Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2007) **16**, 381–393

RESEARCH PAPER

Altered stream-flow regimes and invasive plant species: the *Tamarix* case

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ABSTRACT

Aim To test the hypothesis that anthropogenic alteration of stream-flow regimes is a key driver of compositional shifts from native to introduced riparian plant species.

Location The arid south-western United States; 24 river reaches in the Gila and Lower Colorado drainage basins of Arizona.

Methods We compared the abundance of three dominant woody riparian taxa (native *Populus fremontii* and *Salix gooddingii*, and introduced *Tamarix*) between river reaches that varied in stream-flow permanence (perennial vs. intermittent), presence or absence of an upstream flow-regulating dam, and presence or absence of municipal effluent as a stream water source.

Results *Populus* and *Salix* were the dominant pioneer trees along the reaches with perennial flow and a natural flood regime. In contrast, *Tamarix* had high abundance (patch area and basal area) along reaches with intermittent stream flows (caused by natural and cultural factors), as well as those with dam-regulated flows.

Main conclusions Stream-flow regimes are strong determinants of riparian vegetation structure, and hydrological alterations can drive dominance shifts to introduced species that have an adaptive suite of traits. Deep alluvial groundwater on intermittent rivers favours the deep-rooted, stress-adapted *Tamarix* over the shallower-rooted and more competitive *Populus* and *Salix*. On flow-regulated rivers, shifts in flood timing favour the reproductively opportunistic *Tamarix* over *Populus* and *Salix*, both of which have narrow germination windows. The prevailing hydrological conditions thus favour a new dominant pioneer species in the riparian corridors of the American Southwest. These results reaffirm the importance of reinstating stream-flow regimes (inclusive of groundwater flows) for re-establishing the native pioneer trees as the dominant forest type.

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Keywords
Aridity, flood disturbance, hydrology, invasion, novel ecosystems, riparian, stream-flow regime, vegetation.

INTRODUCTION

As frequently disturbed corridors whose community composition is largely driven by immigration processes, there are many opportunities for new species to become established in riparian ecosystems (Brown & Peet, 2003). Flooding and drought create fluxes in resource availability, while high connectivity between a river and its watershed provides for continuous inflow and outflow of seeds via flood waters, wind or migrating animals (Davis *et al.*, 2000; Tabacchi *et al.*, 2005). At the same time, the intensive use of riverine habitats as agricultural lands, urban areas and transportation routes has provided new sources of seeds. Thus, many introduced species occur in riparian landscapes (Stohlgren *et al.*, 1998; Hood & Naiman, 2000). However, the processes that allow for the establishment of new species differ from those that drive changes in species dominance, and most introduced species remain relatively rare.

Hydrological and geomorphic processes are key drivers of vegetation dynamics in riparian ecosystems and, as these physical factors change, so does the biota (Poff *et al.*, 1997; Nilsson & Svedmark, 2002; Steiger *et al.*, 2005). Shifts in hydrological and geomorphic regimes can alter water resource levels, and timing of

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DOI: 10.1111/j.1466-8238.2007.00297.x
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resource availability and disturbance regimes; these in turn can alter competitive hierarchies and favour species with a different suite of life-history traits (Tickner *et al.*, 2001). For example, reduced groundwater levels can select for deeper-rooted or more stress-tolerant species, while reduced flood frequency or intensity can shift species composition towards later-successional species. The compositional shifts can arise due to *in situ* conversions, with subdominant species becoming dominant, or can arise as a result of migration of species from other locales. Indeed, many introduced aquatic, wetland or riparian plant species have been observed to increase in association with riverine alterations including reductions in permanence of flow, river channelization, stabilized water levels, reduced frequency of inundation and altered timing of water and sediment flows (Howell & Benson, 2000; Aguiar *et al.*, 2001; Taylor & Garf, 2005).

One introduced taxon that has become dominant along the rivers of western North America is *Tamarix* (*Tamarix ramosissima*, *Tamarix chinensis* and their hybrid). Introduced to the United States from Asia in the late 1800s for the control of soil erosion and landscaping purposes, it is now the third most prevalent woody riparian species in the western United States (Friedman *et al.*, 2005). It is also present in western Australia and northern and central Mexico (http://www.issg.org/database/). A plethora of articles have been published in the popular and scientific press about the causes and consequences of the spread of *Tamarix*. In part because of its notoriety, scientific findings on this species have wide-ranging implications both for river restoration and management of invasive species.

A key question underpinning research on species invasions is, 'What site factors, and what species factors, are associated with range expansions and population increases?' For *Tamarix* in western North America, altered flood cycles below dams, reservoir development above dams, reduction of stream flow from groundwater pumping and stream diversion, salinization of floodplain soils and livestock grazing all are implicated as contributing factors (Harris, 1966; Everitt, 1980; Graf, 1982; Di Tomaso, 1998; Stromberg, 1998; Zavaleta, 2000; Ladenburger *et al.*, 2006). These same site factors have contributed to the decline of *Populus* and *Salix* along many rivers in western North America (Rood & Mahoney, 1990; Howe & Knopf, 1991; Busch & Smith, 1995; Pataki *et al.* 2005). A fortuitous suite of physiological and morphological traits, in concert with the 'bottom-up' changes in resource levels and 'top-down' changes in levels of herbivory, have contributed to the population increase of *Tamarix*. Like other members of its genus (He *et al.*, 2003), *T. ramosissima* is a stress-tolerant, reproductively opportunistic pioneer species. Although not particularly competitive against *Populus* and *Salix* under well-watered conditions (Sher *et al.*, 2000), *Tamarix*'s deep roots, drought tolerance, salt tolerance, prolonged period of seed dispersal and unpalatability to livestock allow it to occupy sites that no longer sustain the native, shallow-rooted, hydromesic pioneer trees (Glenn & Nagler, 2005).

Certainly, *Tamarix* is not restricted to sites in North America with a high degree of human influence. But, despite the many review articles and river-specific studies, multiriver comparisons of the abundance patterns of *Tamarix*, *Populus* and *Salix* within a region have not been undertaken. The hypothesis that alteration of flow regime is a key driver of compositional shifts from *Populus* and *Salix* (the historically common riparian trees in the desert Southwest) to introduced *Tamarix* remains untested. The goal of this study was to test this hypothesis by interpreting vegetation patterns of riparian pioneer tree species as a function of natural and altered hydrological patterns of rivers in the Sonoran Desert region of south-western United States. Our specific objective was to determine whether the abundance of *Tamarix*, *Populus* and *Salix* varies between reaches with (1) perennial versus intermittent flow (resulting from stream diversion, groundwater pumping or hydrogeomorphic setting) and between reaches with (2) unregulated versus regulated flow (resulting from dam operation). Additionally, we explored the effects of municipal effluent as a stream-water source. We expected that *Populus–Salix* would be the dominant forest type along hydrologically unaltered rivers, and that *Tamarix* would dominate along rivers with reduced water availability and with altered temporal flow patterns.

