we calculated area (hectares) of abandoned floodplain and riparian surfaces to analyse the relative contribution to the bottomland.

Field sampling

Six field sites were randomly selected within each abandoned floodplain and adjacent surface category along the Bill Williams River using generalized random-tessellation stratified design (Stevens and Olsen, 2004). Potential field sites were defined as polygons at least 30 m wide and at least 100 m long. Abandoned floodplain sampling was concentrated between Planet Valley and the canyon immediately below the dam (Figure 1). We omitted surfaces that were current or former agricultural lands, thus excluding the lowest 24 river kilometres, as well as a few isolated areas upstream of Planet Valley. Because riparian and upland polygons were large and contiguous, sample sites were chosen on the basis of randomly selected distances upstream from the mouth of the river, and site locations were placed alternately on river left and river right. Upland sites were placed 20 m away from the closest upland-terrace surface border. For ephemeral tributary washes, all tributaries were identified, and sites were selected as for abandoned floodplains.

For each study site, a 100-m transect was placed in the approximate centre of the surface polygon and oriented parallel to the long axis of the surface. For upland and ephemeral wash sites, a 100-m transect was placed 20 m away from the border between the neighbouring surface and oriented parallel to the active river or tributary channel. We measured substrate grain sizes using Wolman pebble counts along each transect and calculated the per cent of substrate in each of five grain size categories: sand or finer (<2 mm diameter), fine gravel (2–16 mm), coarse gravel (16–64 mm), cobble (64–256 mm) and boulders (>256 mm) (Wolman, 1954). Cover by herbaceous species was estimated along each transect in six 1×1 m plots spaced every 20 m. Woody shrub and tree cover was measured using the line-intercept method along the length of the transect (Canfield, 1941). We also compiled a list of shrub and tree species that were observed on each surface during sampling but did not occur in the plots or along the transect; these species were added to our richness calculation and species lists for surfaces but not other analyses. Stem density and basal area of trees were measured using the point-centred quarter method where stem density plots were centred on the 0-m, 50-m and 100-m marks along the transect (Cottam and Curtis, 1956).

Plant species were identified and characterized as native or exotic, perennial or annual/biennial. Nomenclature follows the USDA PLANTS Database (USDA, 2010). Plot-level species diversity values were calculated using the Shannon–Wiener index ($H' = -\sum p_i \ln p_i$) (where species cover was used as p_i) (Magurran, 1988).

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During the field sampling effort, it was observed that surface sediment particle size, tree stem densities and relative elevation above the channel were very similar between abandoned '53 and abandoned '64, between terraces 1 and 2 and between terraces 3 and 4. A pre-analysis of data from these surfaces confirmed the similarities observed in the field (see Results section for statistical details). Therefore, to simplify data analysis and interpretation, data from abandoned '53 and '64 were grouped to make an 'abandoned channel and floodplain' (ACF) category, data from terraces 1 and 2 were grouped to make a 'low terrace' category and data from terraces 3 and 4 were combined to make a 'high terrace' category (Figure 1).

Statistical analysis

To compare substrate grain size between surface types, we calculated per cent of each grain size category (sand or finer, fine gravel, coarse gravel, cobble and boulder) for each transect within each surface. We then analysed the three most abundant categories: sand or finer, fine gravel and coarse gravel, to test for differences between surfaces. These variables required a log-transformation to attain normality. We then used an analysis of variance (ANOVA) and Tukey multiple comparisons of means to determine the effect of surface on grain size (Crawley, 2007).

To compare species lists between surfaces, we combined herbaceous and woody species lists and calculated Jaccard similarity indices for each surface-to-surface pair combination. To characterize combined herbaceous and woody plant communities, we used PRIMER v6 software to square-root transform the data to down-weight abundant species, calculate Bray–Curtis similarity values and calculate species contributions to dissimilarity percentages (Simper analysis) between surface types (Clarke and Gorley, 2006).

We then separated the woody and herbaceous components of the plant communities and analysed differences between surfaces using non-metric multidimensional scaling (NMDS; Clarke and Gorley, 2006). We also conducted an analysis of similarity (ANOSIM) between surface types on herbaceous and woody vegetation separately. ANOSIM tests for differences by calculating an R statistic: R values of 1 indicate complete difference in species composition, and R values of 0 indicate no difference in species composition. R values >0.15 typically indicate substantial differences (Clarke and Gorley, 2006).

For the remaining univariate analyses, we used R statistical software (R Development Core Team, 2011). To analyse the effect of surface on total cover, per cent perennial species, species richness and diversity of herbaceous and woody vegetation, we used a univariate ANOVA and Tukey multiple comparisons of means to inspect effects of individual surfaces on cover, richness and diversity (Crawley, 2007). Variables were tested for normality and transformed with a log-transformation when necessary.

To compare tree stems between surface types, we calculated average stem diameter, average stem density per square metre and average basal area per square metre for each surface. All of these variables required a log-transformation to attain normality. We then used an ANOVA and Tukey multiple comparisons of means to determine the effect of surface on stem diameter, stem density and basal area (Crawley, 2007).

RESULTS

Abandoned floodplain and active floodplain extent

Our estimates of the spatial extent of ACF, terrace and riparian surfaces along the full length of the Bill Williams River below Alamo Dam (58.7 river km) indicated that riparian surfaces comprise 31.6% of the bottomland. Thus, all abandoned floodplain surfaces are nearly 70% of the modern bottomland landscape. Surfaces that were active channel or floodplain in 1953 or 1964 but not since then (ACF) comprise 54.7% of the bottomland. Terraces (low and high) that were inundated only during large floods prior to dam installation comprise 13.6 % of the bottomland (Table I, Figure 1). Riparian and terrace surfaces comprise slightly more, and ACFs comprise slightly less of the bottomland along our 25-km study reach than the rest of the river (Table I).

