

Shifting dominance of riparian *Populus* and *Tamarix* along gradients of flow alteration in western North American rivers

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Abstract. *Tamarix ramosissima* is a naturalized, nonnative plant species which has become widespread along riparian corridors throughout the western United States. We test the hypothesis that the distribution and success of *Tamarix* result from human modification of river-flow regimes. We conducted a natural experiment in eight ecoregions in arid and semiarid portions of the western United States, measuring *Tamarix* and native *Populus* recruitment and abundance at 64 sites along 13 perennial rivers spanning a range of altered flow regimes. We quantified biologically relevant attributes of flow alteration as an integrated measure (the index of flow modification, IFM), which was then used to explain between-site variation in abundance and recruitment of native and nonnative riparian plant species.

We found the likelihood of successful recruitment of *Tamarix* to be highest along unregulated river reaches and to remain high across a gradient of regulated flows. Recruitment probability for *Populus*, in contrast, was highest under free-flowing conditions and declined abruptly under even slight flow modification (IFM > 0.1). Adult *Tamarix* was most abundant at intermediate levels of IFM. *Populus* abundance declined sharply with modest flow regulation (IFM > 0.2) and was not present at the most flow-regulated sites. Dominance of *Tamarix* was highest along rivers with the most altered flow regimes. At the 16 least regulated sites, *Tamarix* and *Populus* were equally abundant.

Given observed patterns of *Tamarix* recruitment and abundance, we infer that *Tamarix* would likely have naturalized, spread, and established widely in riparian communities in the absence of dam construction, diversions, and flow regulation in western North America. However, *Tamarix* dominance over native species would likely be less extensive in the absence of human alteration of river-flow regimes. Restoration that combines active mechanical removal of established stands of *Tamarix* with a program of flow releases conducive to native species establishment and persistence is hypothesized to facilitate the codominance of *Populus* in reaches where it has become rare. Our findings have implications for planning flow-related stream restoration, for developing realistic expectations for yield on investment in prescribed flow releases, and for planning flow-related interventions that might be possible if control and management of invasive plant species along rivers is a goal.

Key words: dams; flow management; flow regime; index of flow modification; invasive species; *Populus*; river management; river restoration; tamarisk; *Tamarix ramosissima*; vegetation change; water development.

INTRODUCTION

River bottomlands and riparian habitats serve as key corridors for the establishment and spread of introduced species (Planty-Tabacchi et al. 1996, Stohlgren et al. 1999, Brown and Peet 2003) for many of the same reasons that they harbor disproportionately diverse assemblages of plants relative to uplands worldwide (Naiman et al. 1993, Naiman and Décamps 1997, NRC 2002). Fluvial disturbance, habitat heterogeneity, varied flow regime and hydrologic gradients, and connectivity through landscapes maintain high species diversity and

also provide opportunities for the spread of nonnative, ruderal species (Pyšek and Prach 1993, 1994, Hood and Naiman 2000, Aguiar et al. 2001). Although debate over the relative importance of species traits vs. site characteristics in explaining the causes and consequences of plant invasion is far from resolved (Levine and D'Antonio 1999, Levine et al. 2003, 2004), it is clear that disruption or modification of natural disturbance processes (e.g., fire and flow regimes) can render some ecosystems more vulnerable to invasion by nonnative species (Vitousek et al. 1997, Lonsdale 1999, Thuiller et al. 2006). Once established, species that regulate disturbance processes (e.g., increase fire frequency or intensity) tend to cause the greatest degree of change within an ecosystem into which they become established (Busch

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and Smith 1993, Levine et al. 2003, Brooks et al. 2004). Because patterns of fluvial disturbance, stream flow, and groundwater regime structure the habitat template upon which riparian plant communities form, changes in these hydrologic and channel processes can have significant negative effects on native, flow-regime-adapted taxa (Braatne et al. 1996, Stromberg 2001) and may increase the susceptibility of these systems to invasion by generalist, invasive, and ruderal plant species.

Worldwide development of rivers for water resources and flood control represents one of the most deliberate and pervasive human alterations of natural processes. Over half of the world's largest river systems are regulated and fragmented by dams and storage reservoirs which cumulatively detain ~15% of the total global river runoff annually (Nilsson et al. 2005) and significantly alter natural hydrologic regimes. In the western United States the 15 000 dams >2 m high and tens of thousands more smaller dams and diversions were constructed over the course of the 20th century to provide municipal and agricultural water supplies, recreation, enhanced navigation, hydroelectric power, and flood control (Graf 1999, Lytle and Merritt 2004, NID 2004). Changes to hydrologic and sediment regimes on regulated rivers around the world have induced shifts in the distributions of plant populations (Busch and Smith 1995, Scott et al. 1997, Lonsdale 1999), altered plant community composition (Nilsson et al. 1997, Jansson et al. 2000, Merritt and Cooper 2000, Merritt and Wohl 2006), diminished plant species diversity (Nilsson et al. 1997, Jansson et al. 2000), and modified ecosystem processes (Molles et al. 1998, Valett et al. 2005). Altering the timing, magnitude, duration, and interannual variability in flow regimes can be detrimental to species that have phenologic and physiological adaptations to the characteristics of natural flow regimes (Lytle and Poff 2004) and may advantage generalist and ruderal species.

Over the last 50 years along regulated rivers throughout western North America, some native riparian tree species, such as cottonwood (*Populus deltoides* Bartram ex Marsh. and subspecies), have declined dramatically, in concurrence with the rapid invasion of Eurasian saltcedar, or *Tamarix* (Friedman et al. 2005). Because *Populus* (and some other native species) has reproductive and physiological adaptations synchronized with the regional timing, magnitude, duration, and interannual variability of historic stream flow (Karrenberg et al. 2002, Lytle and Poff 2004, Stella et al. 2006), flow alteration has contributed directly to declines in the regeneration, persistence, and population structure of these taxa (Poff et al. 1997, Rood et al. 2003, Lytle and Merritt 2004). Thus, a widely held view is that the dramatic decline in *Populus* over the last 50 years reflects extensive regional flow alteration (Rood and Mahoney 1990).

However, flow alteration can also influence patterns, rate, and extent of colonization of exotic species along

rivers by creating new habitat, displacing native species, and providing conditions that suit the nonnative species' life-history requirements (Thébaud and Debussche 1991, Pyšek and Prach 1994). Therefore, some have argued that regional flow-regime modification has facilitated the spread of *Tamarix* (Shafroth et al. 1998, Stromberg et al. 2007). As many as a dozen species of *Tamarix* have been introduced from southern Europe and Asia into western North America over the past century and a half. Widely introduced for horticulture, as windbreaks, and to stabilize river banks, *Tamarix* (primarily the hybrid *T. ramosissima* Ledeb. × *T. chinensis* Lour.) rapidly naturalized and spread, now occupying an estimated 500 000 (Robinson 1965, Everitt 1980, Gaskin and Schaal 2002) to 1 000 000 ha (Brock 1994, Zavaleta 2000) in an area of North America ranging from Kansas to coastal California and from northern Mexico to northern Montana (Friedman et al. 2005).

The presence and spread of *Tamarix* has been associated with a variety of contentious scientific and social issues, ranging from the compromised health and collapse of native riparian ecosystems to economic implications about water use and water availability along rivers in the western United States (Di Tomaso 1998). Perceptions and concerns have led to large-scale efforts to salvage water and manage invasive species through *Tamarix* removal (Graf 1981, Culler et al. 1982, Zavaleta 2000). In the popular and peer-reviewed literature, *Tamarix* has been implicated as a major driver of environmental change: increasing salinity of floodplain soil, depleting soil and groundwater and reducing stream flow (attributed to increased evapotranspiration by *Tamarix*), increasing fuel loading and fire intensity, displacing native species, reducing habitat quality, and suppressing species diversity (Cleverly et al. 1997, Di Tomaso 1998, Pataki et al. 2005). Despite these concerns, empirical data directly linking *Tamarix* to such ecosystem changes are surprisingly sparse or absent, and conclusions about cause and effect remain largely speculative. The presumed ecological and economic costs associated with the presence of *Tamarix* (Zavaleta 2000) have resulted in an expenditure of tens of millions of U.S. dollars at local, state, and federal levels annually for *Tamarix* control and "restoration," aimed primarily at removing *Tamarix* to salvage water, restoring native plant assemblages, and supporting the fundamental goal of invasive species management (Hart et al. 2005, Shafroth et al. 2005, U.S. House of Representatives 2005–2006).

