Distribution of invasive and native riparian woody plants across the western USA in relation to climate, river flow, floodplain geometry and patterns of introduction

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Management of riparian plant invasions across the landscape requires understanding the combined influence of climate, hydrology, geologic constraints and patterns of introduction. We measured abundance of nine riparian woody taxa at 456 stream gages across the western USA. We constructed conditional inference recursive binary partitioning models to discriminate the influence of eleven environmental variables on plant occurrence and abundance, focusing on the two most abundant non-native taxa, *Tamarix* spp. and *Elaeagnus angustifolia*, and their native competitor *Populus deltoides*. River reaches in this study were distributed along a composite gradient from cooler, wetter higher-elevation reaches with higher stream power and earlier snowmelt flood peaks to warmer, drier lower-elevation reaches with lower power and later peaks. Plant distributions were strongly related to climate, hydrologic and geomorphic factors, and introduction history. The strongest associations were with temperature and then precipitation. Among hydrologic and geomorphic variables, stream power, peak flow timing and 10-yr flood magnitude had stronger associations than did peak flow predictability, low-flow magnitude, mean annual flow and channel confinement. Nearby intentional planting of *Elaeagnus* was the best predictor of its occurrence, but planting of *Tamarix* was rare. Higher temperatures were associated with greater abundance of *Tamarix* relative to *P. deltoides*, and greater abundance of *P. deltoides* relative to *Elaeagnus*. *Populus deltoides* abundance was more strongly related to peak flow timing than was that of *Elaeagnus* or *Tamarix*. Higher stream power and larger 10-yr floods were associated with greater abundance of *P. deltoides* and *Tamarix* relative to *Elaeagnus*. Therefore, increases in temperature could increase abundance of *Tamarix* and decrease that of *Elaeagnus* relative to *P. deltoides*, changes in peak flow timing caused by climate change or dam operations could increase abundance of both invasive taxa, and dam-induced reductions in flood peaks could increase abundance of *Elaeagnus* relative to *Tamarix* and *P. deltoides*.

Rivers are sources of water and nutrients, agents of physical disturbance and corridors for dispersal, rendering floodplains susceptible to biotic invasion (DeFerrari and Naiman 1994, Stohlgren et al. 1998), with consequences for ecosystem function and services (Gregory et al. 1991, Strange et al. 1999). Climate, flow of water and sediment, floodplain geometry, land-use management and patterns of introduction interact to control plant invasions along river corridors (Corenblit et al. 2007, Araujo and Peterson 2012). Despite this interaction, these factors are infrequently examined together to understand spatial patterns of native and non-native plants.

Distributions of riparian species are strongly influenced by interactions between physical and ecological processes (Patten 1998, Nilsson and Svedmark 2002, Merritt et al. 2010). For example, patterns of establishment in any year are influenced by propagule dispersal in relation to flow timing, magnitude and duration, as well as channel geometry

and weather (White 1979, Scott et al. 1996, Auble and Scott 1998, Mahoney and Rood 1998). Understanding these pattern–process relationships is necessary to design water management strategies that promote native species, or to predict how a change in climate or land-use management would affect populations of target species (Palmer et al. 2009, Perry et al. 2012).

Riparian ecosystems of interior western North America provide an excellent opportunity to examine how these interacting factors influence occurrence and abundance of native and non-native woody plants. Introduced trees and shrubs dominate many riparian ecosystems across the region. In particular, the introduced saltcedar *Tamarix* spp. and Russian-olive *Elaeagnus angustifolia* are now the third and fourth most frequently occurring (i.e. percentage of the sites surveyed where they were present), and the second and fifth most abundant woody riparian plants across this landscape, replacing woodlands once dominated by cottonwood

Populus spp. (Friedman et al. 2005). The successful invasions of *Tamarix* and *Elaeagnus* have been linked to climate, flow variability and intentional introduction (Nagler et al. 2011). Finally, analyses of relationships between flow and vegetation in the region are facilitated by a system of abundant stream gages, many in continuous operation for over twenty years, with uniform data collection overseen by the U.S. Geological Survey.

Tamarix and *Elaeagnus* were introduced to North America as drought-tolerant trees for landscaping and erosion control. *Tamarix* was naturalized in the western USA by the late 1800s (Chew 2009), and *Elaeagnus* by the early 1900s (Katz and Shafroth 2003). Both plants were distributed extensively to construct shelterbelts for controlling wind erosion during and after the Dust Bowl (Read 1958), *Tamarix* was planted widely to combat fluvial erosion (Robinson 1965), and *Elaeagnus* was promoted to provide edible fruit and woody cover for birds (Christensen 1963). More recently, because of concerns about water use and habitat degradation, governmental promotion of these plants has ended in the western USA, although both are still offered for sale. Both plants are targets of eradication campaigns, and *Tamarix* is the target of a biocontrol program (Nagler et al. 2014). Examples of dramatic spread of both plants following local introduction have been reported (Graf 1978, Lesica and Miles 1999, Pearce and Smith 2003), but it is unknown to what extent planting continues to influence their spread at the sub-continental scale. In comparison to *Tamarix*, *Elaeagnus* should have relatively slow dispersal because it produces small numbers of less mobile seeds, although edible fruits can aid *Elaeagnus* dispersal (Katz and Shafroth 2003). In the western USA, the two taxa have similar frequency of occurrence, but *Tamarix* occupies a much larger area (Friedman et al. 2005). This pattern may suggest that the total suitable area is less for *Elaeagnus* than for *Tamarix*. Alternatively, it may suggest that the more slowly dispersed *Elaeagnus* is at an earlier phase of its invasion with a greater potential for future increases in area.