We present this as a regional case study, emblematic of an approach for embedding invasive species issues into the larger context of ecosystem restoration. Ecosystem restoration projects are under way on many rivers, many with a goal of replacing introduced plant species with the historically common vegetation types. In the western United States, for example, many of the river restoration projects strive to increase the abundance of *Populus–Salix* forests and reduce the abundance of *Tamarix*. Reinstating hydrological regimes and other key drivers of ecosystem structure and function is recognized as important for the success of restoration (Ward *et al.*, 2001; Rood *et al.*, 2005) but is not always considered in invasive species management projects. We intend our study to contribute information that can be used in a restoration context.

METHODS AND STUDY SITES

Study sites

Data were obtained for 24 river reaches distributed among 10 rivers (Table 1 & Fig. 1). The reaches were selected to span a range of hydrological alterations. All are within the Sonoran Desert (or Sonoran/Chihuahuan or Sonoran/Mojave transition zones) of Arizona. Eight rivers are in the Salt Gila drainage basin: two (Bill Williams and Santa Maria) are in the Lower Colorado drainage basin, immediately to the north. The elevation of the reaches ranges from 152 (Bill Williams) to 1288 (upper San Pedro) m a.s.l. Mean annual rainfall ranges among reaches from 14 cm (Bouse station, near Bill Williams River) to 42 cm (Nogales station, near upper Santa Cruz River). River reaches were not always spatially contiguous (i.e. some perennial stretches were separated by intervening intermittent stretches) but were uniform with respect to stream hydrology. *Tamarix* became established on the study reaches as early as the 1910s (Gila River) to as late as the 1950s (San Pedro; Stromberg, 1998).

River reaches were classified into stream-flow permanence categories (perennial vs. intermittent) using data from USGS stream gauges or collected by study authors or preserve managers.

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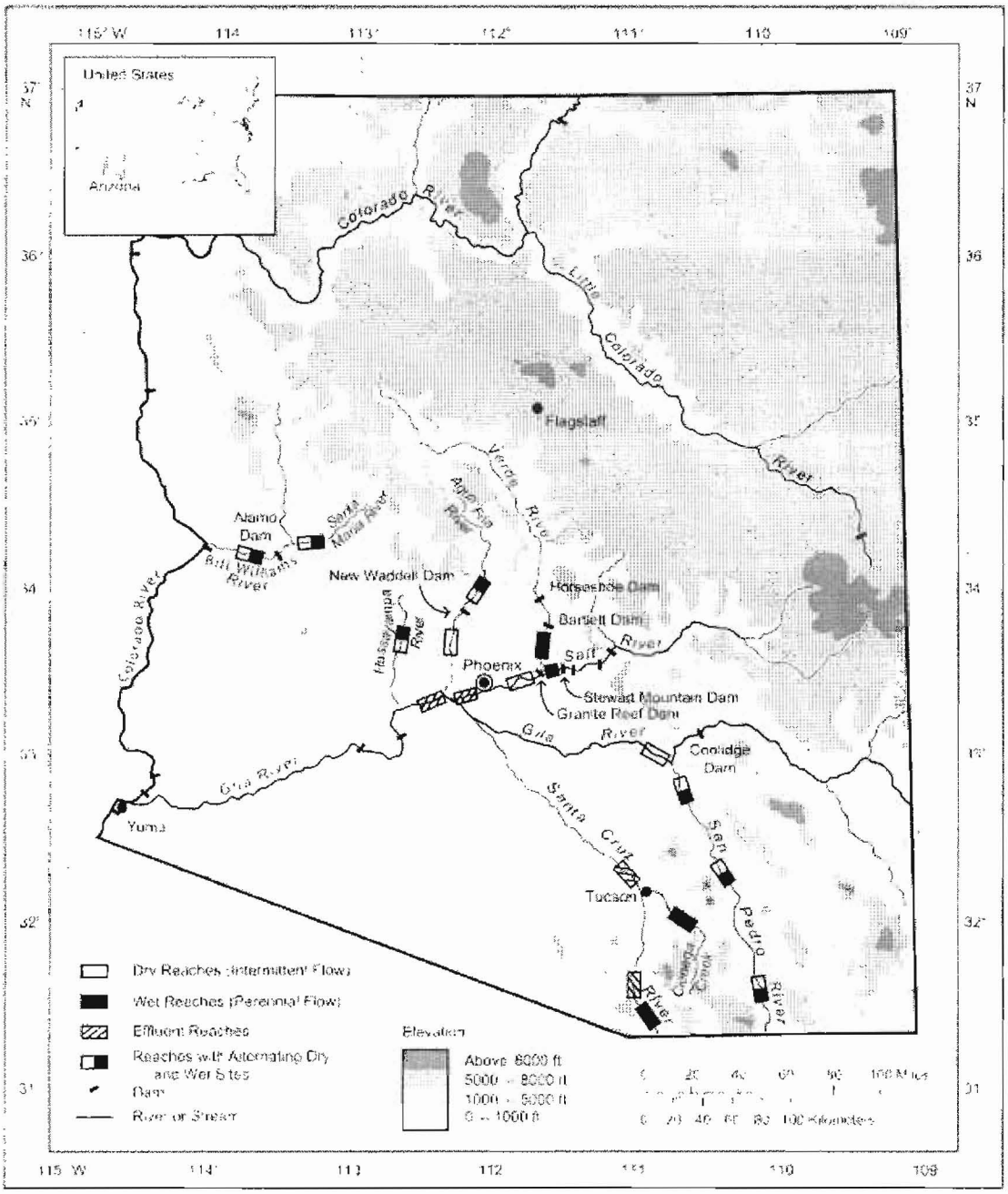

Figure 1 Location of the 24 study reaches in Arizona, USA. Also shown are the locations of major dams. (The map is based on templates provided by Arizona Geographic Alliance)

Perennial streams by definition have surface flow year-round; we also included quasi-perennial reaches (those with flow at least 90% of the time) in this category. Intermittent streams can have surface flow for several months but are dry for much of the year; no-flow days in Sonoran desert rivers are most common in early summer (May, June) and late autumn (October, November). Some reaches were dry due to their hydrogeomorphic setting; others have become intermittent due to groundwater pumping or stream-flow diversion for irrigated agriculture, municipal use or mining activities.