In this study, our goal was to disentangle the poorly understood relationships between flow regulation, *Tamarix* spread, and *Populus* decline. We tested the hypotheses that the dominance of *Tamarix* relative to *Populus* (and by implication other native riparian species) is a function of the degree of hydrologic alteration caused by dams and that successful recruitment of *Tamarix* is a function of flow alteration (Fig. 1). Despite the widely held belief that altered hydrologic

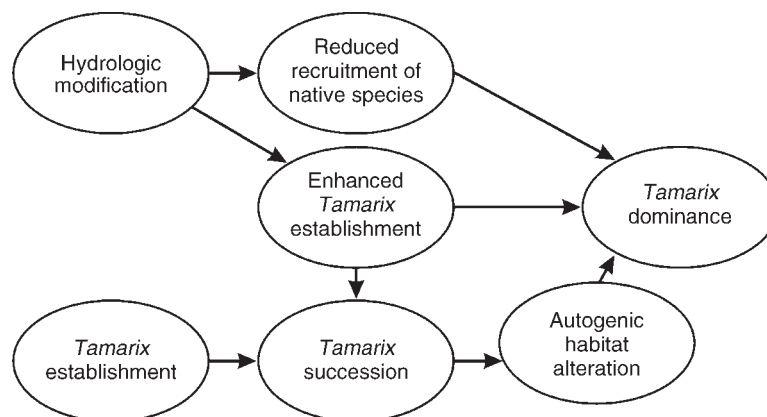


FIG. 1. Possible pathways leading to *Tamarix* dominance. Hydrologic modification may lead to the decline of native species, allowing *Tamarix* to occupy new space which can lead to *Tamarix* dominance of habitat formerly dominated by native species. Alternatively, hydrologic alteration may facilitate the establishment of *Tamarix* by creating conditions to which *Tamarix* is better suited than native species, leading either directly to dominance by *Tamarix* or to the initiation of autogenic processes (changes in soil properties, litter accumulation, soil moisture or groundwater levels, light availability, and so forth) that inhibit native species and lead to dominance. A third alternative pathway to *Tamarix* dominance is that inherent traits of *Tamarix*, rather than some connection to hydrologic alterations, facilitate its spread and initiate autogenic processes that inhibit native species and lead to *Tamarix* dominance.

regimes are a principal mechanism facilitating dominance shifts toward *Tamarix*, supporting evidence has been based either on small-scale experiments (Shafroth et al. 1995, Sher et al. 2000, Beauchamp and Stromberg 2007) or on examination of dammed and undammed river segments in a particular area (Stromberg et al. 2007). Therefore, to test this hypothesis we conducted an extensive, regional analysis along 13 rivers in five states with different degrees of flow alteration by dams and other water infrastructure. Previous regional analyses have been either small in extent and limited to intermittent vs. perennial classes of streams (Stromberg et al. 2007) or geographically extensive but designed to examine the relationship between *Tamarix* dominance with flow-regime alteration (Friedman et al. 2005). Our approach enabled us to conduct a “natural experiment” across a wide range of conditions, capturing both catchment and local-scale environmental variables along a gradient of flow regulation. We expected evidence in support of our hypothesis to manifest as increasing recruitment success and abundance of *Tamarix* along a gradient of intensifying flow regulation. Similarly, we predicted *Populus* would have greater success under the least altered conditions, as has been suggested elsewhere (Stromberg et al. 2007). One goal of this work is to gain insight into the possible efficacy of active stream flow management to control the abundance of *Tamarix* and to restore native *Populus* on dam-modified rivers in the arid and semiarid western United States.

METHODS

Sites and geographical extent

Major perennial rivers from each of eight arid and semiarid ecoregions west of the 100th meridian and east of the Sierra Nevada Mountains were selected for

measurement of *Tamarix* and *Populus* recruitment and abundance (Fig. 2). Perennial rivers of varying degrees of flow regulation were selected in the following ecoregions (sensu Bailey 1995): American semidesert and desert (includes the Mojave, Colorado, and Sonoran Deserts); Arizona–New Mexico semidesert open woodland–coniferous forest–alpine meadow; Chihuahuan semidesert; Colorado Plateau semidesert; intermountain semidesert and desert; intermountain semidesert; southern Rocky Mountain steppe–open woodland–coniferous forest–alpine meadow; and southwest plateau and plains dry steppe and shrub. The region surveyed includes the most arid portion of North America. The sites that we surveyed spanned an elevation gradient of 79–1989 m above mean sea level and ranged in annual precipitation from 102 to 424 mm. As in many other arid and semiarid regions of the world, the perennial desert streams sampled derive flows primarily from snowmelt in mountainous headwaters, although in the southernmost ecoregions summer monsoons also influence late-season flows. Most of these rivers flow from narrow, confined mountain channels out onto broad alluvial valleys. Segments of each river were selected to represent varying levels of flow modification ranging from nearly free-flowing (the upper Colorado, upper Gila, San Miguel, and Yampa Rivers), to moderately regulated by dams (upper Humboldt and upper Pecos Rivers), to heavily regulated (lower Colorado, middle Rio Grande, Little Colorado, and lower Pecos Rivers; Table 1). Once a sampling segment was identified (based upon degree of regulation, accessibility, and permission for access), each was systematically sampled by randomly choosing an initial point and evenly spacing sampling reaches along the segment. In this study, a river segment is a length of

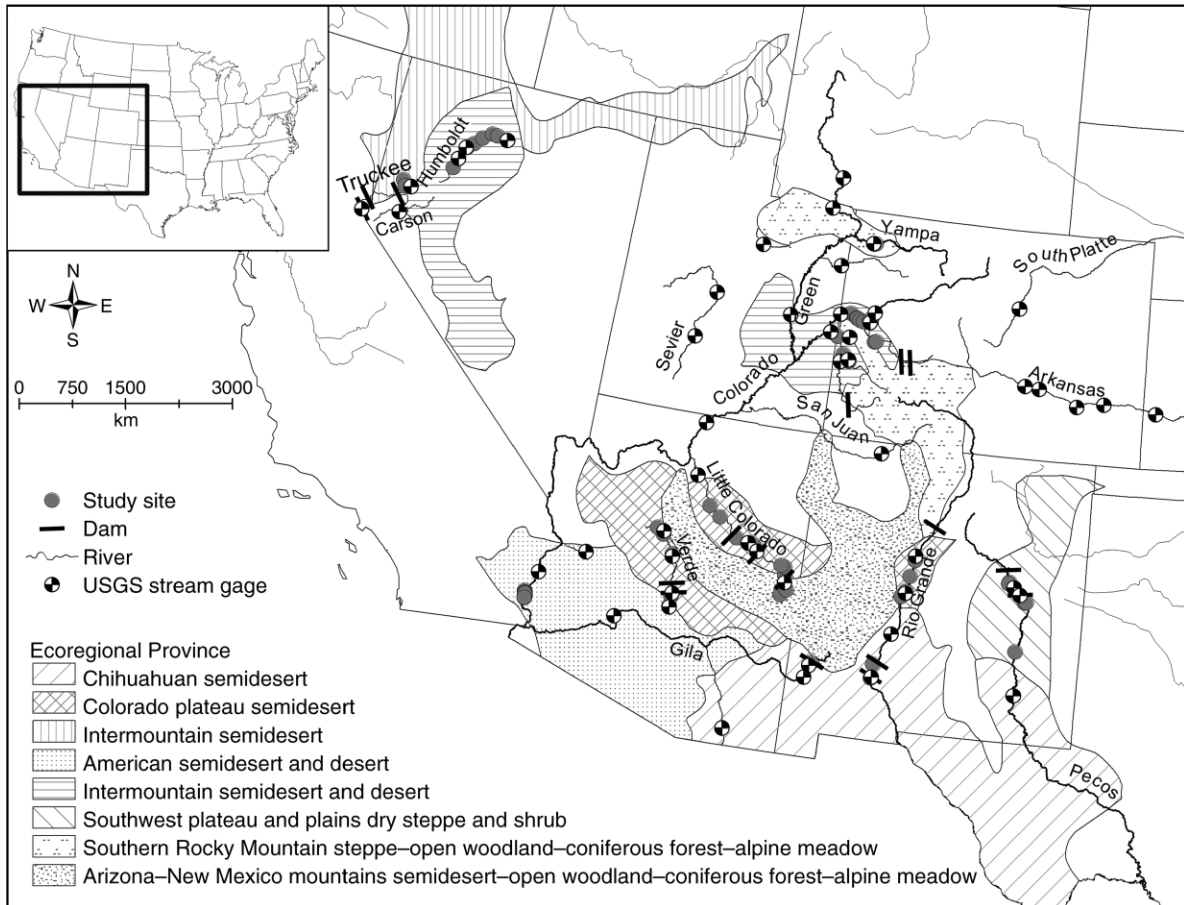


FIG. 2. Study-site map showing the western United States. Only rivers included in the analysis are included in the diagram. USGS stream flow gauges are indicated with black and white symbols, dams are indicated by black lines normal to streams, and gray dots indicate *Tamarix* sampling sites.

stream separated from another by a dam or a major tributary.

Sampling of recruitment and abundance of Tamarix and Populus

We inventoried recruitment and abundance of *Tamarix* and *Populus* along 64 river reaches on 13 perennial rivers in the western United States (Fig. 2). Inventories were conducted during the growing seasons in 1999–2003. At each sampling reach, a 200-m transect was established parallel to the river channel at the margin of the active channel. Locations of candidate 200-m transects were systematically selected by dividing each river segment into 0.5-km intervals on 1:300 000 scale topographic maps. Subsampling of candidate sites (every other site) was necessary in some cases due to time constraints. In the field, the beginning point of the 200-m reaches was chosen to be representative of the larger stream segment. Along each reach, we collected recruitment and abundance data for *Tamarix* and *Populus*.

Recruitment was determined by census of 2–5 year-old saplings of *Tamarix* and *Populus* along both river margins along the 200-m reach; a single presence constituted positive recruitment. Ages were verified by excavating and taking a cross section of the stem of the oldest individual in the plot and counting annual growth rings. In cases when *Populus* was present but not abundant, rather than excavating individuals, we made the assumption that saplings 5 mm or more in diameter at their base were within the 2–5 year range.