Physiological studies provide clear expectations about the effect of climate on distribution of *Populus*, *Tamarix* and *Elaeagnus*. Relative to *Populus*, *Tamarix* is more tolerant of summer drought and high salinity (Busch and Smith 1995). For example, when grown in 4 ppt NaCl, *Populus* from the Colorado River Delta wilted at 10% soil moisture while *Tamarix* wilted at 3% (Vandersande et al. 2001). This leads to the expectation that, all other factors being equal, *Tamarix* should be favored over *Populus* by higher temperature and lower precipitation. At the other temperature extreme, *Tamarix* is relatively intolerant of winter cold. *Tamarix* from latitude 35°N was killed in midwinter by a temperature of −41°C, while *Populus deltoides* from the same latitude survived at −70°C (Friedman et al. 2011), and *Elaeagnus* from latitude 52°N survived down to −55°C (Gusta et al. 1983), suggesting that cold temperatures should favor *Populus* and *Elaeagnus* over *Tamarix*.

Differential effects of flow on survival and reproduction of *Populus*, *Tamarix* and *Elaeagnus* should also separate these taxa along hydrologic gradients. The superior drought tolerance of *Tamarix* should favor it relative to *Populus* where low flows are extreme (Busch and Smith 1995, Glenn and Nagler 2005). As pioneers, both *Populus* and *Tamarix* produce many small seeds that disperse readily by wind and water to become established on bare, moist surfaces such as recently deposited alluvial sediment (Auble and Scott 1998, Merritt and Poff 2010). *Populus* seeds are released in early summer, often at the time of peak flows in snowmelt-dominated systems (Scott et al. 1997, Mahoney and Rood 1998). *Tamarix* has a later and more prolonged period of seed release, which may provide an advantage in systems with less predictable flow peaks or along regulated rivers experiencing delayed peaks (Glenn and Nagler 2005). In contrast to *Populus* and *Tamarix*, *Elaeagnus* produces fewer, larger dormant seeds with sufficient energy reserves to enable establishment beneath existing vegetation (Katz et al. 2001). Therefore, *Elaeagnus* should not be strongly influenced by flow timing. Finally, fewer seeds and slower dispersal may disadvantage *Elaeagnus* relative to *P. deltoides* and *Tamarix* when site disturbance is frequent (Katz and Shafroth 2003).

Climate, streamflow, floodplain geometry and the history of introduction have been examined as predictors of introduced and native species distribution individually and in limited combinations. These factors are not well-studied in conjunction, however, especially at the regional to continental scale. Reach-scale studies describing riparian vegetation patterns have emphasized flood disturbance and moisture availability as the principal drivers of establishment and persistence (Scott et al. 1997, Cooper et al. 2003, Webb and Leake 2006). At the scale of a drainage network, theoretical and remote-sensing studies have identified strong links between species incidence and hydrologic and geomorphic gradients (Muneepeerakul et al. 2007, 2008). Regional-scale studies have shown effects of hydrologic alteration from reservoir construction on relative abundance of *Populus* and *Tamarix* (Friedman et al. 1998, Stromberg et al. 2007, Merritt and Poff 2010, Mortenson and Weisberg 2010). Yet, small sample sizes, non-random sampling, incomplete sets of environmental variables and limited spatial extent limit the conclusions that can be drawn from these studies. The most extensive analysis to date, a survey of invasive plants in twelve western states on 1316 stream reaches at least 160 m long (Ringold et al. 2008), found downstream increases in riparian invasive species, but did not relate this pattern to flow. Multivariate distribution models constructed for these plants at the sub-continental scale have shown strong effects of temperature, precipitation and sometimes distance to water (Morisette et al. 2006, Evangelista et al. 2008, Jarnevich et al. 2011, Nagler et al. 2011), but have not considered flow variability, channel dimensions or patterns of introduction.

Accordingly, we used a large sample size and random sampling across a large area (the western USA) to ensure a representative sample and to overcome local correlations among environmental variables. Sites were located close to long-term U.S. Geological Survey stream gages to permit the detailed characterization of flow regime attributes, and we implemented a hierarchical variable partitioning approach (Hothorn et al. 2006) suited to distinguishing among multiple environmental controls in the presence of non-linearity, correlation among variables and hierarchical effects. We modeled the occurrence and abundance of nine widespread riparian trees and shrubs, emphasizing *Elaeagnus*, *Tamarix* and *P. deltoides*, given their broad management importance.

This analysis tested the following specific hypotheses: 1) *Tamarix* is more abundant than *P. deltoides* or *Elaeagnus* in hotter, drier climates; 2) extreme low flows (relative to the mean) favor *Tamarix* relative to *P. deltoides*; 3) flood disturbance favors *Tamarix* and *P. deltoides* over *Elaeagnus*; 4) *P. deltoides* is more sensitive than *Tamarix* or *Elaeagnus* to flood timing and is favored by earlier peak flows (relative to the date of the last frost); and 5) occurrence of introduced *Elaeagnus* and *Tamarix* is strongly associated with intentional planting.