Substrate grain size

Substrate grain size distribution varied significantly between surfaces with respect to the three most abundant grain sizes: per cent sand or finer ($F = 16.72_{5,49}$, $p < 0.0001$), per cent

Table I. Summary of total area and per cent of the total bottomland area for the total river and the study reach for each floodplain and terrace surface type along the Bill Williams River, Arizona

Surface	Total area (ha)	Per cent of total river	Area (ha) within study reach	Per cent of study reach
Active channel and floodplain (riparian)	1745.2	31.6	978.8	47.4
Abandoned channel and floodplain (ACF)	3016.1	54.7	701.7	34
Low terrace	449.2	8.1	191.8	9.3
High terrace	301.9	5.5	191.0	9.3
Total bottomland area	5,515.4	100	2,063.3	100

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fine gravel ($F = 8.95_{5,49}$, $p < 0.0001$) and per cent coarse gravel ($F = 16.39_{5,49}$, $p < 0.0001$, Figure 2). In general, riparian, ACF and low terrace surfaces had similar grain size distributions with 60–70% sand and finer grains and 25–35% gravels (Figure 2). High terraces were predominantly sand and finer-grained substrates, with few other grain sizes. Ephemeral wash and upland sites had the coarsest grains, with more gravels than the other surfaces and the appearance of boulders in the uplands (Figure 2).

Overall species composition

Results of the Simper analysis within surface types indicated that riparian surfaces were characterized by the exotic plants *Tamarix* and *Cynodon dactylon* and the native *Salix gooddingii*. ACFs and low terrace surfaces are characterized by similar grasses and herbs, whereas *Tamarix* is the typical woody plant on ACF surfaces and *Prosopis* on low terrace surfaces. High terraces had fewer characteristic species: mainly *Prosopis* and the annual *Amsinckia* species. Ephemeral washes and uplands also shared many of their characteristic herbaceous species with ACF and terraces; however, their woody vegetation was dominated by *Lycium* spp., *Larrea tridentata* and *Acacia greggii* (Table II, Appendix).

When species lists were compared between surfaces using the Jaccard index, riparian areas were the most distinct compared with the other surfaces with Jaccard indices ≤14. Other non-riparian surfaces compared with each other had Jaccard indexes in the range of 20–50. There were

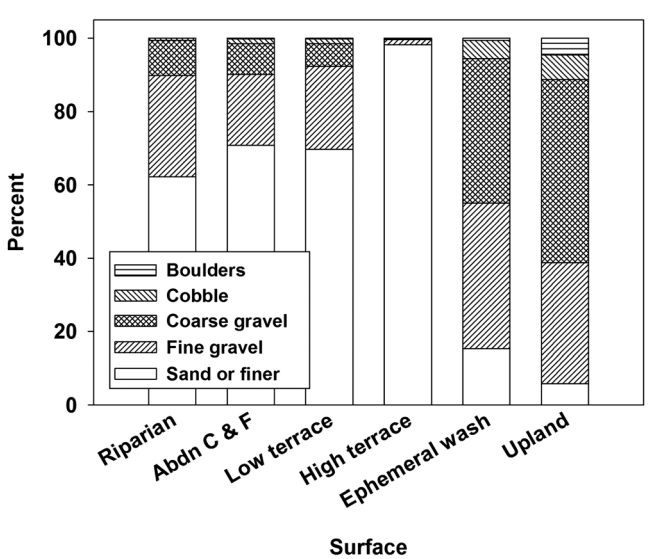

Figure 2. Average percentage of surficial grain sizes indicated by different shading (sand or finer, fine gravel, coarse gravel, cobble and boulders) among abandoned floodplain and adjacent surface types along the Bill Williams River below Alamo Dam, Arizona. Surface types include riparian, abandoned channel and floodplains (Abnd C & F), low terraces, high terraces, ephemeral washes and uplands

significant differences in total richness and native richness across surfaces (total richness one-way ANOVA: $F = 13.32_{5,49}$, $p < 0.001$; native richness one-way ANOVA: $F = 15.71_{5,49}$, $p < 0.001$). Tukey multiple comparisons of means indicated that total and native richness on riparian and high terrace surfaces was significantly lower than on ephemeral wash and upland surfaces (Figure 3). ACF and low terrace surfaces had moderate levels of total and native richness. Exotic richness was moderately different across surfaces (exotic richness one-way ANOVA: $F = 3.62_{5,49}$, $p = 0.007$); only riparian surfaces were significantly higher in exotic richness than both terraces and uplands according to Tukey multiple comparisons of means (Figure 3, Appendix).

Herbaceous vegetation

Results from an NMDS analysis of herbaceous vegetation between surface types indicated that upland and ephemeral wash plant communities are distinct from riparian communities and that ACF, low and high terrace surfaces fall somewhat in between and somewhat separately from these two extremes, although with more overlap with the upland and ephemeral wash surfaces (Figure 4). Most of the separation between herbaceous communities occurred along axis 1 of the NMDS. A one-way ANOSIM indicated significant differences between herbaceous community composition between surfaces (global $R = 0.37$, $p < 0.001$). Our data contained one outlier that could not be included in the ordination because it shared no species with any other plots: a riparian site, which was composed mostly of sedges (*Carex* spp.) found only at that site.

Total herbaceous cover among surfaces was not significantly different (one-way ANOVA; $F = 1.00_{5,49}$, $p = 0.43$, Figure 5). However, perennial cover on riparian surfaces was significantly higher than perennial cover on the other surfaces (one-way ANOVA; $F = 5.15_{5,49}$, $P < 0.001$, Figure 5).