The reaches were classified as flow-regulated if an upstream dam influenced their flows. The nature and extent of the alterations to a river's hydrograph vary depending on the intent of a dam (e.g. hydropower production, water supply) and the storage capacity of its reservoir, but we treated this as a dichotomous variable (flow-regulated vs. free-flowing). Sixteen of the 24 reaches were free-flowing (nine with perennial flow and seven with intermittent flow). Eight of the 24 reaches were flow-regulated (five with perennial flow and three with intermittent flow). These included two reaches of the Bill Williams River, downstream of

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Table 1 Attributes of the 24 study reaches

River name	Dam-influenced?	Stream-low regime	Effluent-influenced?	Reach elevation (m)	Mean transect width (m)
San Pedro-Lower	No	Perennial	No	604 - 643	350
San Pedro Middle	No	Perennial	No	931 - 949	313
San Pedro Upper	No	Perennial	No	1212 - 1288	290
Santa Maria	No	Perennial	No	314 – 539	370
Agua Fria	No	Perennial	No	490	117
Hassayampa	No	Perennial	No	570 – 598	164
Cienega Creek	No	Perennial	No	1010 - 1060	113
Santa Cruz, Lower	No	Perennial	Yes	575 - 578	156
Santa Cruz, Upper	No	Perennial	Yes	956 – 1050	238
San Pedro, Lower	No	Intermittent	No	783 – 811	324
San Pedro, Middle	No	Intermittent	No	951 – 1152	215
San Pedro, Upper	No	Intermittent	No	1122 - 1166	263
Santa Maria	No	Intermittent	No	314 - 539	305
Agua Fria	No	Intermittent	No	490	115
Hassayampa	No	Intermittent	No	607	332
Santa Cruz, Upper	No	Intermittent	No	1071 - 1140	203
Bill Williams	Yes	Perennial	No	152 - 271	282
Verde	Yes	Perennial	No	458 - 464	428
Salt, east of Phoenix	Yes	Perennial	No	408 - 409	415
Salt, west of Phoenix	Yes	Perennial	Yes	290 – 291	1224
Gila, west of Phoenix	Yes	Perennial	Yes	264 – 283	785
Bill Williams	Yes	Intermittent	No	152 – 271	401
Gila-Winkelman	Yes	Intermittent	No	536 - 680	495
Agua Fria	Yes	Intermittent	No	440	237

Alamo Dam, which is operated for flood control, reservoir recreation and riparian conservation (Shafroth *et al.*, 2002); one reach of the Salt River below Stewart Mountain Dam and one on the Verde River below Bartlett Dam, both operated mainly for water storage and controlled delivery to downstream urban and agricultural users; and one reach of the Gila River below Coolidge Dam operated primarily as an agricultural water supply dam. Also included in this category was a reach of the Agua Fria below New Waddell Dam. This dam is a diversion structure and the entire stream flow (including water imported from the Colorado River) is routed into canals. The study reach just downstream of New Waddell Dam was classified as intermittent, due to seepage from the dam. In addition, there were two effluent-dominated flow-regulated reaches.

Reaches were classified as effluent-dominated if most or all of their dry-season flow was derived from the release of treated municipal wastewater directly into the stream channel. The four effluent-dominated reaches were: (1) the free-flowing Santa Cruz River near Tubac, flows of which have been augmented by effluent discharge since 1948, (2) the historically dewatered but undammed Santa Cruz River north of Tucson into which effluent has been discharged since the 1970s, (3) a 7-km reach of the Salt River west of Phoenix and downstream of the Multi-cities Wastewater Treatment Plant into which effluent has been discharged since the 1950s, and (4) a 12-km reach of the Gila River located downstream of the Salt–Gila confluence. These latter two reaches were classified as flow-regulated, because upstream dams influence their flood regimes.

Data were obtained on two other site factors that can influence forest composition. Elevation above sea level was determined for each reach from topographical maps. Mean values for specific conductance of stream water (a measure of salinity) were obtained from USGS stream gauges located in or near study reaches for representative 2-year time periods (averages of 11 to 27 values per station). Water quality data were not available for all gauges and periods of record varied, and the data do not provide a direct measure of the water used by riparian trees. Because of these limitations, salinity data were summarized but not included in statistical analyses.

Most of the study reaches are not currently grazed by livestock, however, all have been grazed at some point over the past century, some at very high stocking rates. Other notable land management actions include the clearing of *Tamarix* from the perennial reach of the Hassayampa River by the Nature Conservancy. Data for this reach are graphically portrayed but not included in statistical analyses.

Vegetation sampling

In each river reach, two to 10 transects were established. The transects were perpendicular to the drainage and encompassed the river and its floodplain. We defined the floodplain as that portion of the riparian zone that includes fluvial surfaces built of sediments deposited in the present regime of the river and that are periodically inundated under the present regime. This encompassed the area vegetated by pioneer trees and shrubs and by young, successional trees such as *Prosopis velutina*, but excluded the terraces that are no longer inundated by the river. The transects

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were separated by a minimum of 100 m. Data were collected in different years among reaches, during the period 1996 to 2005.

Riparian vegetation consists of a mosaic of patches, with each patch developing after some disturbance event and each reflecting differences in fluvial conditions at the time of establishment (Bagstad *et al.*, 2006). The various trees and shrubs can form single-species patches or can grow in multispecies stands, often with one species dominating. Vegetation was sampled along the transects to obtain data on (1) the percentage of the patches in the floodplain dominated by each tree species and (2) the basal area of each tree species. A species was considered to dominate a patch if it had the greatest basal area in the sampled quadrat that represented the patch. To obtain the data, the transects were subjectively delineated into patches based on observed differences in woody vegetation structure (i.e. canopy cover, species composition, tree age as inferred from trunk diameter). Quadrats were then sampled along the transect line in stratified random fashion (one 100-m^2 quadrat per patch or one 40-m^2 quadrat per patch, depending on the river). Stem diameter, by species, was measured in each quadrat to obtain basal area values. The basal area data were scaled to the floodplain level by weighting plot values by the relative length of the patch along the transect line. To obtain patch area values, the lengths of all the patches dominated by a particular species along the transect line were summed and expressed as a percentage of the transect length. We report basal area and patch area data for the three most prevalent pioneer tree species (*Populus fremontii*, *Salix gooddingii* and *Tamarix* spp.). Patch areas of *P. fremontii* and *S. gooddingii* were combined because both trees have similar morphology, life history and environmental tolerances. Basal area data were not obtained for one intermittent, flow-regulated river reach (Gila River–Winkelman). Here, patch dominance was defined by the species with the greatest canopy cover (as visually estimated).

Data analysis

Six dependent variables were analysed, representing absolute and relative abundance of *Tamarix* and *Populus–Salix*: *Tamarix* patch area (% of floodplain), *Populus–Salix* patch area, patch area of *Tamarix* relative to that of *Populus–Salix*, *Tamarix* basal area (m^2 ha^{-1}), *Populus–Salix* basal area, and *Tamarix* basal area relative to that of *Populus–Salix*. The measures of relative abundance provide indicators of dominance. Because of small sample size, nonparametric tests were used to make comparisons between river reach types. Within the subset of free-flowing non-effluent rivers, the Wilcoxon signed rank test was used to compare the six variables between pairs of intermittent ($n = 5$) and perennial reaches ($n = 5$). For this test, each pair was located on the same river; these matched-pair comparisons were made because they controlled for river-scale factors that might influence the vegetation. Sample size was too small to allow for analysis of matched above-dam and below-dam pairs within rivers. Thus, within the subset of perennial reaches, the Kruskal–Wallis test was used to compare variables between free-flowing ($n = 8$) and flow-regulated ($n = 5$) reaches (these samples each include two effluent-dominated perennial reaches). The significance level for these tests was set at $P = 0.10$.