Methods

Occurrence and abundance data

During 1997–2002, we surveyed the occurrence and abundance of 44 riparian trees and shrubs within 456 floodplains near U.S. Geological Survey gaging stations in the 17 western states. The study area was the dry inland western USA, including all of the conterminous USA west of the 100th meridian except for the humid zones west of the Cascade Range in Washington and Oregon and the northern Sierra Nevada in California (Fig. 1). Sites were randomly selected from the set of all gages in this area with at least 20 yr of daily discharge data during 1965–1994. The data and a detailed description of field methods are included in Auble et al. (2012). In this study, we modeled the nine most frequently occurring trees and shrubs (Table 1): the natives *Acer negundo*, *Cornus sericea*, *Fraxinus pennsylvanica*, *Salix amygdaloides*, *S. exigua*, *Populus angustifolia* and *P. deltoides*; and the non-natives *Elaeagnus angustifolia* and *Tamarix* spp., which included the closely related *T. ramosissima*, *T. chinensis* and their hybrids, but not *T. parviflora* or *T. aphylla* (Friedman et al. 2005, Gaskin and Kazmer 2009, Auble et al. 2012). Taxonomic nomenclature follows NRCS (2014) with two exceptions necessitated by the difficulty of making
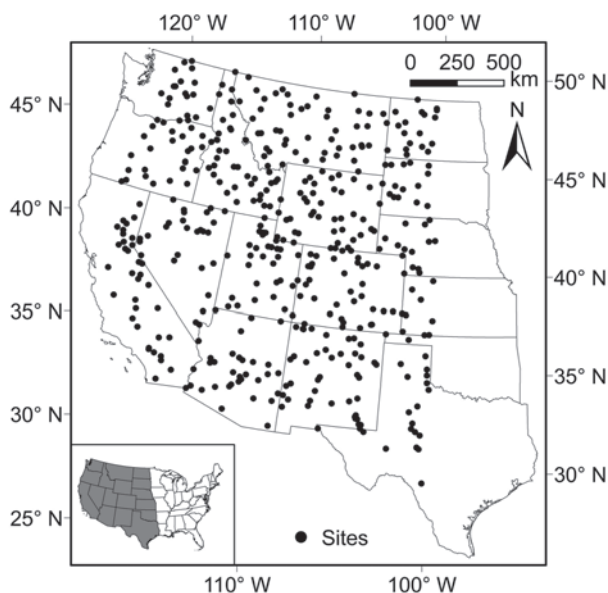
Table 1. Descriptive statistics for nine taxa and eleven environmental variables used in the analysis. Taxonomic nomenclature follows NRCS (2014). Median and range data for each taxon refer to its abundance (percentage of the floodplain area at a site covered by the canopy of that taxon) only at sites where it occurred; n = the number of presences for each taxon at 456 sites.

	n	Median	Range
Populus deltoides ssp. *monilifera* (Aiton) Eckenw. and ssp. *wislizeni* (Watson) Eckenw., and *P. fremontii*	186	10.6	<0.01–73.0
Elaeagnus angustifolia L.	139	0.9	<0.01–73.4
Tamarix ramosissima Ledeb., *T. chinensis* Lour. and hybrids	140	13.2	<0.01–95.0
Acer negundo L.	95	2.8	<0.01–60.0
Cornus sericea L.	110	1.4	<0.01–72.2
Fraxinus pennsylvanica Marsh.	75	1.5	<0.01–50.0
Populus angustifolia James	83	17.5	<0.01–85.0
Salix amygdaloides Anderss.	109	2.3	<0.01–50.0
Salix exigua Nutt.	299	3.9	<0.01–100
Growing degree-days (°C-days)		1327.5	196–4744
Mean annual precipitation (mm)		358.5	75–2175
Peak flow timing (days)		4.29	–176.7–181.0
Peak flow predictability (0–1)		0.74	0.07–0.99
Seasonal low flow[a]		0.15	0.00–1.50
Mean annual flow (m³ s⁻¹)		4.15	<0.01–3205.2
10-yr flood[a]		19.5	1.68–43947.1
Stream power (N m⁻¹ s⁻¹)		59.9	0.17–2366.6
Channel confinement (m m⁻¹)		5.42	0.97–416.1
Past grazing (1, 2, 3, 4)		1	1–4
Observation of *Elaeagnus* planted near site (0, 1)	129[b]	0	0–1

[a]Scaled to mean annual flow, and hence dimensionless.
[b]Number of sites where intentional planting was observed nearby.

unambiguous distinctions in the field: we lumped *Salix interior* and *S. melanopsis* with *S. exigua*, and we lumped *Populus fremontii* with *P. deltoides*. Abundance was measured as the percentage of the floodplain area at a site covered by the canopy of each taxon.

Environmental variables

We analyzed plant occurrence and abundance relative to two climatic variables, seven hydrogeomorphic variables, two variables indicating patterns of non-native plant introduction, and one variable indicating intensity of livestock grazing (Table 1). By hydrogeomorphic variables, we mean variables related to streamflow, floodplain geometry or both. We obtained the climatic variables growing degree-days and mean annual precipitation from gridded weather station data at 2-km resolution collected from 1961–1990 (The Climate Source, Corvallis, OR, USA; <www.climatesource.com/>). Although temperature and precipitation influence plant physiology in many ways, the overall influence of climate on vegetation is two-dimensional (Stephenson 1998). Therefore, to avoid inclusion of highly correlated climate variables in our models, we winnowed the set of potential temperature and precipitation variables to two (growing degree-days and mean annual precipitation) that

Figure 1. Study area in the western USA showing the 456 sites surveyed (Auble et al. 2012).

were physiologically relevant and highly correlated with vegetation gradients throughout the study region.