Woody vegetation

Results from an NMDS analysis of woody vegetation between surfaces indicated that, similar to the herbaceous vegetation, upland and ephemeral wash woody communities are distinct from those on riparian surfaces, ACF and terrace surfaces fall in between these two extremes and most of the separation falls along axis 1 of the NMDS (Figure 4). However, differentiation between surfaces, especially between riparian and upland, is greater than it was for herbaceous vegetation (Figure 4). A one-way ANOSIM indicated significant differences between woody community composition between surfaces (global $R = 0.53$, $p < 0.001$). We omitted two ACF sites from our woody plant cover data analysis where there was zero woody cover.

Total woody cover among surfaces was significantly different (one-way ANOVA; $F = 10.58_{5,49}$, $p < 0.001$, Figure 6),

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Table II. Average abundances (Av. abund.), average similarities (Av. Sim.) and per cent contributions to similarity of the species that contribute at least 75% within surface plant communities

Species	Av.Abund	Av.Sim	Similarity contribution%	Cumulative contribution%
Riparian surfaces				
Average within-surface similarity: 38.01				
Tamarix sp.	5.77	26.57	69.91	69.91
Cynodon dactylon	1.65	4.61	12.13	82.05
Salix gooddingii	2.32	3.57	9.38	91.43
Abandoned channel and floodplains				
Average within-surface similarity: 29.48				
Schismus barbatus	2.32	6.62	22.45	22.45
Cryptantha gracilis	1.46	4.04	13.69	36.14
Pectocarya recurvata	2.23	3.92	13.29	49.43
Amsinckia menziesii var. intermedia	1.49	3.56	12.09	61.52
Tamarix sp.	1.97	2.97	10.07	71.58
Hymenoclea monogyra	1.23	2.26	7.68	79.26
Low terraces				
Average within-surface similarity: 32.68				
Schismus barbatus	2.53	7.15	21.87	21.87
Pectocarya recurvata	1.88	5.42	16.57	38.44
Prosopis glandulosa	3.01	5.29	16.19	54.63
Amsinckia menziesii var. intermedia	2.15	4.82	14.76	69.38
Cryptantha gracilis	0.78	2.05	6.28	75.67
High terraces				
Average within-surface similarity: 44.31				
Prosopis glandulosa	6.85	23.40	52.81	52.81
Amsinckia menziesii var. intermedia	2.57	6.79	15.33	68.13
Pluchea sericea	2.54	4.30	9.70	77.83
Ephemeral washes				
Average within-surface similarity: 37.03				
Cryptantha sp.	1.41	5.28	14.26	14.26
Amsinckia menziesii var. intermedia	1.64	5.03	13.59	27.85
Lycium sp.	2.28	4.65	12.57	40.42
Schismus barbatus	1.73	4.31	11.63	52.06
Larrea tridentata	1.35	2.92	7.87	59.93
Acacia greggii	1.61	2.69	7.27	67.20
Vulpia octoflora	1.07	2.66	7.18	74.38
Pectocarya recurvata	1.16	2.58	6.96	81.34
Uplands				
Average within-surface similarity: 52.91				
Pectocarya recurvata	3.46	11.44	21.62	21.62
Larrea tridentata	2.73	9.28	17.53	39.15
Amsinckia menziesii var. intermedia	1.92	5.90	11.15	50.31
Encelia farinosa	1.58	4.81	9.08	59.39
Plantago patagonica	1.20	3.90	7.37	66.76
Cylindropuntia versicolor	1.23	3.45	6.52	73.28
Vulpia octoflora	1.34	3.32	6.27	79.55

with a Tukey multiple comparisons of means showing that high terraces had significantly higher cover than the other surfaces, which were not different.

Tree stem diameters differed across geomorphic surfaces ($F = 25.66_{5,159}$, $p < 0.0001$) with riparian surfaces having smaller trees, ACF and low terraces having moderate-sized trees and high terraces having the largest trees (Figure 6). Ephemeral washes also had larger trees, whereas uplands tended to have moderate-sized trees. Surface also significantly affected tree stem density (stems/ha, $F = 13.67_{5,159}$,

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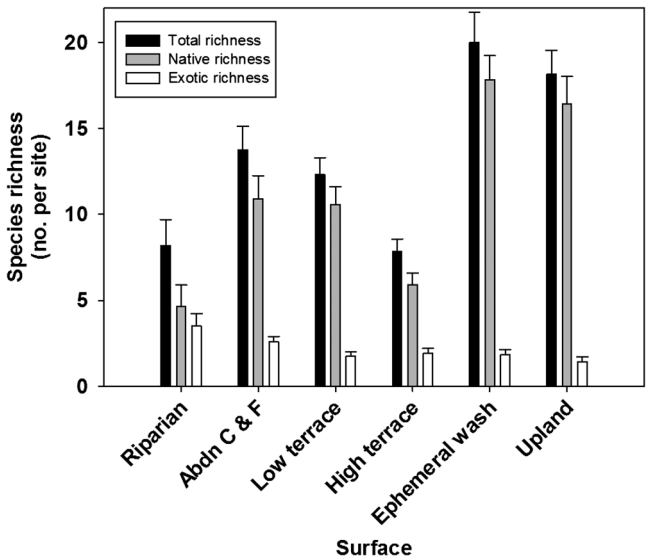

Figure 3. Average species richness for all species (herbaceous and woody) among abandoned floodplain and adjacent surface types along the Bill Williams River below Alamo Dam, Arizona. Average values are shown with ±1 SE bars. Surface types include riparian, abandoned channel and floodplains (Abnd C & F), low terraces, high terraces, ephemeral washes and uplands

$p < 0.0001$) with riparian surfaces having significantly higher stem densities than the other surfaces, which did not differ from each other (Figure 6). Tree stem basal area (m^2/ha) also varied by surface ($F = 8.40_{5,159}$, $p < 0.0001$) with riparian, ACF, ephemeral wash and upland surfaces having generally lower tree basal areas and terrace habitats having higher tree basal areas (Figure 6).