Correlation analysis (Pearson product-moment) was used to explore the relationships of *Tamarix* relative patch area ($n = 23$) and basal area ($n = 22$) to site elevation. Multiple regression analysis was used to test for significant effects on relative patch cover ($n = 23$) and relative basal area ($n = 22$) of *Tamarix* of three independent variables: reach elevation, flow permanence (categorical variable) and flow regulation (categorical variable). Because of the larger sample size and greater statistical power, the significance level for these tests was set at $P = 0.05$.

RESULTS

Perennial vs. intermittent flow

Populus fremontii and *S. gooddingii* were the dominant tree species in the floodplains of the perennial, free-flowing river reaches (Fig. 2). *Populus–Salix* patches had significantly greater cover on perennial reaches than on matched intermittent reaches ($n = 5$, $P = 0.05$), and *Populus* and *Salix* had greater combined basal area on perennial than intermittent ($n = 5$, $P = 0.05$) reaches (Fig. 3, left panel). *Tamarix* showed the opposite trend, but patterns were more variable. *Tamarix* patches had greater cover on the intermittent reaches than on the matched perennial reaches ($n = 5$, $P = 0.08$), but differences for basal area were weaker between the intermittent and perennial reaches ($n = 5$; $P = 0.13$). *Tamarix* patches covered less than 10% of the floodplain at all perennial, free-flowing reaches except one (middle San Pedro, 18%). The relative *Tamarix* patch area was significantly greater on the intermittent reaches than perennial reaches, as was the relative *Tamarix* basal area (Table 2). Forest patterns on the two effluent-dominated, free-flowing perennial rivers were similar to those on the non-effluent, free-flowing perennial rivers: *Populus–Salix* was the dominant patch type and *Tamarix* patches had low cover.

Table 2 Abundance of *Tamarix*, relative to the combined abundance of *Populus* and *Salix*, within hydrological reach types. Values are means plus or minus one standard deviation. *P* values indicate the difference between reach types (i.e. between perennial and intermittent reaches, within the free-flowing subset, and between free-flowing and regulated reaches, within the perennial subset)

	Free-flowing perennial	*n*	Free-flowing intermittent	*n*	*P* value	Free-flowing perennial	*n*	Regulated perennial	*n*	*P* value
Relative *Tamarix* patch area	16 ± 10	5	46 ± 27	5	0.08	12 ± 10	8	59 ± 22	5	<0.01
Relative *Tamarix* basal area	12 ± 9	5	39 ± 31	5	0.08	8 ± 9	8	53 ± 28	5	0.01

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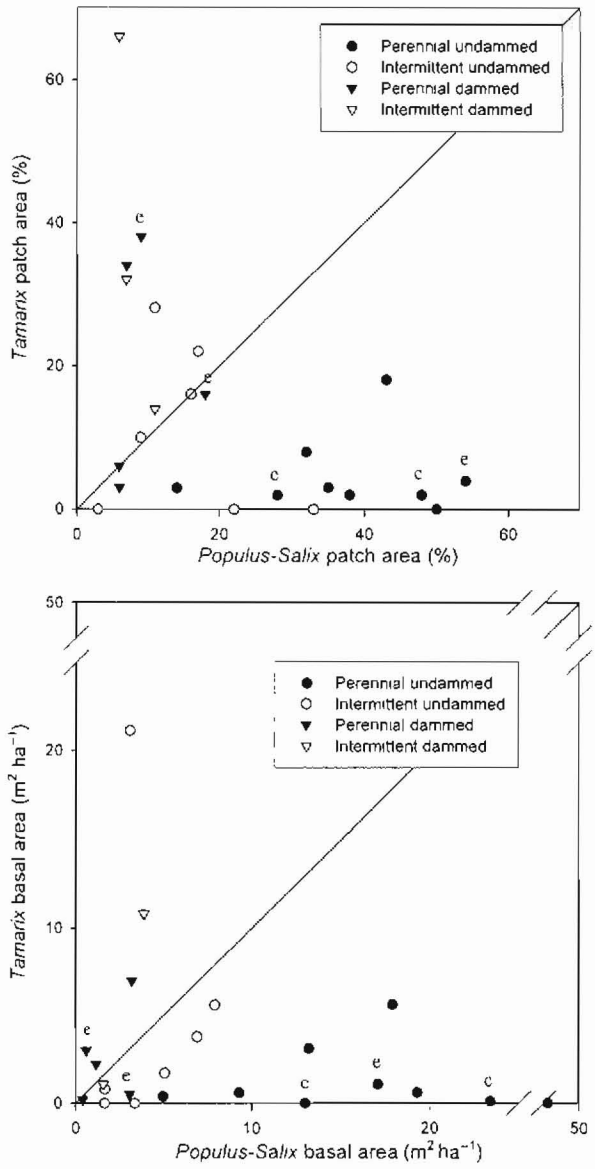

Figure 2 Top: Percentage of the floodplain occupied by *Tamarix*-dominated patches plotted against the percentage of the floodplain occupied by *Populus–Salix*-dominated patches. Bottom: Basal area of *Tamarix* on the floodplain plotted against the combined basal area of *Populus* and *Salix*. Each data point represents a study site (24 sites on the top panel, 23 on the bottom panel). Sites above the diagonal line have greater relative abundance of *Tamarix*, those below the line have greater relative abundance of *Populus–Salix*. 'c' denotes a site from which *Tamarix* has been cleared, 'e' denotes an effluent-dominated site.