We produced hydrogeomorphic variables from the daily discharge record associated with each site in combination with aerial photographs and topographic maps (Auble et al. 2012). The success of seedling establishment is influenced by timing of peak flows relative to timing of seed dispersal. Timing of seed dispersal for our sites is unknown, and accurate phenological models for predicting it are unavailable. Therefore, to capture the relationship between peak flow timing and plant reproduction, we measured the average annual difference between the Julian Day of instantaneous peak flow and that of last frost (peak flow timing). To characterize interannual variation in the Julian Day of instantaneous peak flow (peak flow predictability), we calculated the relative length of the circular vector (Zar 2009), with values increasing from 0 to 1 as annual peak flows occurred on increasingly similar dates. We calculated mean annual flow ($m^3 \, s^{-1}$) by averaging over all records. We computed the 10th percentile of mean daily flow during the growing season (seasonal low flow) and the 10-yr recurrence interval annual peak flow (10-yr flood) (USGS 1982); both variables were scaled to mean annual flow. We calculated unit stream power, the rate of energy expenditure per unit area of channel boundary (Bagnold 1966), from channel gradient, active channel width (Hedman and Osterkamp 1982), and the annual peak flow with a 2-yr recurrence interval (USGS 1982). We estimated channel confinement by dividing floodplain width by active channel width, with values increasing as channels became decreasingly confined. We recorded the occurrence of intentionally planted *Elaeagnus* and *Tamarix* within 5 km of a site; however, planted *Tamarix* was found to be rare (< 2% of sites), so we removed this variable from the analysis. Finally, we characterized long-term intensity of grazing by livestock and wild ungulates (past grazing) on an ordinal scale of 1 to 4 based on the extent of grazing-induced anatomical alterations to shrubs, prominence of annual and biennial species favored by grazing, abundance of shrub regeneration, and erosion of banks due to trampling (Auble et al. 2012).

Statistical analyses

In a preliminary analysis, we evaluated Spearman's rank correlations among the environmental variables to assess the degree of multicollinearity (Supplementary material Appendix 1, Table A1). We used R for all statistical analyses (R Development Core Team; <www.r-project.org/>). We fit univariate logistic regressions of taxon occurrence against each factor to reveal basic patterns in the data (Supplementary material Appendix 1, Table A2; glm function in R stats package), and we conducted a canonical correspondence analysis to examine the overall relationships between occurrence and composite environmental gradients (cca function in R vegan package).

The set of environmental variables in this analysis included both continuous and categorical variables. At the sub-continental scale, they were sometimes moderately correlated (Supplementary material Appendix 1, Table A1), and often had non-linear or hierarchical relationships with plant distribution. Therefore, we applied conditional inference (CI) binary recursive partitioning (Hothorn et al. 2006) to investigate our hypotheses and to identify and quantify hierarchical thresholds in the environmental variables related to occurrence, abundance and relative abundance. This modeling technique accommodates a range of variable types and distributions as well as non-linear variable interactions. Like standard classification and regression tree techniques (De'ath and Fabricius 2000), CI trees are fit iteratively, but for each hierarchical set of observations, a permutation test is evaluated relative to the null hypothesis of independence between the response and each predictor at a pre-specified significance level (e.g. $\alpha = 0.05$); we applied a Bonferroni correction method to the significance level to maintain the family-wise error rate for multiple hypothesis tests. If the null hypothesis is rejected, the observations are split into the most homogenous groups (nodes) that can be produced for a value of the most significant covariate, and splitting continues until the null hypothesis is no longer rejected. We also constructed CI forests (Strobl et al. 2007) to reveal environmental variables that were masked by the highest ranked covariate for a particular split in the individual CI trees. A conditional inference forest adapts the random forests method (Cutler et al. 2007) by generating multiple CI tree models from random subsets of explanatory variables. The result is a table ranking the environmental variables by their overall importance across all trees. To model CI trees and forests, we used the ctree and cforest functions in the R party package.

We built CI tree and forest models for occurrence of each taxon on the ten variables describing climate, hydrogeomorphology and grazing, and we fit an extra CI tree model of *Elaeagnus* occurrence that also included a variable for intentionally planted *Elaeagnus*. We constructed CI models with abundance as a response for the same ten variables for *P. deltoides*, *Elaeagnus* and *Tamarix*. We also modeled the abundance of *P. deltoides* relative to *Elaeagnus* and *Tamarix* to more directly test our hypotheses on relative abundance. Because *P. deltoides* is long-lived (Merigliano et al. 2013), presence of old trees may reflect hydrologic events prior to the 30-yr period of streamflow records examined in this study. Taking advantage of the fact that cottonwood age can be visually estimated from size and bark characteristics (Merigliano et al. 2013), we separately quantified abundance of trees older and younger than 30 yr, and separately modeled the abundance of *P. deltoides* stands in these two age-classes.

Results

Patterns of occurrence

Tamarix occurred at the warmest sites (growing degree-days = 2677°C-days), which averaged about 1000 more growing degree-days than sites occupied by *P. deltoides* or *Elaeagnus* (Table 2). *Elaeagnus* and *Tamarix* occurred at the driest sites (mean annual precipitation = 283 and 291 mm), which averaged around 65 mm less precipitation than sites occupied by *P. deltoides*. *Cornus sericea* and *P. angustifolia* occupied the coldest sites (growing degree-days = 877 and 916°C-days), while *C. sericea*, *Fraxinus pennsylvanica* and *Acer negundo* occupied the wettest sites

Table 2. Descriptive statistics (means) for ten environmental variables at sites where any of the nine taxa occurred. Means for each taxon are weighted by its abundance at sites where it occurred. The most extreme values for each variable are shown in bold.