DISCUSSION

The large extent of Bill Williams' abandoned floodplains is comparable with that of other regulated rivers. On 36 large, dam-regulated rivers in North America, 'inactive floodplains' (comparable with our ACF and terraces) increased 236% in frequency and 363% in area following dam installations (Graf, 2006). Worldwide, floodplain loss, including abandonment, is most extensive in Europe and North America, with Southeast Asia, the USA and Africa showing accelerating rates of floodplain loss (Tockner and Stanford, 2002).

Our study suggests that abandoned floodplains support distinct plant communities because they have been altered physically from their historic state and support different combinations of plants, soils and hydrology. The few other studies around the world that have investigated abandoned floodplains have also found intermediate plant communities containing both riparian and upland species (Deiller *et al.*, 2001; Start and Handasyde, 2002; Beauchamp and Shafroth, 2011; Johnson *et al.*, 2012). In addition to unique plant assemblages, we also found distinct surface sediment composition and hydrology. Because of the presence of the upstream dam, these surfaces no longer flood yet contain relatively coarse alluvial substrates. As long as current dam operations exist, these surfaces will remain disconnected from the flooding that historically reworked surface sediments, removed vegetation and provided periodic influxes of river water and nutrients.

Flooding history has influenced surface substrates on ACFs and terraces and contributes to the differentiation between surfaces. Grain size was coarsest in ephemeral wash and upland sites and the finest on the highest terraces. More gravels occurred moving down the elevation gradient from the high terraces to ACFs, reflecting the increase in flood energy with closer proximity to the active channel (Knighton, 1998). Fine substrates are common on high terraces, because of the upward fining pattern away from the river, but ACF and low terrace grain sizes are notable because of their relatively coarse composition. Naturally occurring abandoned floodplains usually have finer textures because they were formerly true floodplains, rather than abandoned channels and low floodplains such as in our study (Graf, 1988).

Potential access to alluvial ground water also makes these surfaces unusual. Similar surfaces exist along unregulated rivers but with drier hydrology (Graf, 1988). As with many dam-regulated rivers, management of the Bill Williams in recent decades has emphasized high base flow releases, which have increased the extent of perennial flow compared with the pre-dam era when seasonally intermittent reaches were common (Shafroth *et al.*, 2002, 2010; Graf, 2006). Although we did not collect data on ground water levels on our surfaces, previous investigations suggest that higher base flows lead to higher ground water levels than existed historically for adjacent terrace and ACFs (Shafroth *et al.*, 2000; House *et al.*, 2006; Shafroth and Beauchamp, 2006) and that these levels should be within the rooting depth of some of the riparian plants that occupy these surfaces (Stromberg *et al.*, 1996).

Abandoned channel and floodplains and terraces on the Bill Williams River support distinct combinations of plant species. Herbaceous plant communities were more similar to uplands and ephemeral washes, whereas woody plant communities fell between riparian and upland and ephemeral wash communities (Figure 4, Table II). Differences in herbaceous and woody community patterns across surfaces are likely due to a lag effect in species turn-over for the longer-lived woody species. Also, the deep-rooted woody species we found on abandoned floodplain surfaces have access to riparian ground water, whereas herbaceous species persist in the upper soil layers, which are significantly drier in the absence of flooding. It is possible that ACF and

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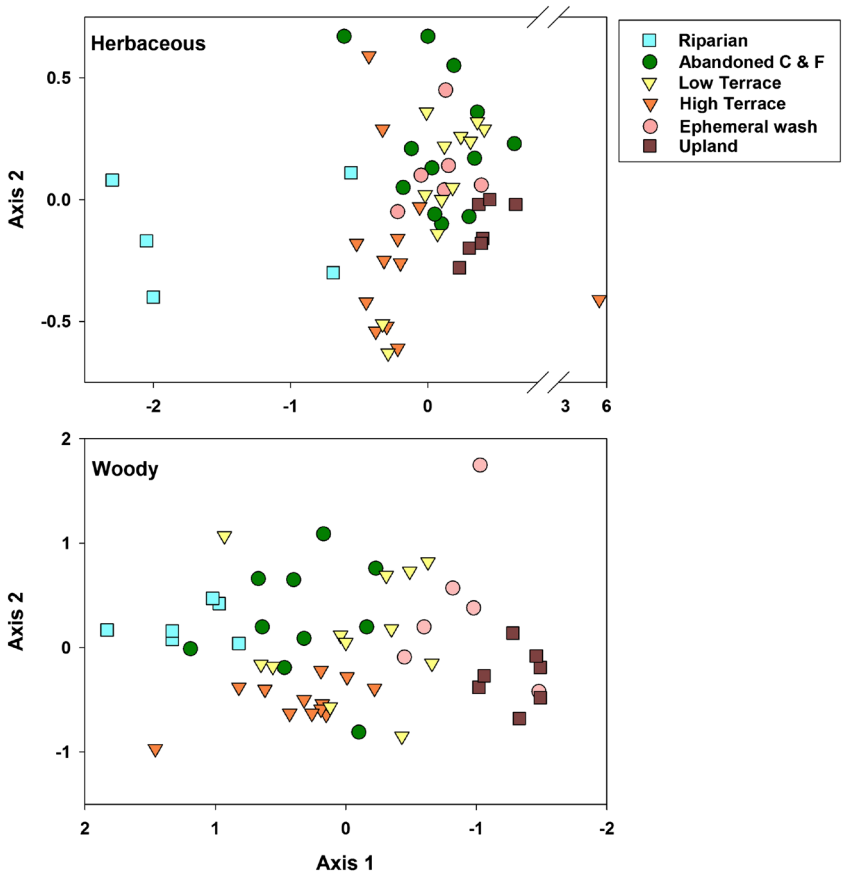

Figure 4. Results of a non-metric multidimensional scaling analysis of herbaceous (upper panel) and woody (lower panel) community composition comparing different abandoned floodplain and adjacent surface types along the Bill Williams River below Alamo Dam, Arizona. Different surface types are noted in ordination space with different symbols and colours. Surface types include riparian, abandoned channel and floodplains (abandoned C & F), low terraces, high terraces, ephemeral washes and uplands. This figure is available in colour online at wileyonlinelibrary.com/journal/rra

terrace surfaces are supporting novel ecosystems with new combinations of surface sediments and vegetation communities as a result of the dam. However, we cannot confirm that they are entirely novel without historic pre-dam data or data from a reference river for comparison.