Abundance of the two species at the segment scale was based on estimates derived from a census of the presence–absence of adults (>5 years old) at 1-m intervals along the 200-m transect. We recorded the presence of *Tamarix* or *Populus* within a 1 m wide belt (positioned perpendicular to the 200-m transect) visually extended across the entire floodplain. Lengths of the belts varied from 100 to 400 m depending on the width of the valley bottom along the reach. Abundances of *Tamarix* and *Populus* were calculated as the proportion of occurrences in the 200 1 m wide belts (i.e., the occurrence of at least one individual in each belt would

yield an abundance of 1.00). This did not provide an aerial estimate of abundance, but rather an indication of occurrence along river bottomlands (presence–absence across the entire floodplain). Relative abundance of the two species was calculated as the abundance of the species plus one divided by the abundance of the other species plus one. Relative abundance is a measure of dominance.

Several local environmental variables were also recorded at sampled sites. Soil grab samples (upper 15 cm) were collected in two randomly located points along the 200-m transects; river morphology at the scale of the reach was recorded and dominant land-use patterns were noted (presence of recent fire, grazing, and agriculture). In the laboratory, soil samples were analyzed for pH by the soil paste method (Richards 1954). Salinity (electrical conductivity) and concentrations of B, Na⁺, Ca²⁺, K, and Mg²⁺ were determined using inductively coupled plasma (ICP) analysis on an extraction of the soil paste. Sodium absorption ratio was calculated using the formula $\text{Na}^+ / [0.5(\text{Ca}^{2+} + \text{Mg}^{2+})]^{0.5}$ (Harron et al. 1983). Salinity of the catchment above the sample site was estimated by examining the mean salinity of grid cells within a 100-m buffer of all USGS National Hydrography dataset for stream channels in the watershed upstream of the sample reach (USGS 1999). The USGS National Hydrography data set (NHD, 1:100 000 scale; USGS 1999) was used for stream coverage and the U.S. General Soil Map (STATSGO) salinity data set was used to calculate mean salinity in the upstream watershed (data *available online*).⁶ Estimates of mean annual precipitation for the period 1970–2000 at each site was derived from PRISM climatic data (Daly et al. 2001). Valley width through the reach was measured from 1:300 000 scale topographical maps and latitude and elevation were included in the data set for each of the 64 reaches sampled.

Index of flow modification (IFM)

We obtained stream flow data from the U.S. Geological Survey for the period of record available from 26 gages on the 13 rivers nearest the sampling sites (USGS 2002; Table 1). Dam locations, date of construction, and purpose for construction were obtained from the National Inventory of Dams database (NID 2004). For each sampled river segment, we used existing stream flow records to develop a composite metric of the degree of flow modification compared to a relatively unregulated (pre-dam) condition based on biologically relevant flow metrics that we could extract from the hydrologic records. We first summarized the daily mean flow data for the period before and after dam construction. The mean number of pre-dam flow records was 31 years (range 12–111 years) and the mean number of post-dam years of flow record was 49 years (range 21–

70 years). Dams were built between 1905 and 1984. We fitted flood-frequency curves to instantaneous peak-flow series for each river segment studied. Log Pearson Type III distributions were fitted to series of annual instantaneous peak flow using methods outlined by the U.S. Geological Survey (USGS 1981).

For each sampling site, we developed a profile of eight biologically relevant hydrologic variables to characterize alterations associated with river regulation. For regulated systems, the date of upstream dam installation was obtained and the pre-dam record compared to the post-dam record. For relatively free-flowing river segments, the entire hydrologic record was divided into two equal time periods, and the absolute or percentage change from the first half to the second half of the record was calculated. The “modification” or change represented by the difference in the two equal time periods represents natural variation in the unregulated rivers and incorporates climatically and human-caused changes in flow regime. Dams have a much larger effect on modifying flow regimes over the 20th century than do decadal-scale changes attributable to climate variability (Poff et al. 2007).

The biologically relevant hydrologic variables included in this analysis represented key flow-regime components. *Magnitude* and *frequency* of high and low flows comprised six metrics based on percentage change in spring flow (mean of April through June), summer flow (mean of July through September), low flow (mean of October through February flows), and the 2-, 10-, and 25-year recurrence-interval peak flows. *Timing* variables included change in the number of days of minimum flow (number of days shifted) and change in maximum flow.

FloodFreq software (version 4.1) was used to calculate flood frequency (USGS 2002). All other flow-related summary statistics were calculated using Indicators of Hydrologic Alteration software (Richter et al. 1996). To see if there was an association between recent flooding and *Tamarix* and *Populus* recruitment, we determined the number of times that the 5-year recurrence-interval flood had been exceeded in the 5-year period 1998–2002 (Table 1).

Principal components analysis (PCA) was conducted using the eight flow variables from the 26 gages representing all of the study sites (Table 1). To better represent the full range of altered flow regimes in rivers in the western United States, we also included gage records from 21 additional regulated rivers (not field sampled) for which long-term stream flow data were available (Table 2). The broken-stick rule was used to determine the statistical significance of the principal component axes (Jackson 1993): In this rule, eigenvalues from the PCA are compared to eigenvalues from randomly generated data. Only significant axes ($P < 0.05$) were included in the calculation of index of hydrologic modification.

We developed an index of flow modification (IFM) by calculating the Euclidean distance of each observation

⁶ (<http://soildatamart.nrcs.usda.gov>)

TABLE 1. Attributes of U.S. Geological Survey stream flow gages that represent each of the sampled segments in western North American rivers.

River (gage no.)	Catchment area (km ²)	Elevation (m)	Sites at gage no.	Ecoregion†	Dam constructed (year)	Five-year peak exceeded‡	IFM
Gunnison (9128000)	14 576	1564	2	ISDD	1966	0	0.18
Rio Grande (8332010)	49 806	1440	3	CPSD	1973	0	0.43
Rio Grande (8358400)	71 899	1358	1	CSD	1938	0	0.28
Rio Grande (8362500)	79 514	1262	1	CSD	1938	0	0.25
Pecos (8383500)	10 282	1314	2	SPPS	1979	0	0.18
Pecos (8384500)	11 370	1262	3	SPPS	1937	0	0.53
Colorado (9095500)	20 849	1467	2	ISDD	NA	0	0.07
Colorado (9163500)	46 212	1091	4	ISDD	1966	0	0.05
Colorado (9429100)	471 880	79	14	ASDD	1938	1	0.18
Dolores (9169500)	5242	1506	2	ISDD	1984	0	0.21
San Miguel (9177000)	3882	1524	1	ISDD	NA	0	0.07
Dolores (9180000)	11 862	1269	1	ISDD	1984	0	0.12
Yampa (9251000)	19 839	1783	3	SRMS	NA	1	0.04
Little Colorado (9384000)	1823	1832	2	CPSD	NA	0	0.19
Little Colorado (9388000)	2608	1694	3	CPSD	1912	0	0.59
Little Colorado (9394500)	20 903	1563	3	CPSD	1939	0	0.53
Little Colorado (9402000)	68 526	1213	2	CPSD	1939	0	0.15
Gila (9430500)	4828	1482	1	CSD	NA	0	0.12
Verde (9504000)	8091	1067	2	CPSD	NA	0	0.22
Verde (9506000)	12 030	876	1	CPSD	NA	0	0.09
Verde (9511300)	17 132	402	2	ASDD	1939	1	0.16
Humboldt (10327500)	31 649	1329	5	ISDD	NA	1	0.12
Humboldt (10335000)	41 697	1240	2	ISDD	1936	1	0.08
Truckee (10351700)	4341	1255	2	ISDD	1905	0	0.31

Notes: Index of flow modification (IFM) is calculated by examining pre- and post-impact change in eight biologically relevant flow attributes. Elevation is above mean sea level. Values reported for *Tamarix* and *Populus* recruitment, abundance, and dominance are the means for sites along each segment. Abundance is a proportion; recruitment is a probability; and dominance is a ratio of abundance of one species relative to abundance of the other.

† Ecoregion abbreviations are ISDD, intermountain semidesert and desert; CPSD, Colorado plateau semidesert; ASDD, American semidesert and desert; CSD, Chihuahuan semidesert; SRMS, southern Rocky Mountain steppe–open woodland–coniferous forest–alpine meadow; and SPPS, southwest plateau and plains dry steppe and shrub.

‡ Number of times the five-year recurrence-interval flow occurred within the five years prior to sampling.

(study reach) from the centroid of the significant PCA axis scores of relatively unregulated rivers (no major dams) for the eight hydrologic metrics (Fig. 3). Because hydrologic changes on unregulated systems were relatively small between the earlier and later periods, the unregulated streams (upper Colorado, upper Gila, San Miguel, and Yampa Rivers) clustered together in the ordination. The more significant the change in hydrologic alteration of a particular reach, the further the observations lie from the centroid of unregulated sites. IFM was rescaled from 0 to 1.0 using the most flow-modified segment (Bill Williams River) as the maximum. IFM was determined for each of the 64 reaches sampled for *Tamarix* and *Populus* in the field. Multiple reaches located along segments between dams were assigned equal IFM values.