	Growing degree-days	Mean annual precipitation	Peak flow timing	Peak flow predictability	Seasonal low flow	Mean annual flow	10-yr flood	Stream power	Channel confinement	Past grazing
P. deltoides	1681	352	36.9	0.68	0.22	43	115	129	16	1.5
E. angustifolia	1614	**283**	26.3	0.73	0.23	32	43	117	13	1.4
Tamarix spp.	**2677**	291	**60.4**	**0.61**	**0.14**	33	**246**	93	18	1.2
A. negundo	1305	425	−3.7	0.72	0.15	13	67	102	19	1.3
C. sericea	**877**	**439**	**−27.2**	0.81	**0.37**	**13**	**19**	181	**5**	**1.1**
F. pennsylvanica	1478	428	4.7	0.67	0.19	28	84	**47**	**24**	1.5
P. angustifolia	916	368	0.3	**0.86**	0.37	16	25	**211**	15	1.3
S. amygdaloides	1371	361	4.0	0.70	0.28	42	41	131	16	**1.5**
S. exigua	1203	363	−2.2	0.76	0.25	**44**	34	137	8	1.3

(mean annual precipitation = 439, 428 and 425 mm). *Cornus sericea* also occurred at sites with the earliest timing of peak flow relative to last frost (−27 d). Sites occupied by *Elaeagnus*, *P. deltoides* and *Tamarix* experienced flooding an average of 26, 37 and 60 d after last frost. *Tamarix* also occupied sites exhibiting the least interannual consistency in peak flow timing on average (peak flow predictability = 0.61), whereas sites occupied by *P. angustifolia* displayed the greatest average regularity (peak flow predictability = 0.86). *Salix exigua*, *P. deltoides* and *S. amygdaloides* occurred at sites with the largest average mean annual flow (44, 43 and 42 m³ s⁻¹), whereas *Tamarix* occurred at sites with both the lowest average seasonal low flow (0.14 × mean annual flow) and the highest 10-yr flood (246 × mean annual flow). Sites occupied by *F. pennsylvanica* had the lowest average stream power (47 N m⁻¹ s⁻¹) and channel confinement (24), whereas *P. angustifolia* and *C. sericea* occurred at sites having the highest average stream power (211 N m⁻¹ s⁻¹) and channel confinement (5), respectively.

Occurrence models for nine taxa

Variation in vegetation and environment was dominated by a single composite gradient from cool, wet sites with high stream power and early, predictable floods to warm, dry sites with low power and late or unpredictable floods. In the canonical correspondence analysis (Fig. 2), this primary axis ($\lambda = 0.336$) accounted for more than eight times as much environmental variation as the second axis ($\lambda = 0.041$). *Tamarix* was positioned at the warm end of this gradient, followed by *P. deltoides* and *Elaeagnus* (Fig. 2). *Cornus sericea* and *P. angustifolia* fell at the cool extreme, with *Salix exigua*, *S. amygdaloides*, *Fraxinus pennsylvanica* and *Acer negundo* occupying intermediate positions (Fig. 2).

Temperature and precipitation were usually the most important environmental variables in conditional inference (CI) models of occurrence. Growing degree-days was the most important environmental variable in CI forest models for six of nine taxa and was among the top three variables for all nine taxa (Table 3). Conditional inference tree models for occurrence of *P. deltoides* and *Tamarix* contained significant splits on growing degree-days; the CI tree of *Elaeagnus* occurrence also included a significant split on growing degree-days, but only when the variable for intentional *Elaeagnus* planting was included (Fig. 3). All three

of these taxa occurred more frequently at higher temperatures (Fig. 3). Precipitation ranked among the three most important variables for five of nine taxa, including *Tamarix* (Table 3), which occurred more frequently at lower mean annual precipitation (Fig. 3). Precipitation was not, however, one of the three most important environmental variables in CI forest models for occurrence of *P. deltoides* or *Elaeagnus* (Table 3), and there were no significant splits on mean annual precipitation in the CI tree models for either taxon (Fig. 3).

Hydrogeomorphic variables also exhibited strong relationships with plant occurrence. Stream power was among the three most important environmental variables in CI forests for occurrence of four of nine taxa, including *Elaeagnus* (Table 3). There was a significant split on this variable in the CI tree for *Elaeagnus*, but not for *P. deltoides* or *Tamarix* (Fig. 3). Peak flow timing was among the three most important environmental variables in CI forests for occurrence of five of nine taxa, including *P. deltoides*, *Tamarix* and *Elaeagnus* (Table 3). This variable produced a significant split in the CI tree of *Elaeagnus* occurrence, but was masked by growing degree-days at splits in CI trees for occurrence of *P. deltoides* and *Tamarix* (Fig. 3). Other hydrogeomorphic variables had weaker relationships with occurrence. Peak
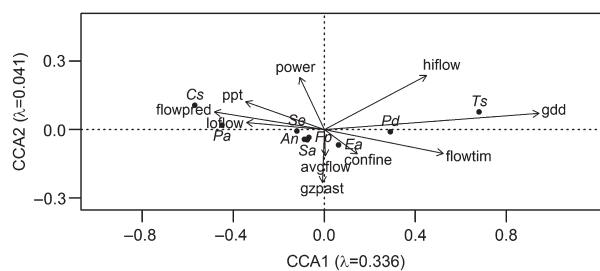

Figure 2. Canonical correspondence analysis (CCA) of occurrence of the nine taxa on ten environmental variables. Eigenvalues are displayed in parentheses on the axes. The taxa and environmental scores are indicated with bullets and arrows. An = *Acer negundo*, Cs = *Cornus sericea*, Ea = *Elaeagnus angustifolia*, Fp = *Fraxinus pennsylvanica*, Pa = *Populus angustifolia*, Pd = *P. deltoides*, Sa = *Salix amygdaloides*, Se = *S. exigua*, Ts = *Tamarix* spp., gdd = growing degree-days, ppt = mean annual precipitation, flowtim = peak flow timing, flowpred = peak flow predictability, loflow = seasonal low flow, avgflow = mean annual flow, hiflow = 10-yr flood, power = stream power, confine = channel confinement, gzpast = past grazing.