Riparian areas have been found to be havens for exotic species (Stohlgren *et al*., 1998; Hood and Naiman, 2000) and also often harbour relatively high total species richness (DeFerrari and Naiman, 1994; Friedman *et al*., 1996; Brown and Peet, 2003). Our findings corresponded to the literature with high exotic species richness, but in contrast, our riparian surfaces had lower native and total species richness than most of the other surfaces. Our results were more consistent with work showing that riparian areas may not necessarily have high richness but contribute unique species to the landscape (Deiller *et al*., 2001; Sabo *et al*., 2005). Further, riparian areas along regulated rivers such as the Bill Williams River can have lower diversity compared with unregulated river reaches (Uowolo *et al*., 2005; Stromberg *et al*., 2012). Because we sampled after a wet winter and subsequent spring flooding, it is likely that diversity in the uplands and ephemeral washes was relatively high because of increased soil moisture from precipitation and relatively low in the riparian areas because of recent flooding disturbance and associated understory vegetation removal. Older soil seed banks on upland surfaces (compared with riparian surfaces) may also contribute to higher richness in wet years. These findings are in line with results from dryland rivers where richness was greater in upland and ephemeral stream sites compared with riparian and perennial stream sites but only in wet years (Stromberg, 2007; Stromberg *et al*., 2009).

Our sampling approach also may have contributed to relatively low species richness on riparian surfaces. For consistency across surfaces, we sampled in the centre of and along the long-axis of each surface. This may have caused us to miss some of the topographic variation that is often pronounced on riparian surfaces compared with terraces. In another study along the Bill Williams River, Stromberg *et al*. (2012) sampled more intensively along the transverse gradient and found on average

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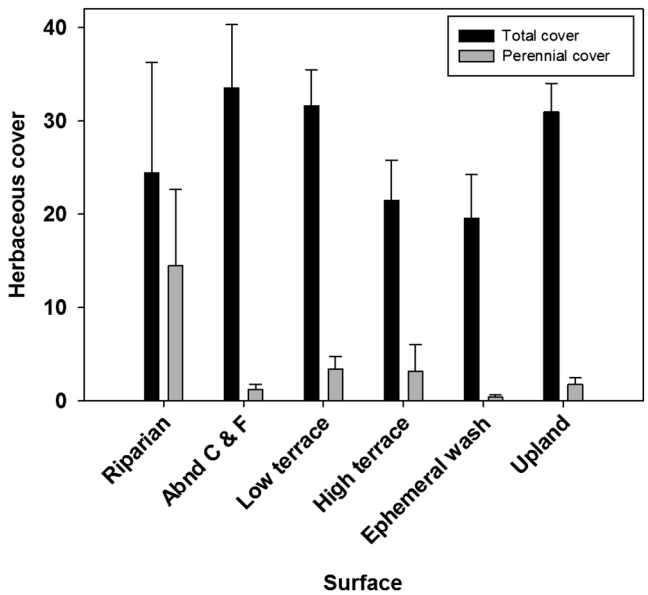

Figure 5. Average per cent herbaceous cover of all species (black bars) and perennial species (grey bars) among abandoned floodplain and adjacent surface types along the Bill Williams River below Alamo Dam, Arizona. Average values are shown with ±1 SE bars. Surface types include riparian, abandoned channel and floodplains (Abnd C & F), low terraces, high terraces, ephemeral washes and uplands

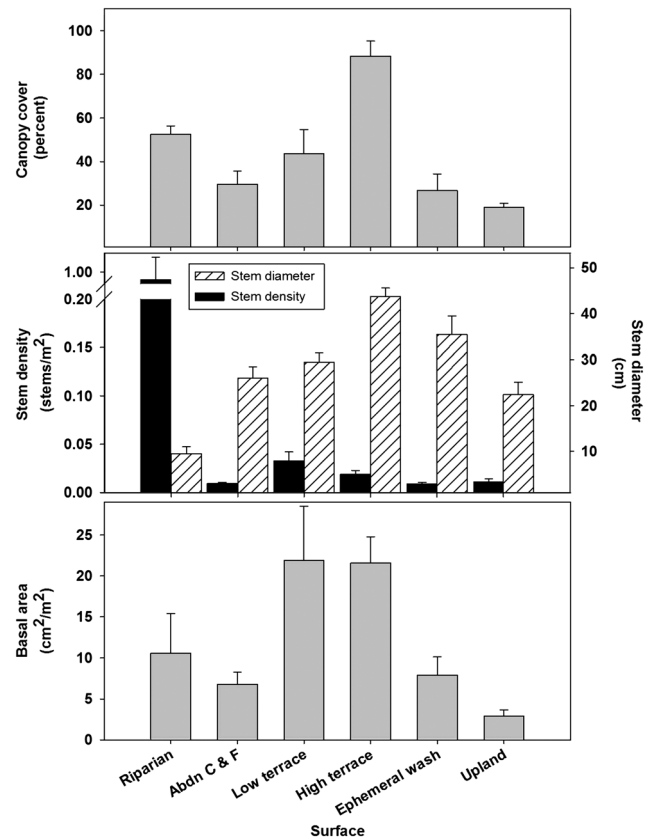

Figure 6. Average per cent canopy cover (±SE, upper panel), average stem density (stems/m^2, black bars, left axis, middle panel) and average stem diameter (cm ± SE, hatched bars, right axis, middle panel) and average basal area (cm^2/m^2 ± SE, lower panel) among abandoned floodplain and adjacent surface types along the Bill Williams River below Alamo Dam, Arizona. Surface types include riparian, abandoned channel and floodplains (Abnd C & F), low terraces, high terraces, ephemeral washes and uplands

14–32 species per riparian site depending on the year, season and location.