Statistical analysis

We developed models to test *Tamarix* and *Populus* response to flow alteration (IFM) in terms of three response variables: recruitment, abundance, and dominance. For recruitment we used logistic regression to test the hypotheses that *Tamarix* recruitment increases as a function of flow modification and *Populus* recruitment decreases as a function of flow modification. After fitting fixed-effects models and determining that models were

significant, we accounted for the lack of independence between sites within a river or within a river segment in order to more accurately estimate variance components (SAS Institute 2004). We added the random effects RIVER and SEGMENT nested within RIVER in the logistic regression models and compared the fixed-effects and mixed models using corrected Akaike's information criterion (AIC_c; Burnham and Anderson 2002).

For the abundance and dominance response variable, we first used locally weighted regression (LOESS) as an exploratory approach (Cleveland et al. 1988, Cohen 1999) to determine the form of the relationship between IFM and the abundance of *Populus* and *Tamarix*. We then used linear or nonlinear regression as appropriate to test the hypothesis that *Tamarix* and *Populus* abundance at the sites is related to flow alteration. For each analysis of abundance, we first fitted fixed-effects models with IFM (adding quadratic terms as appropriate) and then added the random effect RIVER followed by the SEGMENT nested within RIVER term if it improved the model, using AIC_c as the criterion (SAS Institute 2004).

We were also interested in determining which combinations of the measured environmental variables at the site and segment scale accounted for variability in recruitment and abundance of *Tamarix* and *Populus*.

TABLE 1. Extended.

Recruitment		Abundance		Dominance	
<i>Tamarix</i>	<i>Populus</i>	<i>Tamarix</i>	<i>Populus</i>	<i>Tamarix</i>	<i>Populus</i>
1.00	0.28	0.50	0.00	1.58	0.64
1.00	0.25	1.00	0.00	1.60	0.63
1.00	0.00	0.00	0.00	2.00	0.50
0.98	0.40	1.00	0.00	1.41	0.71
0.95	0.30	1.00	0.00	1.52	0.67
0.92	0.03	0.67	0.00	1.86	0.54
0.77	0.74	1.00	1.00	1.04	1.00
0.75	0.68	1.00	0.25	1.05	0.96
1.00	0.00	1.00	0.00	2.00	0.50
0.85	0.30	1.00	0.00	1.42	0.70
0.60	0.75	1.00	1.00	0.91	1.09
0.98	0.00	1.00	0.00	1.98	0.51
0.09	0.75	1.00	1.00	0.65	1.62
0.00	0.21	0.00	0.00	0.85	1.21
0.37	0.00	0.33	0.00	1.37	0.80
0.94	0.12	0.67	0.00	1.78	0.58
0.90	0.00	0.50	0.00	1.90	0.53
0.30	0.85	1.00	1.00	0.70	1.42
0.69	0.31	0.00	0.00	1.29	0.77
0.01	0.10	1.00	1.00	0.92	1.09
0.84	1.00	0.50	0.50	0.92	1.09
0.61	0.00	0.60	0.00	1.61	0.66
0.76	0.04	1.00	0.00	1.70	0.60
0.36	0.00	0.00	0.50	1.36	0.76

First, we constructed fixed-effects models using stepwise selection in both logistic regression (for recruitment) and linear regression (for abundance). Variables included the following site attributes: latitude, longitude, drainage area, elevation, valley width, mean annual precipitation, estimated salinity from STATSGO maps. The following soil anions and cations were included in model selection: CO_3 , HCO_3 , NO_3 , NO_3N , and SO_4 . Electrical conductivity (EC) was highly correlated with B, Ca, K, Mg, Na, Cl; so only EC was included in model selection. Sodium absorption ratio and pH were also included. We also included the percentage change in pre- to post-flow regulation percentage for April to June flow, July to September flow, and October to February flow, as well as the 2-, 10-, and 25-year recurrence interval flows and the change in the number of days in minimum and maximum flows. After selecting the most parsimonious model, we entered the random effects terms and removed fixed effects that were insignificant after accounting for variation due to random effects.

SAS/STAT version 9.1 was used to perform all statistical analyses (SAS Institute 2004). Adjusted R^2 model selection in REG procedure was used to select variables to be included in mixed linear models; LOESS procedure was used for locally weighted regression; NLIN procedure was used to fit nonlinear models; and stepwise selection in LOGISTIC procedure was used to select variables for inclusion in logistic regression models. MIXED procedure was used for mixed linear modeling, and GLIMMIX procedure was used for mixed logistic regression modeling (Littell et al. 1996). Independent variables were transformed to natural

logarithm or square root when necessary to more closely meet the assumptions of normality and homogeneity of variance.

RESULTS

Index of flow modification

The first three axes of the PCA were significant ($P < 0.05$, broken-stick model) and cumulatively accounted for 74% of the variation in the hydrologic data. Axis 1 represents increases in flood magnitudes (2-, 10-, and 25-year recurrence interval flows) and earlier minimum flow. Axis 2 represents an increase in summer flow, a reduction in 10- and 25-year flows, and an earlier minimum and maximum flow. Axis 3 represents elevated summer flow and later maximum and minimum flows (Fig. 3).

Relationships between IFM and Populus and Tamarix recruitment and abundance

Tamarix recruitment was negatively associated with flow modification but not significantly so (rescaled $R^2 = 0.07$, likelihood ratio (LR) $\chi^2 = 3.1$, $P = 0.08$). The probability of recruitment was highest (up to 0.8) along unaltered stream segments and declined as a function of IFM (Fig. 4). Inclusion of a quadratic term did not improve model fit, nor did inclusion of random effects (RIVER and SEGMENT nested within RIVER).

Tamarix abundance (proportion of mature individuals occurring in 200-m transects) was significantly higher on average (0.75) than *Populus* (0.26) over the 64 sites.

TABLE 2. Attributes of U.S. Geological Survey (USGS) stream flow gages used to get full representation of modified river flow regimes throughout the study region (no sites sampled along these segments).

River (USGS gage no.)	Catchment area (km ²)	Elevation (m)	IFM
Strawberry (9285000)	111	2243	0.50
Truckee (10337500)	1313	1867	0.42
San Pedro (9471000)	3196	1205	0.17
Carson (10312000)	3372	1274	0.43
Sevier (10191500)	6322	1804	0.07
Sevier (10217000)	12745	1532	0.44
Gila (9431500)	7327	1247	0.14
Gila (9519500)	128 592	230	0.67
South Platte (6710000)	7948	1617	0.31
San Juan (9355500)	8443	1723	0.29
White River (9306500)	10 411	1508	0.15
Bill Williams (9426000)	11 999	295	0.99
Arkansas (7099400)	12 328	1445	0.17
Arkansas (7109500)	16 386	1374	0.18
Arkansas (7123000)	31 623	1232	0.26
Arkansas (7130500)	48 989	1139	0.71
Arkansas (7138000)	61 916	978	0.35
Green (9217000)	25 226	1847	0.05
Green (9315000)	116 161	1231	0.10
Pecos (8396500)	39 626	1003	0.29
Colorado (9380000)	289 560	947	0.37

Notes: Index of flow modification (IFM) is calculated by examining pre- and post-impact (dams) change in eight biologically relevant flow attributes. Elevation is above mean sea level.