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Table 3. Ranking by importance of ten environmental variables in conditional inference (CI) forest models for occurrence of the nine taxa. Only the top five variables for each taxon are shown. See Fig. 3 for the corresponding CI tree models.

	Growing degree-days	Mean annual precipitation	Peak flow timing	Peak flow predictability	Seasonal low flow	Mean annual flow	10-yr flood	Stream power	Channel confinement	Past grazing
P. deltoides	1		2	4		5			3	
E. angustifolia	3		1			5		2	4	
Tamarix spp.	1	3	2	4	5					
A. negundo	1	2	5					3	4	
C. sericea	1	5	3				4			2
F. pennsylvanica	3	2				5	4	1		
P. angustifolia	1	5	3	2					4	
S. amygdaloides	2	3				5		1	4	
S. exigua	1	2				5		3	4	

flow predictability, the 10-yr flood and channel confinement were each among the three most important environmental variables in CI forests for occurrence of one of the nine taxa (Table 3), and there was a significant split on the 10-yr flood in the CI tree for *P. deltoides* (Fig. 3). Seasonal low flow and mean annual flow were not important in CI forests for occurrence of any of the nine taxa (Table 3), and did not produce significant splits in CI trees for occurrence of *P. deltoides*, *Elaeagnus* or *Tamarix* (Fig. 3).

Past grazing was the second most important environmental variable in the CI forest for *Cornus sericea* (Table 3), and was associated with reduced occurrence of this species (Table 2). Grazing was not a strong predictor of occurrence of any other taxa (Table 3).

Abundance models for three focal taxa

Abundance was also strongly related to climatic and hydrogeomorphic variables (Table 4; Fig. 4). Indeed, for *P. deltoides* and *Tamarix*, hydrogeomorphic variables were more strongly associated with abundance than with occurrence. Peak
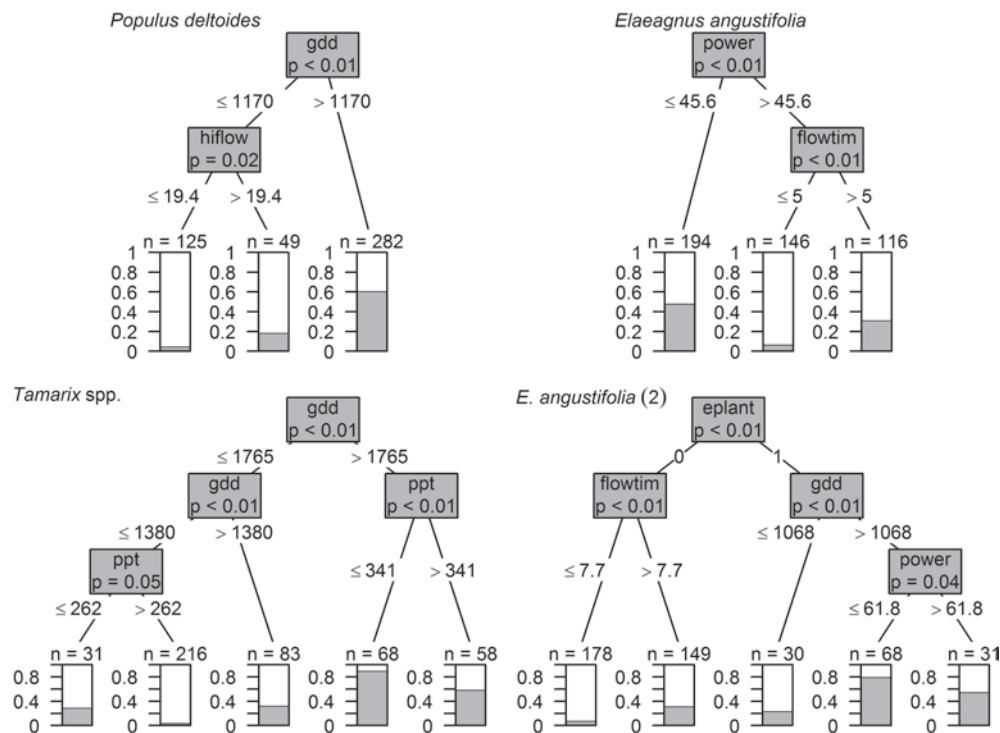

Figure 3. Conditional inference tree models relating ten environmental variables to occurrence of *Populus deltoides*, *Tamarix* spp. and *Elaeagnus angustifolia*. The second model for *Elaeagnus* also included the variable for intentional *Elaeagnus* planting. gdd = growing degree-days, ppt = mean annual precipitation, flowtim = peak flow timing, hiflow = 10-yr flood, power = stream power, eplant = *Elaeagnus* intentionally planted nearby. Gray boxes designate the most significant covariate associated with partitioning the response at an intermediate node, and the value producing the most homogenous split is indicated on the links below. Vertical bars show the proportion of absences (white) and presences (gray) for each taxon at the sites within a terminal node; n = the number of sites within a terminal node. At terminal nodes, no covariate had a significant relationship to the response (given the pre-defined α = 0.05), so further subdivision was not warranted. Tree models are interpreted by considering the combination of factors leading to the proportion of presences and absences within a particular node.

Table 4. Ranking by importance of ten environmental variables in CI forest models for abundance of the focal taxa *Elaeagnus angustifolia* and *Tamarix* spp. and two age-classes of *Populus deltoides* ([< 30] or [> 30] = less or greater than 30 yr old). The last four models are for abundance of the two age-classes of *P. deltoides* relative to *Elaeagnus* and *Tamarix*. Relative abundance was calculated as the abundance of *P. deltoides* at each site divided by the summed abundance of *P. deltoides* and either *Elaeagnus* or *Tamarix*. Only the top five variables for each taxon are shown. See Fig. 4, 5 for the corresponding CI tree models.