Species richness was also low on high terraces, which is likely due to the dense canopy cover and dominance of *Prosopis* in the woody community. The fact that richness was lowest on surfaces with high canopy cover, woody stem density and basal area (riparian and high terraces) is consistent with other studies indicating that herbaceous communities are limited by light, potentially high amounts of leaf litter and, in the case of riparian surfaces, recent flooding (Stromberg, 2007; Stromberg *et al*., 2012).

Abundant, large-diameter trees occurred on high terraces, likely because of the availability of alluvial ground water, supplemental surface water runoff from the uplands, fine-grained substrates that help retain soil moisture and absence of flood disturbance. Conversely, on riparian surfaces, frequent flooding and new tree establishment in recent years (Shafroth *et al*., 2010) resulted in stands with high densities of smaller trees. Other studies on the Bill Williams River have reported similar or higher stem densities and basal areas in riparian areas (Shafroth *et al*., 2002; Stromberg *et al*., 2012).

Despite the absence of flooding, ACF and terrace surfaces are likely to retain some riparian qualities especially in the woody plant communities, as long as there is access to alluvial ground water (Merritt and Cooper, 2000; Boudell and Stromberg, 2008). Further, shallow ground water is likely to exist along the Bill Williams River provided that base flows of sufficient magnitude are released from the dam (Shafroth *et al*., 2000; House *et al*., 2006). Over long time scales, though, riparian species will not be able to regenerate on these surfaces without flood disturbance, and they will transition to include increasingly more upland species (Cooper and Andersen, 2012).

Abandoned floodplain surfaces are often the targets of riparian restoration because they commonly occur along human-impacted rivers (Tockner and Stanford, 2002; Hughes and Rood, 2003; Beauchamp and Shafroth, 2011). In order to plan effective restoration, managers must understand the biological and physical peculiarities of abandoned floodplain surfaces (Hughes *et al*., 2001; Cooper and Andersen, 2012). Restoring historic riparian communities on these surfaces will be challenging because of their altered hydrology (Reynolds and Cooper, 2011; Cooper and Andersen, 2012). However, it is likely that restoration aimed at establishing xeric species

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would have greater success. Where riparian ground water is relatively shallow because of high base flows, restoration techniques such as pole plantings of mesic trees could be a way to maintain riparian forests on abandoned floodplain surfaces that cannot support natural establishment via flooding (Shafroth *et al*., 2008).

Abandoned floodplains are already extensive on other rivers worldwide, especially those with dam-regulated flow regimes (Deiller *et al*., 2001; Start and Handasyde, 2002; Hughes and Rood, 2003). Projections for increased water demand and drier climate conditions in arid regions may lead to reduced flows and expansion of abandoned floodplain surfaces (Wehner *et al*., 2011; Jerla *et al*., 2012). To better understand the ecological dynamics, functions and values of these surfaces and their associated plant and animal communities, further study is warranted across a broad array of river systems.

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APPENDIX
Species lists for habitat types

Table A1. Species list, including Wetland indicator score (WIS) and Nativity (native (N) or exotic (E)) for plots in riparian surfaces.

Herbaceous species	WIS	Native or exotic	Woody species	WIS	Native?
Amsinckia menziesii (Lehm.) A. Nelson & J.F. Macbr. var. *intermedia* (Fischer & C.A. Meyer) Ganders	N/A	N	*Acacia greggii* A. Gray	5	N
Cryptantha sp.	N/A	N	*Baccharis salicifolia* (Ruiz & Pav.) Pers.	2	N
Cynodon dactylon (L.) Pers.	3	E	*Hymenoclea monogyra* Torr. & A. Gray	N/A	N
Lactuca serriola L.	4	E	*Pluchea sericea* (Nutt.) Coville	2	N
Lactuca sp.	N/A	E	*Populus fremontii* S. Watson	2	N
Medicago spp.	N/A	E	*Prosopis glandulosa* Torr.	N/A	N
Melilotus indicus (L.) All.	4	E	*Salix exigua* Nutt.	1	N
Mimulus guttatus DC.	1	N	*Salix gooddingii* C.R. Ball	1	N
Schoenoplectus americanus (Pers.) Volkart ex Schinz & R. Keller	1	N	*Tamarix* spp.	2	E
Schismus barbatus (Loefl. ex L.) Thell.	N/A	E			
Sisymbrium irio L.	N/A	E			
Solidago sp.	N/A	N			
Sonchus oleraceus L.	5	E			
Typha sp.	1	N			
Veronica anagallis-aquatica L.	1	N			

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Table A2. Species list, including nativity (native (N) or exotic (E)) for plots on abandoned channel and floodplain (ACF) surfaces.