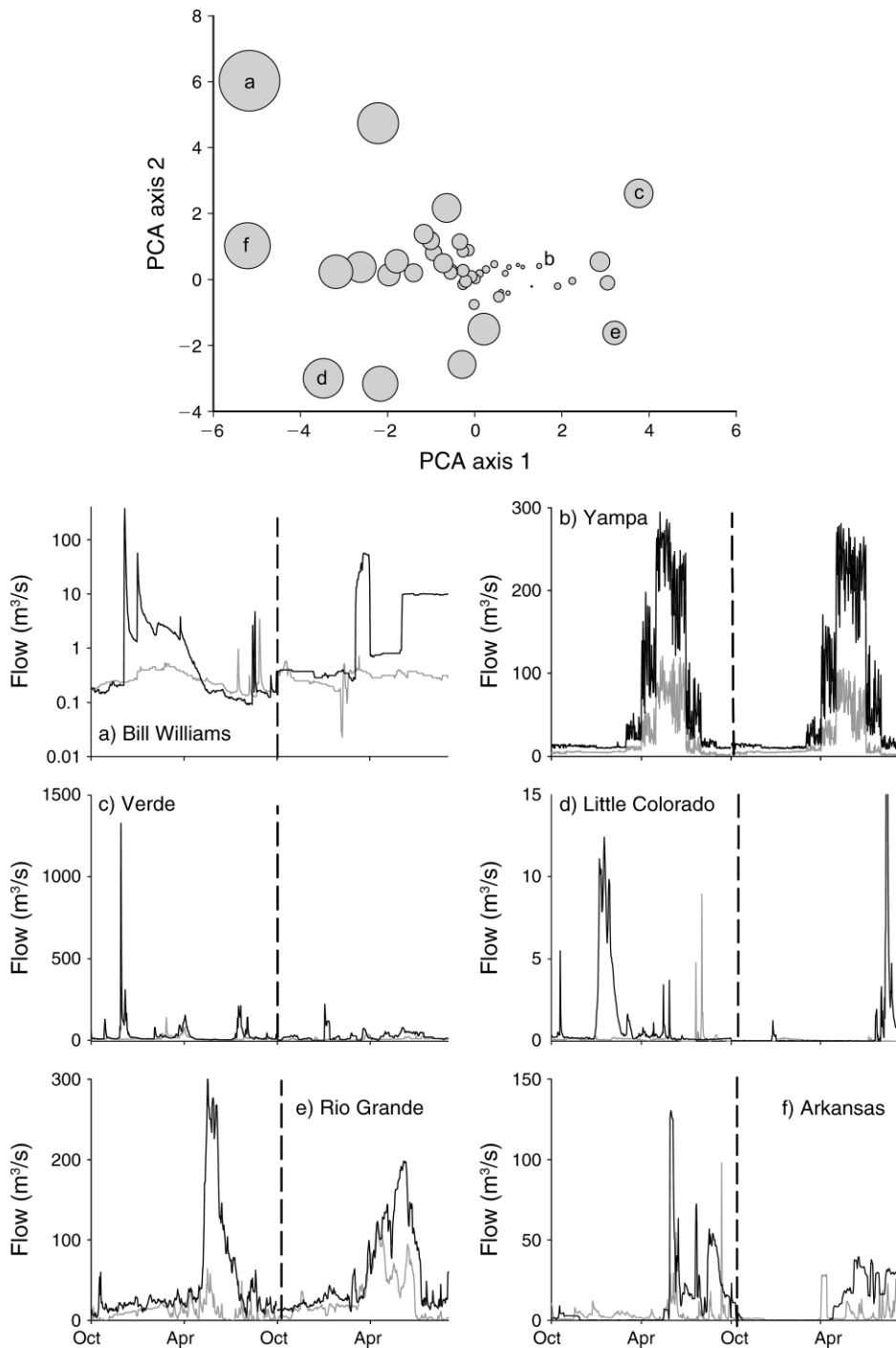


FIG. 3. First two principal component axes (PCA) of biologically relevant attributes of flow regime for 64 river segments in the western United States. Axis 1 represents increases in flood magnitudes (2-, 10-, and 25-year recurrence interval flows) and earlier minimum flow. Axis 2 represents an increase in summer flow, a reduction in 10- and 25-year flows, and an earlier minimum and maximum flow. The size of the circle in the main figure indicates the degree of hydrologic alteration, measured as the Euclidean distance (in three-dimensional flow space) from the centroid of unregulated rivers (generally just right of center). Letters a–f within or beside circles correspond to the hydrograph panels (a)–(f) from selected streams in the PCA. Vertical dashed lines on each hydrograph demarcate the pre-dam and post-dam hydrographs or the first and second half of the flow record for which hydrologic attributes were compared. For the two tracings in the hydrograph panels, the dark lines are a representative hydrographs in the 80th percentile, and the light lines are representative hydrographs for a 10th-percentile daily average flow.

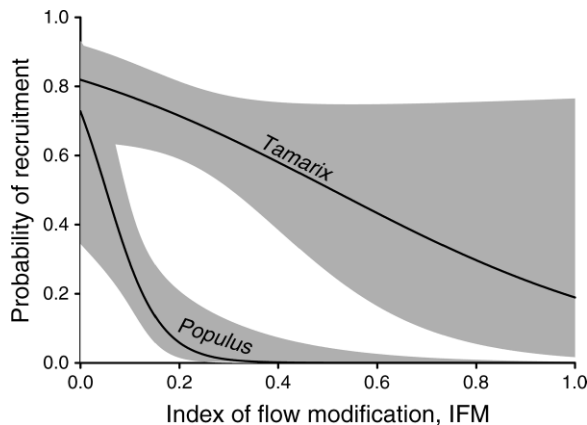


Fig. 4. Logistic regression models of *Populus* and *Tamarix* recruitment as a function of index of flow modification (IFM; shaded area indicates upper and lower 95% confidence intervals). Likelihood ratio tests indicated that *Populus* regeneration is indeed a function of flow modification ($P = 0.0002$), declining rapidly with increasingly altered flows. *Tamarix* recruitment also declined as a function of flow modification, but this relationship was not statistically significant ($P = 0.08$). Index of flow modification is the Euclidean distance (re-scaled from 0 to 1.0) of a stream segment from the centroid of free-flowing (unregulated) streams in ordination space. The variables included in the ordination were changes in eight biologically relevant attributes of flow regime in pre-regulation and post-regulation time periods. Please refer to *Methods: Index of flow modification (IFM)* for details.

Tamarix abundance exhibited a curvilinear form in locally weighted regression, peaking at IFM of ~ 0.3 and dropping off at extreme values of IFM (Fig. 5). Using linear regression with a polynomial term, the index of flow modification was significantly but weakly related to *Tamarix* abundance ($R^2 = 0.12$, $P = 0.02$). Both linear and quadratic terms were significant ($P < 0.007$). Including random effects improved the model fit (AIC_c reduced from 41 to 13) and the fixed-effects IFM and IFM^2 remained significant (Type III test $P < 0.05$; Fig. 5).

Loess regression indicated that a power function was the appropriate form to fit to the *Populus* abundance data. This function had a significant fit ($P < 0.0001$) and was chosen over the polynomial regression (Fig. 5). *Populus* recruitment was significantly inversely related to degree of flow modification (rescaled $R^2 = 0.32$, LR $\chi^2 = 13.7$, $P < 0.0002$). *Populus* recruitment probability was highest (> 0.7) along the least altered stream segments and dropped precipitously to < 0.1 at IFM of 0.2 (Fig. 4).

The quadratic relationship between *Populus* abundance and IFM was also significant ($R^2 = 0.30$, $P < 0.0001$; Fig. 5). *Populus* abundance was highest at very low values of IFM and quickly declined as a function of IFM (Fig. 5). Including the random RIVER effect in the model improved the model (AIC_c reduced from 32.8 to 9.2), and the slope parameter was significantly different than 0 ($P = 0.003$). Adding the SEGMENT nested

within RIVER random effect further improved the model ($AIC_c = -3.3$), but the fixed-effect IFM was not significant after accounting for the variation due to this nested effect (Type III test $P > 0.05$).

Tamarix adults were present at 97% of the sites sampled and showed only a 10% difference in abundance between the lower and upper quantiles of IFM (0.64 and 0.74, respectively). In contrast, *Populus* adults declined in abundance from a mean of 0.45 to 0.26 in the upper and lower quantiles. *Tamarix* was present and abundant in the 16 least regulated segments (median abundance of 0.71). *Populus* abundance was 0.72 along these same segments. Along the nine most regulated segments, *Populus* was absent and *Tamarix* had a median abundance of 0.91. *Tamarix* abundance did not account for a significant proportion of the variation in *Populus* abundance at the sites ($R^2 = 0.02$, $P = 0.32$).

Relationships between site, segment and catchment-scale factors, and Populus and Tamarix recruitment and abundance

Eleven percent of the variation in *Tamarix* recruitment was explained by elevation of the site above mean sea level ($P = 0.02$), and the model was significant (LR $\chi^2 = 7.6$, $P = 0.006$). After adding the random effects to the model, elevation remained significant. Probability of *Tamarix* recruitment declined from a probability of 0.9 to < 0.4 over the range of elevations sampled (79–1989 m above mean sea level). Mean *Tamarix* recruitment was not associated with the occurrence of a 5-year recurrence-interval flood during the 5 years prior to sampling

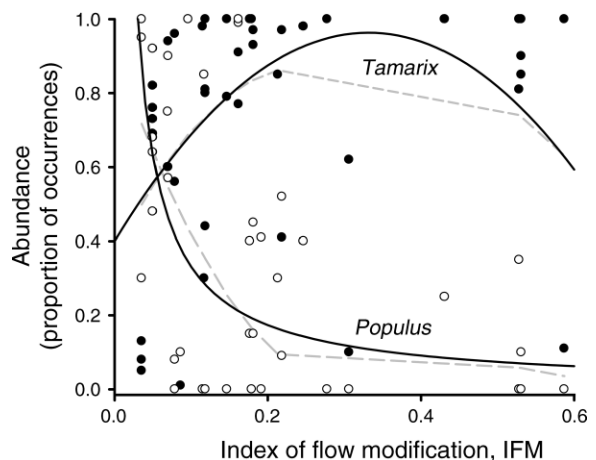


Fig. 5. Models of *Populus* and *Tamarix* abundance as a function of index of flow modification (IFM). Loess regression was used to determine the form of the functions (gray dotted curves, smoothing parameter = 1). The nonlinear power function fitted to *Populus* was significant (solid black line, $P < 0.0001$), indicating that *Populus* abundance declines as a function of flow modification. The polynomial regression fitted to *Tamarix* abundance was also significant ($R^2 = 0.12$, $P = 0.02$), indicating that *Tamarix* abundance is highest at intermediate levels of flow modification. Solid circles represent *Tamarix*, and the open circles show *Populus*.

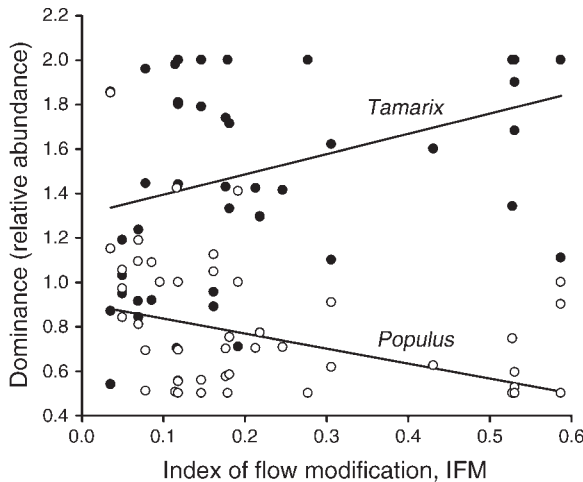


FIG. 6. Models of *Populus* and *Tamarix* dominance (relative abundance) as a function of index of flow modification (IFM). Solid circles represent *Tamarix* and the open circles show *Populus*.