	Growing degree-days	Mean annual precipitation	Peak flow timing	Peak flow predictability	Seasonal low flow	Mean annual flow	10-yr flood	Stream power	Channel confinement	Past grazing
P. deltoides [<30]	3	5	1					2		4
P. deltoides [>30]	3		1			5		2	4	
E. angustifolia	3	1	4	2			5			
Tamarix spp.	1	3	2				5	4		
P. deltoides [<30]/ *E. angustifolia*	1	5			4		2	3		
P. deltoides [>30]/ *E. angustifolia*	1	2		3			4		5	
P. deltoides [<30]/ *Tamarix* spp.	1	2	3				5	4		
P. deltoides [>30]/ *Tamarix* spp.	1	2	3		5		4			

flow timing and stream power produced splits in the CI tree model of *Tamarix* abundance, and were the only variables appearing in the CI abundance trees for both age-classes of *P. deltoides* (Fig. 4). In contrast, the CI tree model of *Tamarix* occurrence contained no splits on hydrogeomorphic variables (Fig. 3), and the primary split in the CI tree of *P. deltoides* occurrence was based on temperature (Fig. 3). Abundance of *Elaeagnus*, however, was less strongly associated with hydrogeomorphic variables than was occurrence (Table 4; Fig. 4), as the only split in the *Elaeagnus* CI abundance tree indicated increased abundance at sites with lower precipitation (Fig. 4).
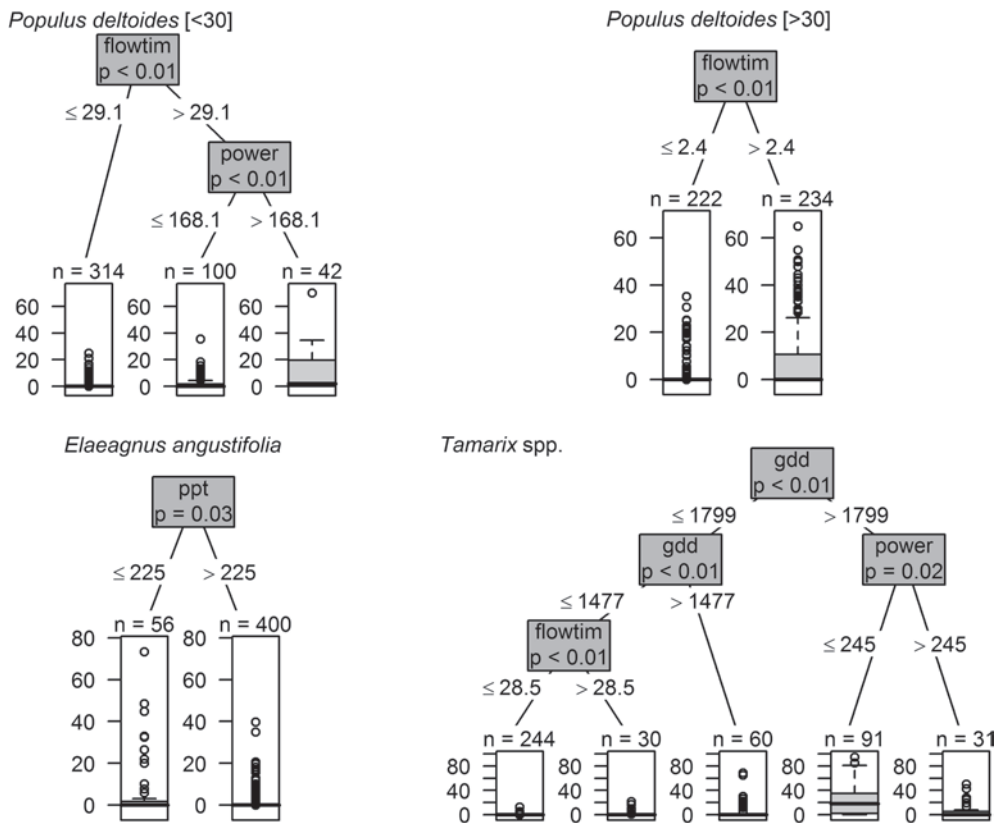

Figure 4. Conditional inference tree models relating ten environmental variables to abundance of *Elaeagnus angustifolia*, *Tamarix* spp. and two age-classes of *Populus deltoides* ([< 30] or [> 30] = less or greater than 30 yr old). gdd = growing degree-days, ppt = mean annual precipitation, flowtim = peak flow timing, power = stream power. Boxplots show the distribution for abundance (percent cover) of each taxon at the sites within a terminal node; n = the number of sites within a terminal node. In terminal nodes, boxes show the median and upper and lower quartiles, whiskers indicate the maximum and minimum (excluding outliers), and dots indicate outliers (> 1.5 times the interquartile range).

Climatic variables accounted for *P. deltoides* abundance relative to *Tamarix* or *Elaeagnus* (Table 4; Fig. 5). In CI trees, relative abundance of *P. deltoides* and *Elaeagnus* was most strongly related to growing degree-days, with a secondary split on stream power or mean annual precipitation, depending on *P. deltoides* age. Relative abundance of *P. deltoides* and *Tamarix* was most strongly related to temperature, and secondarily to precipitation (Table 4; Fig. 5).