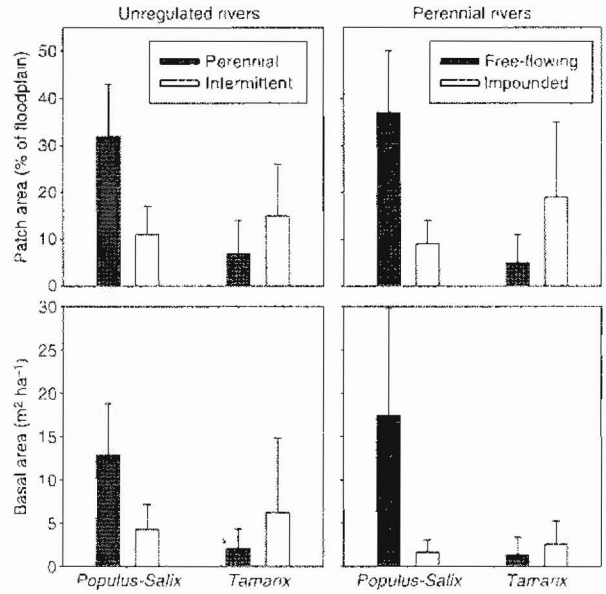

Figure 3 Comparison of abundance of *Populus–Salix* and *Tamarix* between hydrological reach types. Values are means plus one standard deviation. The left panel shows differences between perennial and intermittent reaches, within the free-flowing subset; the right panel shows differences between free-flowing and regulated reaches, within the perennial subset. The two abundance measures are the percentage of the floodplain occupied by each forest type and the basal area of the trees on the floodplain.

Regulated vs. unregulated flow

Populus–Salix patches had significantly greater cover on the free-flowing perennial reaches than on the regulated perennial reaches ($n = 8$ and 5, respectively; $P < 0.01$) (Fig. 3, right panel). Similarly, *Populus* and *Salix* had significantly greater combined basal area on the free-flowing than regulated perennial reaches ($P < 0.01$). *Tamarix* showed the reverse pattern, with less patch cover on the free-flowing than regulated perennial reaches ($P = 0.06$). However, *Tamarix* basal area did not differ significantly between the free-flowing and regulated perennial reaches ($P = 0.46$). Relative *Tamarix* patch area was significantly greater on the regulated than free-flowing perennial reaches, and this pattern persisted for relative *Tamarix* basal area (Table 2).

The intermittent, regulated reaches had very high patch cover of *Tamarix* (37 ± 26%, $n = 3$) compared to *Populus–Salix* (8 ± 3%), with relative patch cover of *Tamarix* averaging 77 ± 18%. Forest composition in the effluent-dominated regulated reaches was similar to that in the non-effluent regulated reaches.

Elevation and salinity

The relative patch area of *Tamarix* was negatively correlated with site elevation ($r = -0.44$, $n = 23$, $P = 0.04$), as was its relative basal area ($r = -0.41$, $n = 22$, $P = 0.06$). In the multiple regression analysis, elevation ($P = 0.69$) was not related to relative *Tamarix* patch area, while flow permanence ($P = 0.013$) and flow regulation ($P = 0.002$) were both significantly related (overall model r^2 of 0.61, F ratio of 15.9). Trends were similar for the *Tamarix* relative basal area model, with elevation not significant ($P = 0.86$) but flow permanence ($P = 0.04$) and flow regulation ($P = 0.02$) both significant (overall model r^2 of 0.48, F ratio of 5.6).

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The stream water of all free-flowing reaches had low electrical conductivity: representative 2-year mean values were 0.4 dS m^{-2} (San Pedro-Tombstone, USGS gauge no. 9471550 and Santa Cruz-Nogales no. 9480500), 0.5 dS m^{-2} (Hassayampa-Box dam site, no. 9515500), and 0.6 dS m^{-2} (Agua Fria-Rock Springs no. 9512800). Mean values on the flow-regulated reaches ranged widely, and were 0.5 dS m^{-2} for Verde-below Bartlett Dam (no. 9510000), 0.8 dS m^{-2} for Salt-below Stewart Mountain Dam (no. 9502000), 1.3 dS m^{-2} for Gila-Winkleman (no. 9470000) and 4.5 dS m^{-2} for Gila-Gillespie (no. 9518000).

DISCUSSION

Rivers in many regions have undergone changes in their flow regimes, leading to changes in the composition of riparian vegetation (Patten, 1998; Tockner & Stanford, 2002; Yoshimura *et al.*, 2005). For the arid rivers addressed in this study, key anthropogenic changes to flow regimes include reduced stream water availability (from groundwater pumping and flow diversion) and altered flood regimes and flow patterns (from damming and flow regulation for water supply). These changes in the flow regime have created conditions that favour a new co-dominant to dominant woody species in the riparian forests. River reaches with perennial flow and a natural flood regime had a high abundance of *Populus* and *Salix*, the historically dominant pioneer riparian trees in the region, and a low abundance of *Tamarix*. In contrast, river reaches with intermittent stream flows (caused by natural and cultural factors), as well as those with dam-regulated flows, were dominated or co-dominated by *Tamarix*, an introduced shrub/tree that is comparatively more stress-adapted and more reproductively opportunistic than *Populus* and *Salix*. These changes in flow regime have facilitated the development of a novel ecosystem (Hobbs *et al.*, 2006), at least with respect to forest composition at the species level.

These compositional shifts are consistent with trends for introduced species to become abundant following anthropogenic habitat changes, including changes to stream-flow regimes (e.g. Bunn & Arthington, 2002). Similarly, they are consistent with trends for altered disturbance regimes or altered resource levels to favour new plant species (Hobbs & Huenneke, 1992; Sher & Hyatt, 1999). Increases or decreases in resource levels can both drive composition shifts, with the latter being at play in the shift from *Populus* to *Tamarix* along dewatered rivers. The abundance of *Tamarix* on the naturally intermittent river reaches suggests that it is intrinsically adapted to the dry conditions that develop on streams of the semi-arid region of the south-western United States. However, water-tables in the floodplains of many formerly perennial river reaches have deepened, thereby favouring stress-adapted species such as *Tamarix* and creating conditions less suitable for drought-intolerant species such as *Populus* and *Salix*. This provides an example of dominance shifts to a new species under conditions of reduced resource availability. The mechanisms for the changes in vegetation on the flow-regulated rivers are more complex, and in part reflect the influence of altered flood regimes on the establishment and survivorship of riparian tree species.

Certainly, physical habitat change is only one of many mechanisms that have been postulated as causes of increased abundance or range expansion of immigrant plant species. For example, a new species may become abundant if it has intrinsically greater fitness than other species (which may occur if introduced into a phylogenetically constrained floristic region), if it produces allelopathic compounds that increase its competitive ability, or if it has escaped from specialized herbivores. Additionally, a species may become abundant if its seed sources have increased (e.g. because of intentional plantings) or because it is able to utilize new and increasing dispersal vectors (such as motor vehicles). However, alteration of the physical environment, which is widespread in riparian corridors of the south-western United States, appears to be a prime driver of the high abundance of *Tamarix*.

Stream dewatering

Many of the rivers in the Basin and Range province of the American Southwest are spatially intermittent, characterized by alternating stretches of perennial and intermittent to ephemeral flow. As the rivers emerge from mountains into dry basins, many lose flow into deep and permeable alluvium, retaining year-round flow only where shallow bedrock forces water to the surface, where major tributaries augment flows or where there is sufficient groundwater inflow from the regional aquifer. The high abundance of *P. fremontii* and *S. gooddingii* on the perennial reaches reflects the presence of sufficient water to sustain these tall, broad-leaved, hydromesic trees. The inflowing groundwater that often maintains the perennial flows also maintains the high water-table in the stream aquifer that allows for survivorship of *Populus* and *Salix* throughout the floodplain (Busch & Smith, 1995; Scott *et al.*, 1999).