($t = 0.2$, $P = 0.9$). Recruitment was present along 69% of river segments that had not experienced a flood during this time and 66% of segments that had flooded (5 of 24 gages experienced a 5-year flood in last 5 years; Table 1).

Forty-nine percent of the variability in adult *Tamarix* abundance was accounted for by five variables and the model was significant ($R^2 = 0.49$, $P < 0.0001$). *Tamarix* was more abundant along higher order streams (larger watershed area, $P = 0.03$), sites with higher soil pH ($P = 0.02$), sites receiving less precipitation ($P = 0.003$), and along segments with elevated late summer flows ($P = 0.004$). *Tamarix* was less abundant along segments that had elevated 10-year recurrence-interval floods in post-dam time periods ($P = 0.0002$). For *Populus*, 66% of the variability in recruitment was accounted for by four variables, and the model was significant (LR $\chi^2 = 28.4$, $P < 0.0001$). *Populus* recruitment was higher along narrower streams ($P = 0.006$), at lower elevations ($P = 0.05$), on stream segments with an earlier minimum flow ($P = 0.02$), and at sites with earlier peak flow relative to pre-dam periods ($P = 0.008$). Mean *Populus* recruitment was not associated with the occurrence of a 5-year recurrence-interval flood during the 5 years prior to sampling ($t = -0.1$, $P = 0.9$). Recruitment averaged 0.34 on segments that had not experienced a flood during this time and 0.36 on segments that had flooded.

Forty-two percent of the variability in adult *Populus* abundance was accounted for by four variables and the model was significant ($R^2 = 0.42$, $P < 0.0001$). *Populus* abundance was highest along streams in areas receiving more precipitation ($P = 0.03$), and areas with earlier peak flow ($P = 0.04$) and earlier minimum flow ($P = 0.0007$). Sites in which the numbers of flow reversals were fewer also had higher *Populus* abundance ($P = 0.04$).

Dominance of *Populus* and *Tamarix*

The IFM explained 9% of the variation in *Tamarix* dominance (relative abundance) across sites ($R^2 = 0.09$, $P = 0.02$; Fig. 6). Stepwise model selection of site and hydrologic factors resulted in a model that included a negative association with precipitation ($P < 0.001$). *Tamarix* dominance was positively associated with delayed date of minimum flow ($P = 0.001$) and delayed date of maximum (peak) flow ($P = 0.0004$; $R^2 = 0.55$, $P < 0.0001$). Dominance of *Populus* declined significantly as a function of IFM ($R^2 = 0.11$, $P < 0.008$; Fig. 6). Variables selected in stepwise analysis included precipitation ($P < 0.0008$), date of peak flow ($P = 0.001$), and date of low flow ($P = 0.01$). *Populus* dominance scores increased across sites as annual precipitation increased, as peak flows occurred earlier, and as the date of minimum flow occurred earlier.

DISCUSSION

An unresolved question is whether the decline in populations of native species and degradation of many *Populus*-dominated riparian ecosystems can be attributed in part to the presence of nonnative *Tamarix* or whether these effects are confounded with, or fundamentally driven by, altered stream flow regimes (Fig. 1). Our approach was to use an index of flow modification (IFM), which integrates biologically meaningful attributes of flow, to quantitatively examine the relationships between recruitment, abundance, and dominance of two riparian plant species. Our findings are consistent with the literature indicating that flow alteration is associated with the decline of native species via reduced recruitment and degradation of river bottomland habitat (Rood and Mahoney 1990, Rood et al. 2003). Certainly, a number of factors other than flow regime influence *Populus* distributions along rivers; however, our data suggest that even slight modifications in flow regime (IFM > 0.2) dramatically reduce the probability of successful *Populus* recruitment and dominance in riparian woodlands across the region (Figs. 4 and 5). Our findings also suggest that native *Populus* forest decline would have occurred independently of *Tamarix* naturalization and spread along rivers throughout the western United States. Furthermore, our findings shed light on and challenge many of the widely held views about the role of flow alteration in *Tamarix* establishment on western river systems by highlighting the inextricable link between flow alteration, native species decline, and the response of species better suited to the new bottomland conditions.

Stream flow alteration and the decline of native species

We found that *Populus* recruitment, abundance, and dominance were all inversely related to flow modification at the regional scale, corroborating other studies that have shown flow alteration (and associated changes in fluvial processes) to be a principal driving factor in *Populus* decline along rivers in the western North

America (Rood and Mahoney 1990, Braatne et al. 1996). Because *Populus* releases its short-lived seeds in synchrony with the falling limb of the natural hydrograph, it is important that open sites with suitable conditions at appropriate locations above the channel are available during the relatively short period of *Populus* seed dispersal (Fenner et al. 1984; reviewed in Lytle and Merritt 2004). Such sites are created by peak flows of sufficient magnitude to create overbank deposits, build depositional bars, and/or to scour existing vegetation creating bare, moist habitat for seedlings to establish (Scott et al. 1996, Karrenberg et al. 2002). If hydrologic conditions are suitable and *Populus* seedlings establish, they are able to grow rapidly and have been shown to compete well with other species for water, light, and nutrients (Sher et al. 2000, 2002).

In addition to providing the regenerative habitat and establishment conditions for *Populus*, flow regime and associated fluvial processes govern soil moisture conditions (seasonal patterns of soil water availability and depth to groundwater) as well as biogeochemical cycling (e.g., floodplain decomposition, nutrient processing), which influence the extent and distribution of *Populus*-dominated forests (Braatne et al. 1996, Molles et al. 1998, Merritt and Cooper 2000, Valett et al. 2005). Our findings reinforce our understanding of the well-documented relationships between flow regime and *Populus* recruitment and abundance in western North America. Understanding the degree of stream flow naturalness (IFM > 0.8) and the key components in the flow regime necessary to maintain *Populus*-dominated forests has implications for both river management and restoration. These findings suggest that *Populus*-dominated forests can be managed while allowing for only a minimal level of flow alteration (Lytle and Merritt 2004).

Stream flow alteration and nonnative species

Our analysis of this extensive regional data set does not support the widely held notion that river regulation of perennial streams has facilitated or promoted the recruitment of *Tamarix*. We found *Tamarix* recruitment along free-flowing streams to equal or exceed that observed on heavily flow-regulated streams. *Tamarix* recruitment tended to be highest on average along the least regulated segments, but this trend was not statistically significant; mean probability of *Tamarix* recruitment across the entire gradient of flow alteration sampled (IFM of ~0–0.6) was 0.70 (Fig. 4). By contrast, the abundance of mature *Tamarix* was a function of degree of flow alteration (Figs. 4 and 5). In addition, *Tamarix* became increasingly dominant over *Populus* along a gradient of flow regulation (Fig. 6). Examining the life-history traits of *Tamarix* as they relate to components of the flow regime helps to explain this pattern in recruitment and dominance of *Tamarix*.

Recruitment.—At the scale of the western landscape, *Tamarix* can be considered a habitat specialist that

recruits in moist areas such as river floodplains, lake and reservoir margins, irrigation ditches, springs, and vernal pools. Within these areas, however, *Tamarix* may be more appropriately described as a habitat generalist. Within the riverine landscape, *Tamarix* has a wide regeneration niche in that its seedlings may become established over a broader range of soil salinities, textures, and soil moistures than *Populus* and other riparian specialists (Shafroth et al. 1995, Cooper et al. 1999). In the field sites sampled in the current work, *Tamarix* recruitment occurred on soils with pH ranging from 7.2 to 8.9, electrical conductivities ranging from 0.4 to 135 mmhos/cm, sodium levels ranging from 14 to 22 038 mg/L, and soil textures ranging from clay to coarse sand–cobble.

Because *Tamarix* flowers and releases seed later and for a longer duration than native disturbance-adapted species such as *Populus*, it has been suggested that delayed peak flows associated with the storage of runoff in reservoirs may put *Tamarix* at a reproductive advantage over native species (Shafroth et al. 1998, Merritt and Wohl 2002, Stromberg et al. 2007). In warmer climates, *Tamarix* individuals may flower multiple times during the growing season and disperse seeds over a period of several months, extending the “window of opportunity” for establishment and the probability that some seeds will encounter suitable germination and establishment sites at some time during the growing season. Delayed peak flow might reasonably be expected to enhance *Tamarix* recruitment. Nonetheless, the sufficient interannual variability in the timing of *Tamarix* seed release and in the timing of peak flows along relatively unregulated rivers appears to allow for successful *Tamarix* recruitment even under free-flowing conditions. Whereas the timing of peak flow is critical for reproductive specialists like *Populus*, our data suggest that *Tamarix* is less sensitive to the timing of peak flows and is not greatly advantaged by delayed or advanced timing of peaks in its naturalized range.