Herbaceous species	Native	Woody species	Native?
Amaranthus albus L.	E	*Acacia greggii* A. Gray	N
Amsinckia menziesii (Lehm.) A. Nelson & J.F. Macbr. var. *intermedia* (Fischer & C.A. Meyer) Ganders	N	*Bebbia juncea* (Benth.) Greene	N
Arabis pendulina Greene	N	*Carnegiea gigantea* (Engelm.) Britton & Rose	N
Brassica tournefortii Gouan	E	*Encelia farinosa* A. Gray ex Torr.	N
Bromus rubens L.	E	*Ephedra* sp.	N
Castilleja exserta (A. Heller) T.I. Chuang & Heckard	N	*Hymenoclea monogyra* Torr. & A. Gray	N
Cryptantha gracilis Osterh.	N	*Hymenoclea salsola* Torr. & A. Gray	N
Cryptantha sp.	N	*Larrea tridentata* (DC.) Coville	N
Descurainia californica (A. Gray) O.E. Schulz	N	*Lycium andersonii* A. Gray	N
Draba sp.	N	*Mentzelia* sp.	N
Emmenanthe penduliflora Benth.	N	*Olneya tesota* A. Gray	N
Eriogonum reniforme Torr. & Frém.	N	*Parkinsonia florida* (Benth. ex A. Gray) S. Watson	N
Eriogonum thomasii Torr.	N	*Pluchea sericea* (Nutt.) Coville	N
Eriophyllum sp.	N		
Erodium cicutarium (L.) L'Hér. ex Aiton	E	*Prosopis glandulosa* Torr.	N
Eschscholzia sp.	N	*Prosopis velutina* Woot.	N
Gilia sp.	N	*Salix gooddingii* C.R. Ball	N
Langloisia setosissima (Torr. & A. Gray ex Torr.) Greene	N	*Suaeda moquinii* (Torr.) Greene	N
Lepidium lasiocarpum Nutt.	N	*Tamarix spp*.	E
Linanthus filiformis (Parry ex A. Gray) J.M. Porter & L.A. Johnson	N		
Malacothrix glabrata (A. Gray ex D.C. Eaton) A. Gray	N		
Mentzelia albicaulis (Hook.) Torr. & A. Gray	N		
Mentzelia sp.	N		
Oenothera sp.	N		
Palafoxia arida B.L. Turner & Morris	N		
Pectocarya recurvata I.M. Johnst.	N		
Plantago patagonica Jacq.	N		
Poa sp.	N		
Salvia columbariae Benth.	N		
Schismus barbatus (Loefl. ex L.) Thell.	E		
Sisymbrium irio L.	E		
Tiquilia plicata (Torr.) A.T. Richardson	N		
Veronica anagallis-aquatica L.	N		
Vulpia octoflora (Walter) Rydb. var. octoflora	N		

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Table A3. Species list, including nativity (native (N) or exotic (E)) for plots on low terrace surfaces.

Herbaceous species	Native	Woody species	Native?
Amaranthus albus L.	E	*Acacia greggii* A. Gray	N
Amsinckia menziesii (Lehm.) A. Nelson & J.F. Macbr. var. *intermedia* (Fischer & C.A. Meyer) Ganders	N	*Bebbia juncea* (Benth.) Greene	N
Arabis pendulina Greene	N	*Carnegiea gigantea* (Engelm.) Britton & Rose	N
Bowlesia incana Ruiz & Pav	N	*Cylindropuntia versicolor* (Engelm. ex J.M. Coult.) F.M. Knuth	N
Bromus rubens L.	E	*Hymenoclea monogyra* Torr. & A. Gray	N
Camissonia contorta (Douglas ex Lehm.) Kearney	N	*Larrea tridentata* (DC.) Coville	N
Chaenactis fremontii A. Gray	N	*Lycium andersonii* A. Gray	N
Chamaesyce polycarpa (Benth.) Millsp. ex Parish	N	*Lycium berlandieri* Dunal	N
Cryptantha gracilis Osterh.	N	*Lycium pallidum* Miers	N
Cryptantha sp.	N	*Olneya tesota* A. Gray	N
Ellisia nyctelea (L.) L.	N	*Parkinsonia florida* (Benth. ex A. Gray) S. Watson	N
Eriogonum reniforme Torr. & Frém.	N	*Parkinsonia microphylla* Torr.	N
Eriogonum thomasii Torr.	N	*Pluchea sericea* (Nutt.) Coville	N
Eriophyllum sp.	N	*Populus fremontii* S. Watson	N
Linanthus filiformis (Parry ex A. Gray) J.M. Porter & L. A. Johnson	N	*Prosopis glandulosa* Torr.	N
Lepidium lasiocarpum Nutt.	N	*Salix gooddingii* C.R. Ball	N
Malacothrix glabrata (A. Gray ex D.C. Eaton) A. Gray	N	*Suaeda moquinii* (Torr.) Greene	N
Mentzelia albicaulis (Hook.) Torr. & A. Gray	N	*Tamarix* spp.	E
Oenothera sp.	N		
Pectocarya recurvata I.M. Johnst.	N		
Schismus barbatus (Loefl. ex L.) Thell.	E		
Sisymbrium irio L.	E		
Tiquilia plicata (Torr.) A.T. Richardson	N		
Vulpia octoflora (Walter) Rydb. var. *octoflora*	N		

Table A4. Species list, including nativity (native (N) or exotic (E)) for plots on high terrace surfaces.