In tandem with increased growth of the human population, the spatial extent of perennial reaches has decreased on many rivers in the arid Southwest as a result of stream-flow diversion and groundwater pumping. Where stream flows are intermittent, the water-table is typically lower and shows more interannual (Fig. 4) and intra-annual fluctuation. As the water-table declines to depths of approximately 3 m or more below the floodplain surface, *Populus* and *Salix*, but not *Tamarix*, are shifted out of their tolerance ranges for root-zone soil moisture (Lite & Stromberg, 2005). *Tamarix* is less susceptible than *Populus* and *Salix* to drought-induced xylem cavitation and canopy dieback, and is more of a facultative phreatophyte (Horton *et al.*, 2001, 2003). The *Tamarix* genus is characterized by deep and extensive root systems (Gries *et al.*, 2003), with rooting depths much greater than *P. fremontii* or *S. gooddingii*. Thus, it can dominate at dry sites where the environmental tolerance ranges of *Populus* and *Salix* have been exceeded.

Although clear patterns were evident, there was high variability in tree abundance patterns within hydrological reach types. For example, *Tamarix* had moderately high abundance at one perennial, free-flowing reach (middle San Pedro). This variability may reflect different relationships between stream-flow permanence and levels of the water-table among sites, with some perennial-flow sites having deeper water-tables than others. The variability

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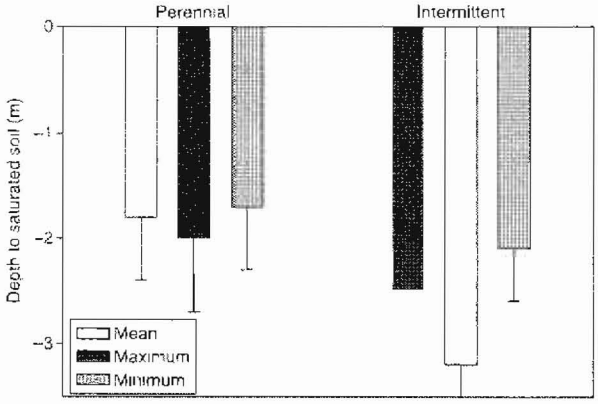

Figure 4 Depth to saturated soil within the floodplain of perennial-flow and intermittent-flow reaches of the upper San Pedro River. Values shown are mean, maximum and minimum values (plus and minus one standard deviation) measured during the 2002 water year. Values are floodplain-weighted averages, based on multiple wells per site (see Leenhouts *et al.*, 2006), for seven perennial-flow sites and eight intermittent-flow sites. Stream flow at the intermittent-flow sites was present for 69 ± 13% of the year.

may also reflect differing hydrological histories. *Populus*, *Salix* and *Tamarix* live for at least a century, and their population structure reflects the influence of past and present environmental conditions. Some of the sites classified as perennial sites are likely to have had deeper water-tables during past decades of drought and intensive agricultural groundwater pumping, conditions which would have favoured survivorship of *Tamarix* over *Populus* and *Salix*.

Flood regime alteration

Floods in Sonoran Desert rivers reflect the largely bimodal rainfall pattern. In late summer, 'flashy' floods of short duration follow localized thunderstorms associated with the monsoonal moisture flow northward from the Gulfs of California and Mexico. Tropical storms cause occasional floods in late summer or autumn. Gentle rains associated with Pacific frontal storm systems periodically saturate the watershed and produce winter floods of high magnitude and long duration. The episodic large autumn and winter floods rework floodplain sediments, creating a patchwork of seed beds on which tree seedlings can establish, without competition from an overstorey. Receding flows in spring moisten the bare sediments during the short period when viable *Populus* and *Salix* seeds are present (Fig. 5), and slow recession of the flood waters and the water-table allows seedling roots to maintain contact with wet soil (Mahoney & Rood, 1998). Over time, subsequent floods cause the channel to migrate or avulse, creating more seed beds. As a result of these dynamic river processes, *Populus–Salix* patches can be abundant on free-flowing, perennial reaches.

Tamarix, like *Populus* and *Salix*, is also a pioneer plant that produces abundant small seeds and establishes on moist mineral soils. Several factors may explain why it remains subdominant to *Populus* and *Salix* on perennial rivers with unaltered flood regimes. First, because *Populus* and *Salix* begin dispersing seeds earlier in the growing season, their seedlings can pre-empt space and out-shade and overtop the later-seeding *Tamarix*. Second, *Tamarix* seedlings are suppressed by *Populus* and *Salix* through competitive interactions. Although *Tamarix* begins dispersing seeds later in the season, its dispersal period does overlap with that of *Populus* and *Salix*, and mixed-species seed beds are common. However, due to evolutionary trade-offs, plants such as *Tamarix* that are stress-adapted often have low competitive ability under conditions of high resource availability. Thus, as a seedling, *Tamarix* is not a strong competitor against co-establishing *Populus* and *Salix* (Sher *et al.*, 2000) and the plants do poorly under a *Populus* canopy (Lesica & Miles, 2001).

As flood waters continue to recede, *Tamarix* seedlings can establish in midsummer on newly exposed surfaces (after *Populus* and *Salix* have ceased germinating). Additionally, they may establish in late summer on surfaces wetted by the often-flashy summer monsoon floods. However, seedlings on near-channel surfaces have a high risk of mortality from flood scour or

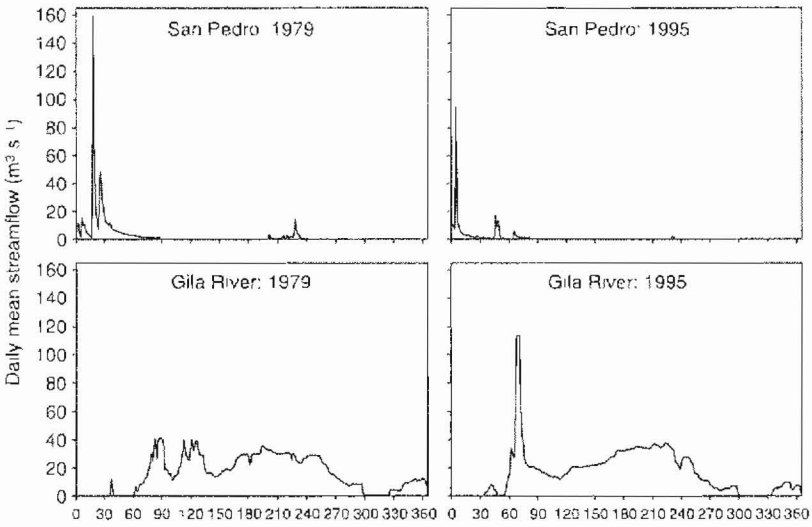

Figure 5 Contrast of annual stream hydrographs between a free-flowing river (San Pedro-Redington, no. 09472000) and a nearby flow-regulated river (Gila River below Coolidge Dam, no. 09469500). Data are shown for two years (1979 and 1995) that regionally were successful seedling establishment years for *Populus fremontii* along free-flowing rivers.