Because shade inhibits *Tamarix* establishment, the loss of *Populus* overstory due to the flow-related disturbance could open up space for *Tamarix* to invade if subsequent fluvial processes and hydrology are conducive to *Tamarix* establishment (Taylor et al. 1999). The presence of *Populus* forests may inhibit *Tamarix* establishment through shading and competition for water, although mixed stands are not uncommon (Stromberg 1998b; D. M. Merritt, *personal observations*). The loss of *Populus* forest overstory may also increase *Tamarix* productivity in established stands due to increased sunlight and elevated transpiration rates. In addition, *Tamarix* rarely recruits into the understory of stands already dominated by *Tamarix*. Therefore, once formerly active channel margins and bottomland habitat are occupied by *Tamarix* or other colonizing species, the rate of establishment in these areas is likely to decline under regulated flow conditions given the absence or reduction of periodic fluvial

disturbance. Recruitment in these areas is then restricted to shade-tolerant, secondary successional species (Dewine and Cooper 2008). For *Tamarix* to continue to successfully recruit in such areas, occasional fluvial disturbance is necessary to form open sites. On free-flowing and semi-naturally flowing rivers, such habitats are likely to be regularly created, providing periodic opportunities for both native and nonnative species to establish and maintain populations. Indeed, the higher probability of *Tamarix* recruitment associated with lower values of IFM may be explained by the more frequent disturbance events and recruitment site creation on free-flowing rivers (Fig. 4).

Abundance.—In contrast to the recruitment results, we found that there is a strong and significant relationship between the degree of flow alteration and abundance of mature *Tamarix* along the rivers sampled, but this relationship is complex (Fig. 5). *Tamarix* is abundant across a wide gradient of flow alteration, even along rivers in which natural patterns of flooding are maintained, but it is highest along reaches with intermediate levels of hydrologic alteration (between IFM of 0.2 and 0.4). Stromberg et al. (2007) found that *Tamarix* was more abundant along intermittent compared to perennial streams in the American southwest, suggesting that extreme flow regulation (e.g., depleting or dewatering of channels), drying climate, and groundwater depletion and decline may facilitate *Tamarix* abundance and/or lead to decline of native riparian species (Baird et al. 2005, Stromberg et al. 2007).

Along perennial streams like the Colorado River, sites experiencing intermediate fluvial disturbance have been shown to be associated with higher frequency and higher cover of *Tamarix* (Tiegs et al. 2005), a finding consistent with our observation that abundance is highest at intermediate values of IFM (Fig. 5). We suspect that the lower *Tamarix* abundance along relatively free-flowing rivers in our study is explained by biological processes (e.g., competition with native species for light), whereas the decline under severely regulated conditions is explained by the interruption of physical processes necessary for recruitment (fluvial disturbance and new site creation).

Dominance.—There is no question that *Tamarix* has been more successful on floodplains in the arid and semiarid American southwest because of the complementary effects of its generalist traits: high fecundity, long dispersal duration, tolerance of salinity, herbivory, fire, flooding, and drought. It is well-established that *Tamarix* is more tolerant of high soil salinity than many native riparian species and is able to establish and persist in sites with such characteristics (Busch and Smith 1995, Shafroth et al. 1995, Arndt et al. 2004). *Tamarix* foliage is not as palatable as many native species to livestock, wildlife, and insects (Andersen and Cooper 2000, Sexton et al. 2006, Mortenson et al. 2008). Release from Eurasian pathogens and insects in its naturalized range may play some role in *Tamarix* abundance relative to

native species in some circumstances (Lonsdale 1999, Shafroth et al. 2005). *Tamarix* suffers lower mortality than native species following wildfire and may quickly resprout from its root system (Busch 1995, McDaniel and Taylor 2003). Despite these confounding factors, we found a strong relationship between flow regulation and *Tamarix* dominance.

Tamarix is recognized as more drought tolerant than native *Populus*, due both to the ability of *Tamarix* to function well at lower soil water potential than *Populus* (Tyree et al. 1994, Cleverly et al. 1997, Pockman and Sperry 2000, Naumburg et al. 2005) and to the fact that *Tamarix* can develop deep taproots (Gries et al. 2003). Drought tolerance relative to native *Populus* enables *Tamarix* to persist at sites though extended periods of drought, periods of dewatering, conversion of streams from perennial to intermittent (Stromberg et al. 2007), or other water-related circumstances that do not permit survival of native phreatophytic species. The implication is that increasing aridity in the southwestern United States due to climate change (Seager et al. 2007) could disadvantage reproductive specialists and favor generalists such as *Tamarix* along rivers and lead to the formation and persistence of *Tamarix*-dominated riparian woodlands.

Because *Tamarix* recruitment and frequency were high even along the least regulated rivers in this study, we hypothesize that, all other factors held constant (e.g., patterns of human introduction), *Tamarix* would likely have naturalized, spread, and established an important role in riparian communities (coexisting with *Populus* and other native riparian woodland species) in the absence of dam construction, diversions, groundwater pumping, and flow regulation along rivers in arid and semiarid regions of western North America. However, the combination of the decline of native species resulting from altered flows and the pre-adaptation (and generalist traits) of *Tamarix* to the habitat associated with rivers and their floodplains in western North America has contributed to *Tamarix* dominance in many western riparian ecosystems. We conclude that the rapid spread and persistent presence of *Tamarix* along western rivers is not simply a consequence of flow regulation by dam building in the 20th century.

Autogenic changes due to Tamarix presence

The potential for *Tamarix* to alter ecosystem structure and function is broadly recognized (Vitousek et al. 1997), though not well demonstrated (but see Whitcraft et al. 2008). Increased soil salinity, inhibited decomposition/reduced organic material processing, altered nutrient status, changes in fire-related disturbance frequency and magnitude, and stream channel form have all been associated with the establishment and presence of *Tamarix* (Graf 1978, Molles et al. 1998, Valett et al. 2005, Follstad Shah and Dahm 2008, Whitcraft et al. 2008).

Salinity.—Because *Tamarix* is better adapted to high soil salinity than *Populus*, its presence in sites with these characteristics has resulted in poorly supported suppositions that *Tamarix* may be the cause of or a contributor to elevated soil salinity (Busch and Smith 1995, Pataki et al. 2005). There is little empirical evidence that *Tamarix* produces allelopathic chemicals or that *Tamarix* actively concentrates salts in the soil at levels that could inhibit establishment of native species (but see Di Tomaso 1998, Laudenberg et al. 2006). *Populus* and other glycophytic riparian species are intolerant of highly saline soils and may suffer from leaf necrosis, reduced transpiration, and inhibited water and nutrient uptake in highly saline soils (Busch and Smith 1993, Chen et al. 2003).

One factor associated with some forms of river regulation is isolation of floodplains from rivers which can result in chronic drying of soils and elevated soil salinity. Soil salinization is a function of reduced flooding, evaporation, agricultural practices, and elevated water table associated with river regulation (Jolly et al. 1993). Indeed, sodium absorption ratio increased as a function of IFM at our sites ($R^2 = 0.11$, $F = 3.3$, $P = 0.04$). Soil salinity and other factors associated with flow regulation may put *Tamarix* at a competitive advantage over some native riparian dominants (e.g., *Pluchea sericea*, *Baccharis salicifolia*, *Populus fremontii*, and *Salix gooddingii*) under conditions of elevated soil salinity and drought stress (Stromberg 1998a, Vandersande et al. 2001). Altered soil properties are likely to contribute to *Tamarix* establishing dominance over native species along regulated rivers (Busch and Smith 1995, Glenn et al. 1998, Lite and Stromberg 2005).

Fire.—It is recognized that invasive nonnative species that modify disturbance regimes can have the greatest impact to ecosystems (D'Antonio 2000). One means by which *Tamarix* and other invasive plant species can affect species composition and ecosystem properties is through its effect on fire regimes in riparian areas. *Tamarix* produces flammable biomass that can influence the frequency and intensity of fires, causing the mortality of fire intolerant native species, such as *Populus* and several species of *Salix* (D'Antonio and Vitousek 1992, Busch 1995). Indirect effects of river damming such as increased fire frequency and intensity due to fuel accumulation in drier riparian habitats may explain the increase in *Tamarix* abundance observed at several sites at the highest levels of flow modification in this regional study (Fig. 5).

Channel narrowing.—There is a perceived linkage between *Tamarix* spread and channel narrowing. This has likely come, in part, from isolated periods of opportunistic establishment along formerly active channel margins immediately following dam closure, as has been reported along regulated rivers throughout the western United States (Graf 1978, 2006, Everitt 1998, Merritt and Cooper 2000). This vegetation may stabilize banks and enhance sediment deposition when flooding

does occur (Allred and Schmidt 1999). Although *Tamarix* may initially take advantage of exposed river margins in the years following dam construction, the opportunities for *Tamarix* establishment diminish through time on regulated rivers (Graf 2006). Our data strongly suggest that *Tamarix* is able to periodically and opportunistically recruit in regulated rivers due to occasional flood-related habitat creation rather than a direct coupling of life-history attributes to regulated conditions under the altered flow regime per se.