Herbaceous species	Native	Woody species	Native?
Amaranthus albus L.	E	*Acacia greggii* A. Gray	N
Amsinckia menziesii (Lehm.) A. Nelson & J.F. Macbr. var. *intermedia* (Fischer & C.A. Meyer) Ganders	N	*Atriplex canescens* (Pursh) Nutt.	N
Bowlesia incana Ruiz & Pav	N	*Cylindropuntia versicolor* (Engelm. ex J.M. Coult.) F.M. Knuth	N
Cryptantha gracilis Osterh.	N	*Larrea tridentata* (DC.) Coville	N
Distichlis spicata (L.) Greene	N	*Lycium andersonii* A. Gray	N
Machaeranthera tagetina Greene	N	*Lycium berlandieri* Dunal	N
Pectocarya recurvata I.M. Johnst.	N	*Lycium parishii* A. Gray	N
Pluchea sericea (Nutt.) Coville	N	*Fouquieria splendens* Engelm.	N
Polygonum persicaria L.	E	*Parkinsonia florida* (Benth. ex A. Gray) S. Watson	N
Schismus barbatus (Loefl. ex L.) Thell.	E	*Phoradendron californicum* Nutt.	N
Sisymbrium altissimum L.	E	*Pluchea sericea* (Nutt.) Coville	N
Sisymbrium irio L.	E	*Prosopis glandulosa* Torr.	N
		Suaeda moquinii (Torr.) Greene	N
		Tamarix spp.	E

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Table A5. Species list, including nativity (native (N) or exotic (E)) for plots on ephemeral wash surfaces.

Herbaceous species	Native	Woody species	Native?
Amaranthus albus L.	E	*Acacia greggii* A. Gray	N
Amsinckia menziesii (Lehm.) A. Nelson & J.F. Macbr. var. *intermedia* (Fischer & C.A. Meyer) Ganders	N	*Atriplex canescens* (Pursh) Nutt.	N
Brassica tournefortii Gouan	E	*Bebbia juncea* (Benth.) Greene	N
Bromus rubens L.	E	*Carnegiea gigantea* (Engelm.) Britton & Rose	N
Chaenactis fremontii A. Gray	N	*Cylindropuntia versicolor* (Engelm. ex J.M. Coult.) F.M. Knuth	N
Cryptantha gracilis Osterh.	N	*Encelia farinosa* A. Gray ex Torr.	N
Cryptantha sp.	N	*Echinocereus engelmannii* (Parry ex Engelm.) Lem.	N
Descurainia sp.	N	*Ferocactus cylindraceus* (Engelm.) Orcutt	N
Draba sp.	N	*Fouquieria splendens* Engelm.	N
Emmenanthe penduliflora Benth.	N	*Hymenoclea salsola* Torr. & A. Gray	N
Eriogonum thomasii Torr.	N	*Hyptis emoryi* Torr.	N
Eriophyllum sp.	N	*Larrea tridentata* (DC.) Coville	N
Erodium cicutarium (L.) L'Hér. ex Aiton	E	*Lycium andersonii* A. Gray	N
Eschscholzia sp.	N	*Lycium berlandieri* Dunal	N
Eucrypta micrantha (Torr.) A. Heller	N	*Olneya tesota* A. Gray	N
Lepidium lasiocarpum Nutt.	N	*Parkinsonia microphylla* Torr.	N
Linanthus filiformis (Parry ex A. Gray) J.M. Porter & L.A. Johnson	N	*Prosopis glandulosa* Torr.	N
Lotus salsuginosus Greene	N		
Lupinus sp.	N		
Mentzelia albicaulis (Hook.) Torr. & A. Gray	N		
Pectocarya recurvata I.M. Johnst.	N		
Perityle emoryi Torr.	N		
Phacelia tanacetifolia Benth.	N		
Plantago patagonica Jacq.	N		
Salvia columbariae Benth.	N		
Schismus barbatus (Loefl. ex L.) Thell.	E		
Sisymbrium irio L.	E		
Vulpia octoflora (Walter) Rydb. var. octoflora	N		

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Table A6. Species list, including nativity (native (N) or exotic (E)) for plots on upland surfaces.

Herbaceous species	Native	Woody species	Native?
Amsinckia menziesii (Lehm.) A. Nelson & J.F. Macbr. var. *intermedia* (Fischer & C.A. Meyer) Ganders	N	*Acacia greggii* A. Gray	N
Borage sp.	N/A	*Ambrosia dumosa* (A. Gray) Payne	N
Bromus rubens L.	E	*Bebbia juncea* (Benth.) Greene	N
Castilleja exserta (A. Heller) T.I. Chuang & Heckard ssp. *exserta*	N	*Carnegiea gigantea* (Engelm.) Britton & Rose	N
Chaenactis douglasii (Hook.) Hook. & Arn.	N	*Cylindropuntia versicolor* (Engelm. ex J.M. Coult.) F.M. Knuth	N
Chaenactis fremontii A. Gray	N	*Echinocereus engelmannii* (Parry ex Engelm.) Lem.	N
Cryptantha gracilis Osterh.	N	*Encelia farinosa* A. Gray ex Torr.	N
Cryptantha micrantha (Torr.) I.M. Johnst.	N	*Ferocactus cylindraceus* (Engelm.) Orcutt	N
Cryptantha sp.	N	*Fagonia laevis* Standl.	N
Eriophyllum sp.	N	*Krameria grayi* Rose & Painter	N
Erodium cicutarium (L.) L'Hér. ex Aiton	E	*Larrea tridentata* (DC.) Coville	N
Lepidium lasiocarpum Nutt.	N	*Lycium andersonii* A. Gray	N
Lotus strigosus (Nutt.) Greene var. *tomentellus* (Greene) Isely	N	*Mammillaria tetrancistra* Engelm.	N
Lotus salsuginosus Greene	N	*Parkinsonia microphylla* Torr.	N
Lupinus sp.	N	*Prosopis glandulosa* Torr.	N
Malacothrix glabrata (A. Gray ex D.C. Eaton) A. Gray	N		
Pectocarya recurvata I.M. Johnst.	N		
Plantago patagonica Jacq.	N		
Polygonum persicaria L.	E		
Salvia columbariae Benth.	N		
Schismus barbatus (Loefl. ex L.) Thell.	E		
Senecio sp.	N		
Vulpia octoflora (Walter) Rydb. var. *octoflora*	N		

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