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sedimentation (Levine & Stromberg, 2001). In general, pioneer tree seedlings have greatest survivorship on surfaces that are sufficiently high to escape mortality from flood scour and that are sufficiently low to avoid mortality from desiccation (Stromberg *et al.*, 1991).

Independent of differences in phenology and spatial establishment zones, it is possible that *Tamarix* is intrinsically less tolerant of flood scour, particularly if competitively suppressed by *Populus* or *Salix* (Everitt, 1980; Stromberg *et al.*, 1993). High investment in adaptations for stress tolerance (such as deep roots) can reduce a plant's ability to survive disturbances. Rea (1988, p. 1399) provides anecdotal evidence: 'The 1965–1966 Christmas–New Year floods [on the Gila River] scoured out much of the vegetation, including most of the impenetrable salt-cedar [*Tamarix*] thickets established in earlier years. The resulting ... sandbars ... proved ideal for establishment of cottonwood and willow stands'. Subsequent flooding in the winters of 1973, 1978, 1979 and late 1983 'scoured salt-cedars along the channels ... leaving most of the willow and cottonwood groves intact'. Studies are needed to compare resistance to flooding of similar-aged populations of *Populus*, *Salix* and *Tamarix*, and more generally of plants adapted for wetter versus drier riparian environments.

Many rivers in the south-western United States have been dammed for water storage and/or flood control (Graf, 1999). Reductions in flood frequency, shifts in flood timing and abrupt decline of flood waters, together with changes in river geomorphology, have contributed to reduced recruitment of *Populus* and *Salix* (in the short term or long term) along many dammed rivers in western North America (e.g. Rood & Mahoney, 1990; Howe & Knopf, 1991; Merritt & Cooper, 2000; Cooper *et al.*, 2003). In this study, as well, *Populus*–*Salix* were less abundant in impounded reaches than in free-flowing river reaches, albeit with high variability within hydrological reach types. Complex interrelationships between floods and droughts structure riparian plant populations and communities, and recruitment and mortality rates of *Populus* and *Salix* vary widely among regulated reaches due to the individualistic nature of rivers and of dam management. For example, in rivers with a low ratio of reservoir storage capacity to watershed runoff (such as on the Verde River), the reservoir can be overwhelmed in wet years, thus allowing the passage of large floods. This can allow for 'run-of-the-river' spring-season hydrographs and successful establishment of *Populus* and *Salix* (Zamora-Arroyo *et al.*, 2001; Stromberg *et al.*, in press). Following these episodic flows that stimulate the establishment of seedlings, reservoir releases that sustain high stream flows and shallow groundwater through the growing season can mitigate the effects of natural drought on seedling mortality (Lytle & Merritt, 2004).

The presence of a flow-regulating dam in this study was associated with abundant patch area (but not high basal area) of *Tamarix*. Many factors may allow for high patch coverage of *Tamarix* on regulated rivers. The reduced abundance of *Populus* and *Salix* may release *Tamarix* from competitive reduction. Additionally, because *Tamarix* disperses seeds over a longer period than do *P. fremontii* and *S. gooddingii* and has less stringent water requirements for seedling survivorship, it can establish where the river flow pattern differs from the climatic norm with respect to flood timing and recession rate. On rivers managed for delivery of irrigation water, opportunities are periodically created for the establishment of late-seeding species on surfaces exposed during late summer drawdowns (Fig. 4). If floods are suppressed for a few years (as is common on regulated rivers), the *Tamarix* seedlings that germinate on the low surfaces can grow to a size that enables high survivorship of subsequent disturbance events (Cooper *et al.*, 2003). If a narrow germination window can be considered as a specialist trait, and a wide germination window as a generalist trait, then the shifts from *Populus*–*Salix* to *Tamarix* on flow-regulated rivers is an example of a specialist species giving way to a generalist species where environments have shifted from the climatic norm.

Flow-regulating dams also can influence vegetation by changing soil salinity levels. Many rivers in the south-western United States have a relatively low solute content, while others, such as some reaches of the Salt and Gila Rivers in Arizona, have high salinity due to passage through ancient marine salt deposits. Discharge of municipal effluent or agricultural tail water, interbasin transport of salty water and an increased rate of evaporation of water due to passage through multiple dam–reservoir systems can further contribute to salinization of stream water. Where floods are reduced in frequency, the salts can accumulate in floodplains, reaching particularly high levels if the source water has a high salt content. Salinity influences riparian vegetation patterns, with salty conditions favouring halophytic species such as *Tamarix* while reducing the germination, productivity and survivorship of glycophytes such as *Populus* and *Salix* (Shafroth *et al.*, 1995; Vandersande *et al.*, 2001; Pataki *et al.*, 2005). Shifts from glycophytic (*Salix* spp.) to halophytic (*Tamarix africana*) riparian species have been observed in the European Mediterranean, in association with increased salinity of the watercourse soils from agricultural activities (Salinas *et al.*, 2000). Our study did not include any free-flowing, salty river reaches, but did include regulated, salty reaches. The high electrical conductivity of the stream water for such reaches may have contributed to the high relative abundance of *Tamarix*.

Stream nutrient levels

Many rivers throughout the world have undergone changes in water quality due to urban, agricultural and industrial activities, and some riparian and wetland ecosystems have become eutrophic. Rivers in the Sonoran Desert typically have low concentrations of nitrogen and phosphorus but nutrients can increase when effluent is discharged from municipal wastewater treatment plants. Eutrophication can modify competitive interactions and favour species with high nitrogen productivity (i.e. high relative growth rate per unit plant nitrogen). In some wetlands, eutrophilic species, some of which are introduced, have become the community dominants (Lake & Leishman, 2004). However, in this study (based on a very small sample of reaches), release of municipal effluent into river channels was not associated with shifts in tree species composition. Although there may be subtle interspecific differences in nutrient uptake and utilization, *Populus*,

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Salix and *Tamarix* seedlings all respond positively to nutrient augmentation (Marler *et al.*, 2001; Adair & Binckley, 2002). The response of the riparian forests in the semi-arid Southwest to effluent discharge appears to be driven more strongly by changes in water quantity rather than by changes in water quality.