The generalist life-history traits of *Tamarix* and its tolerance of high soil salinity, drought, and fire suggest that it could be an “interactive” rather than “competitive” species (sensu Macdougall and Turkington 2005). *Tamarix* may be a passenger, merely establishing dominance due to its wide ecological amplitude and ability to tolerate conditions of both regulated and unregulated systems. There are several examples of *Populus* decline along regulated streams in the absence of *Tamarix*, further suggesting independence in a direct interspecific pattern (Rood et al. 1995, Scott et al. 1997). There is little evidence suggesting that *Populus* and *Tamarix* directly interact for limiting resources; however, is it likely that when water is limiting, *Tamarix* may exacerbate stress to native species through lowering groundwater levels and/or desiccating soils.

Flow regime and implications for Tamarix control and river restoration

There is discussion throughout the western United States and worldwide about implementing prescribed floods to hinder nonnative species establishment or to prevent spread along flow-regulated rivers (Merritt and Wohl 2002, Shafroth et al. 2005, Tieggs et al. 2005, Stromberg et al. 2007). It has been suggested that restoring appropriately timed flooding might inhibit *Tamarix* through interrupting dispersal and establishment (Merritt and Wohl 2002, Harms and Hiebert 2006, Beauchamp and Stromberg 2007). We found no significant repression of *Tamarix* recruitment under even the most “natural” flow regimes examined (Fig. 5). Instead we found the highest recruitment of *Tamarix* at the lowest levels of flow alteration. We attribute this pattern to the characteristics of the regeneration niche of *Tamarix*. Occasional flow-related disturbances create bare patches that are more “invasible” than older patches, providing more opportunities for well-dispersed colonizing species like *Tamarix* to become established along free-flowing river margins compared to more static, stable habitats associated with regulated flows (Planty-Tabacchi et al. 1996).

Flood-driven recruitment of *Tamarix* has been reported for rivers on the Colorado Plateau (Cooper et al. 2003, Birken and Cooper 2006) and in the American semidesert (Whiteman 2006). During our surveys, we aged (using growth ring counts) several *Tamarix* stems along the relatively free-flowing San Miguel River in the upper Colorado River basin and found that a quite

extensive cohort had become established following a year with exceptionally high peak flows and a relatively wet summer (1983). Along the free-flowing Yampa River in the upper Colorado River basin, Cooper et al. (2003) found that *Tamarix* establishment had occurred regularly over the past half-century despite relatively natural flow regimes. Cooper et al. (2003) also noted that *Tamarix* recruitment occurred regularly along the free-flowing pre-dam Green River and occasionally (associated with floods) following dam construction. Another study along the Green River found that 90% of *Tamarix* recruitment occurred in years with floods exceeding the 2.5-year recurrence-interval flow in both pre-dam and post-dam periods (Birken and Cooper 2006). At our sites, *Tamarix* recruitment exceeded that of *Populus* across a broad range of flow alteration, including relatively free-flowing conditions (IFM from 0.04 to 0.59). *Tamarix* has many adaptations to arid riverine environments and natural flow regimes in its Eurasian home-range (Gaskin and Schaal 2002). Indeed, declines of *Tamarix* populations on rivers in northern China have been attributed to flow alterations that include reductions in peak flow (Si et al. 2007).

Given the fact that floods create regenerative habitat for *Tamarix* (as well as for native species) and that successful *Tamarix* recruitment was no lower along the least regulated streams surveyed in this work, we believe care should be taken to develop realistic expectations for the outcome of managed floods downstream from dams. Managed flooding, unless catastrophic or extremely restrictive, is unlikely to significantly hinder *Tamarix* establishment. This has led to some cautionary advice about controlled releases of water under circumstances that could facilitate *Tamarix* establishment (Birken and Cooper 2006). However, we argue that the benefits of using flows to restore native species arguably outweigh the cost of accommodating nonnative species in the process because of the many other ecosystem benefits associated with flooding. For example, flooding is vital to the maintenance and restoration of riparian vegetation that is governed by patterns of natural disturbance, microbial activity, decomposition and nutrient cycling, seed delivery, groundwater recharge, and a host of other flow-driven processes (Junk et al. 1989, Molles et al. 1998, Valett et al. 2005, Follstad Shah and Dahm 2008). Furthermore, based on our extensive survey, overbank flooding benefits *Populus* establishment and abundance and is therefore likely to reduce the likelihood of *Tamarix* becoming dominant over native species in riparian plant communities.

Our findings strongly suggest that restored flooding alone will not serve to remove or eliminate *Tamarix* from western riparian ecosystems; however, high flows are essential for the recruitment and persistence of *Populus* in these ecosystems. Given that mixed *Tamarix*-*Populus* stands have high ecological value (Stromberg 1998b), a reasonable restoration goal for *Tamarix*-dominated ecosystems would be to proactively manage

for *Populus* recruitment and maintenance using prescribed flows. Mechanical removal of dense *Tamarix* stands also may be necessary to open up space for native species, as older stands are relatively resistant to scouring (Friedman and Auble 1999), but control of *Tamarix* alone is unlikely to result in recovery flood-dependent *Populus* in the absence of altered flow management or natural flooding (Nagler et al. 2005).

If the management objective is to recover *Populus* and other native riparian species, the question of what specific attributes of the flow regime (e.g., timing, magnitude, seasonal variation, rates of change) should be restored arises. Some have suggested that high flows precisely timed to the peak of *Populus* seed release could maximize *Populus* recruitment success and inhibit later dispersing *Tamarix* (Levine and Stromberg 2001). However, the seed-release period of *Tamarix* and *Populus* coincide for a portion of the growing season in most regions (Shafroth et al. 1998, Cooper et al. 1999); thus managing flow by rigidly restricting the hydrograph for the sole purpose of inhibiting *Tamarix* is problematic and potentially harmful to *Populus* and other native species. Restricting the hydrograph to one single peak or short duration to advantage *Populus* would likely prove detrimental to many other native species that require gradual drawdown and shallow groundwater for root elongation during early establishment (Mahoney and Rood 1998, Amlin and Rood 2002, Karrenburg et al. 2002). Further, many native riparian species that benefit from or require occasionally late peak flows or drought years would likely be adversely affected by restricted flows designed to accommodate only *Populus* and to inhibit *Tamarix*. We would argue for a more holistic approach to riparian flow management in which managed flows are designed within the natural range of variability in magnitude, timing, and duration of historic peaks, to the benefit of the broader riparian community while ensuring some *Populus* recruitment.

The debate continues as to the relative ecological "value" and function of *Tamarix*-dominated, mixed native and nonnative, and pure native-dominated riparian stands. Some studies suggest that mixed stands of *Tamarix* and native vegetation rival completely native-dominated stands in richness of birds, insects, and rodents (Ellis et al. 1997, Andersen and Nelson 1999, Sogge et al. 2008, van Riper et al. 2008). Stromberg (1998b) suggests that nonnative *Tamarix* stands may be functionally equivalent to native *Populus*-dominated stands. Managing flows to restore functional attributes of riparian areas may prove a preferred alternative to stream flow management aimed at one or a few species.

CONCLUSION

The region we sampled in this study is among the most arid in North America, yet it is experiencing very rapid human population growth rates and an associated

continuing demand for development of water infrastructure (Barnett et al. 2008). Already heavy regional levels of river regulation are expected to increase over the next several decades with potentially serious impacts on riparian ecosystems (Graf 1999, Lytle and Merritt 2004). Depleted streamflow can result in decreased alluvial groundwater levels capable of inducing drought stress on riparian vegetation; reduced frequency of high-magnitude flood events can prevent the creation of regenerative habitat; and, altered timing of flow can decouple flows during key phenological times in plant development and growth (Nilsson and Svedmark 2002). All streams inventoried have some degree of human water development in the form of groundwater pumping, diversions, and dams, and most are subjected to each at some point throughout their drainage networks and demands for water will continue to intensify (Barnett et al. 2008).

Tamarix was present along all rivers sampled in this study. We did not find that *Tamarix* was more abundant along perennial rivers with lower total mean annual discharge; however, we did find significant relationships between the degree of stream flow alteration (IFM) and the relative success of native *Populus* and nonnative *Tamarix*. Understanding patterns and relationships between flow alteration and the recruitment and abundance of nonnative species is critical to informing decision making in river management, especially in this era of environmental flow prescription and experimental flooding to attain ecological goals. Our findings have implications for how we set objectives for the restoration of flow-altered streams, for what sorts of yields we should realistically expect on investments in conducting prescribed flow releases, and for what kinds of interventions may be necessary to control and manage nonnative plant species along western North American rivers where it is desirable. Because plant establishment, vegetation change, and shifts in dominance may be a multi-staged process, there are several mechanisms that explain the invasion success of *Tamarix* into riparian ecosystems of the American southwest. Our findings suggest that implicating *Tamarix* as the sole driver in the decline of western riparian ecosystems is too simplistic. Flow alteration has likely been the principle cause of the decline of native-dominated riparian ecosystems in western North America, and it may have facilitated dominance of some riparian communities by *Tamarix* (Fig. 1). The simultaneous collapse of *Populus*-dominated ecosystems both within and outside of the naturalized range of *Tamarix* suggests that such collapse would likely have occurred in the western United States in the absence of *Tamarix*. Furthermore, the success of *Tamarix* along the entire gradient of flow alteration suggests that *Tamarix* would be an important component of western riparian ecosystems even in the absence of water development. Our findings clearly suggest that active management for natural hydrograph characteristics downstream from dams is likely to decrease the

likelihood of *Tamarix* establishing dominance over native species in riparian ecosystems. Such active management will also provide a range of ecological benefits that removal of invasive species alone will not accomplish.

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