Other influences

Some of the variability in abundance of *Populus*, *Salix* and *Tamarix* within hydrological reach types may have been caused by land-use factors. For example, reach differences in livestock grazing histories may be a cause of some of the variability. By selectively foraging on the more palatable *Populus* and *Salix*, livestock can shift forest composition towards *Tamarix* dominance even at free-flowing perennial rivers. Intense livestock grazing in past decades at some sites may have produced a higher relative abundance of *Tamarix* than would be the case had cattle been excluded from the riparian zone.

Past episodes of riparian land clearing may also have shaped the riparian forests. *Populus* and *Salix* were cleared from the floodplains of some rivers in the Southwest at various times throughout the 20th century, setting the stage for large-scale vegetation replacement. The composition of the colonizing species may have been determined by the timing of the post-clearing flood events relative to the availability of seed sources at the time (Everitt, 1998).

On some rivers, *Tamarix* increases in abundance with distance downstream of the headwaters (Campbell & Dick-Peddie, 1964). The relative abundance of *Tamarix* in this study increased with decreasing elevation, consistent with the general regional trend. The pattern in this study appears to be explained by the tendency for hydrological alterations to increase at lower elevations. However, it may also occur because the upstream reaches are farther from source populations or because they are less favourable climatically.

Patterns in other regions

This study demonstrated that where rivers remain perennial and free-flowing, the native riparian pioneer trees (*Populus* and *Salix*) have high abundance and the introduced pioneer species (*Tamarix*) has low abundance. These results may or may not be representative of other river basins in North America. Birken and Cooper (2006), for example, describe a case of extensive colonization of *Tamarix* along a river in Utah, prior to major dam construction. Whiteman (2006) found *Tamarix* to be abundant along an unregulated river in New Mexico. A study in south-east Montana, however, concluded that the spread of *Tamarix* could be minimized by managing for factors that sustain *Populus* (Lesica & Miles, 2001).

Patterns may vary regionally because of differences in traits of the local species. *Populus fremontii* and *S. gooddingii* have a fairly small geographical range, limited to the south-western United States and northern Mexico, whereas *T. ramosissima* is more broadly distributed in western North America. In much of western North America, *Tamarix* co-occurs with a different species of cottonwood (*Populus deltoides*). Additionally, along some rivers (and lakes), *Tamarix* grows in areas that formerly supported riparian grasslands or shrublands rather than riparian forests (Ladenburger *et al.*, 2006; Sexton *et al.*, 2006).

The degree to which *Tamarix* establishes along free-flowing and undiverted rivers may vary between regions depending on local soil conditions, land uses and flow regimes. For example, if riparian soils in a particular region have very high salt content, *Tamarix* may dominate regardless of flow regime. Or, if the intensity of livestock grazing has been high in the riparian corridor and watershed, *Tamarix* may become very abundant, independent of direct hydrological alteration. Additionally, *Tamarix* abundance may vary regionally with characteristics of the flood regime. Floods in Sonoran Desert rivers are very powerful, transport much sediment and occur in multiple seasons of the year. This frequent scour and sedimentation may contribute to low abundance of *Tamarix* along free-flowing rivers of the Sonoran Desert. *Tamarix* may have greater survivorship where floods are less intense, transport fewer sediments and are restricted to early summer; comparative studies with regions typified by snowmelt-fed rivers and less arid catchments would be beneficial.

Implications for river restoration

The results of this study imply that restoration of *Populus–Salix* forest ecosystems, in the strict sense, will require the return of perennial stream flows, shallow groundwater, and flood timing and intensity in keeping with climatic norms. The study also has implications for the management of *Tamarix*. Efforts at removal of *Tamarix* are under way on many western North American rivers, including those that are free-flowing and perennial. However, under such hydrological conditions our results suggest that *Tamarix* will remain subdominant within the plant community. We draw this conclusion even though *Populus*, *Salix* and *Tamarix* may not have reached quasi-equilibrium at some of our study reaches. For example, the upper San Pedro River is typified by relatively low rates of floodplain turnover and the relatively recent introduction of *Tamarix*; many of the pioneer forest stands established prior to the arrival of *Tamarix* (Stromberg, 1998) and its present density in the floodplain might not be representative of its potential future density. However, the low abundance of *Tamarix* in young age classes (e.g. cohorts from the 1990s and 1980s) at this and other free-flowing rivers (e.g. Santa Maria; Shafroth *et al.*, 2002) suggest that *Tamarix* will remain a subdominant tree where the processes that allow for *Populus–Salix* establishment and survival remain intact. Thus, targeted plant removal seems unnecessary on perennial, free-flowing rivers if the goal is to prevent *Tamarix* from attaining dominance.

On many naturally intermittent, free-flowing rivers, *Tamarix* is co-dominant with *Populus–Salix*. Some *Tamarix* clearing efforts, in this and other settings, are conducted with the goal of removing an 'uninvited' invader. If ecosystems are viewed as open systems, in which immigration is an ongoing process and shifting species assemblages are the norm, then the mere presence of an introduced species is not in itself a call for action. If the new species is causing structural or functional changes in the ecosystem, and if these changes are perceived as negative, this can motivate actions such as clearing (Kennedy *et al.*, 2005).

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Large-scale efforts at *Tamarix* removal, involving bulldozing, aerial herbicide application, fire and use of biocontrol insects are under way at several highly modified rivers in the western United States (McDaniel & Taylor, 2003; Dudley & DeLoach, 2004; Hart *et al.*, 2005; Shafroth *et al.*, 2005). However, on these hydrologically altered rivers, *Tamarix* may fall within the 'invasive species as passenger' rather than the 'invasive species as driver' model of ecosystem degradation (MacDougall & Turkington, 2005). If indeed a passenger, the removal of *Tamarix*, without simultaneous restoration of stream-flow and sediment flow regimes, may not restore the desired conditions. On partially dewatered and flow-regulated river reaches, *Populus*, *Salix* and other hydromesic plants may not establish in abundance barring the restoration of appropriate river flows, and other ecosystem traits (such as species diversity) may not change, barring the restoration of dynamic flood regimes. Furthermore, clearing of vegetation, without other restorative actions, could reduce habitat for the federally endangered south-western willow flycatcher and other bird species that utilize *Tamarix* (Zavaleta *et al.*, 2001; Paradzick & Woodward, 2003). From the perspective of river restoration in south-western North America, it may be most fruitful to view *Tamarix dominance* (not to be confused with *presence*) as an indicator of altered riverine processes. As such, its dominance could serve as a trigger for the restoration of surface and groundwater flows, more natural flood regimes, and, perhaps, more suitable livestock grazing practices.

ACKNOWLEDGEMENTS

Results presented in this study were facilitated by funding provided by the Arizona Game and Fish Department, Arizona Water Protection Fund, the US Environmental Protection Agency, the National Science Foundation's Center for Sustainability of semi-Arid Hydrology and Riparian Areas and the US Bureau of Reclamation.

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BIOSKETCH

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Editor: Martin Sykes

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