Hypothesis 1: *Tamarix* **is more abundant than** P. deltoides **or** Elaeagnus **in hotter, drier climates**

This hypothesis was strongly supported. In CI forest models relating abundance of *P. deltoides* to *Elaeagnus* and *Tamarix*, growing degree-days was the most important variable in all four cases, and mean annual precipitation was the second most important variable in three of four cases (Table 4). Abundance of *Tamarix* was high relative to *P. deltoides* where temperature was higher and precipitation was lower (Fig. 5). In contrast, abundance of *Elaeagnus* was high relative to *P. deltoides* where temperature, precipitation and stream power were all lower (Fig. 5). These differences were consistent with the average climate at sites occupied by the three taxa (Table 2). Conditional inference tree models for occurrence of *Tamarix* and *P. deltoides* were also dominated by growing degree-days, and the threshold value of this variable in the primary split was higher for *Tamarix* (> 1765°C-days) than for *P. deltoides* (> 1170°C-days) (Fig. 3).

Hypothesis 2: extreme low flows favor *Tamarix* relative to P. deltoides

Our analysis only weakly supported this hypothesis. We did observe that *Tamarix* occurred at sites with smaller low flows during the growing season than those at which *P. deltoides* was present (Table 2), and *Tamarix* showed a stronger negative relationship to increasing seasonal low flow (i.e. a more negative regression coefficient; Supplementary material Appendix 1, Table A2). However, seasonal low flow did not appear in CI trees for occurrence or abundance of either taxon (Fig. 3–5), and was a relatively unimportant variable in CI forest models for these same responses (Table 3, 4).

Hypothesis 3: flood disturbance favors *Tamarix* and P. deltoides over Elaeagnus

Our analysis offered strong support for this hypothesis. Because physical disturbance promotes the establishment of *Tamarix* and *P. deltoides*, we expected smaller peak flows and lower stream power to be associated with the more shade-tolerant, animal-dispersed *Elaeagnus*. In agreement with this expectation, sites occupied by *Tamarix* and *P. deltoides* had the largest and second largest 10-yr flood respectively, while sites occupied by *Elaeagnus* had much lower 10-yr flood (Table 2). In CI trees, higher occurrence and abundance of *P. deltoides* was associated with higher stream power (Fig. 3, 4), and higher *Elaeagnus* occurrence was associated with lower stream power (Fig. 3). Most importantly, 10-yr
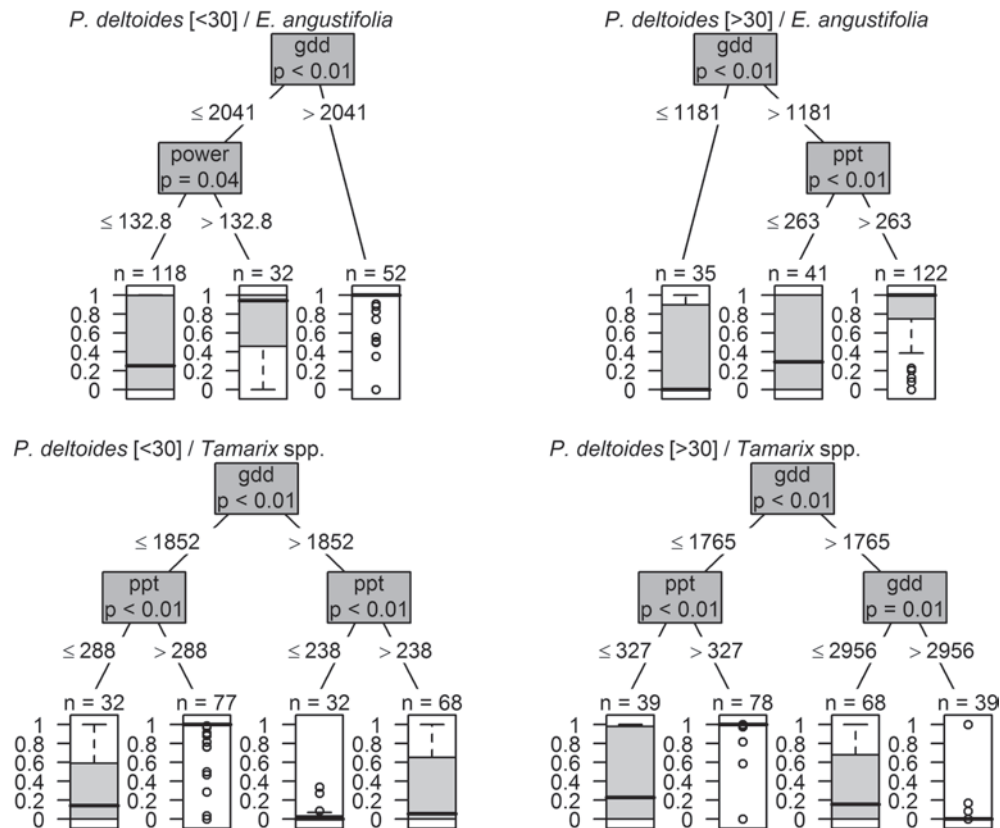

Figure 5. Conditional inference tree models relating ten environmental variables to abundance of two age-classes of *Populus deltoides* ([< 30] or [> 30] = less or greater than 30 yr old) relative to *Elaeagnus angustifolia* and *Tamarix* spp. gdd = growing degree-days, ppt = mean annual precipitation, power = stream power. Relative abundance was calculated as the abundance of *P. deltoides* at each site divided by the summed abundance of *P. deltoides* and either *Elaeagnus* or *Tamarix*. Therefore, boxplots show the distribution for proportional abundance of *P. deltoides* at the sites within a terminal node.

flood was selected as the second and fourth highest ranking variable in CI forest models differentiating the abundance of younger and older *P. deltoides* relative to *Elaeagnus* (Table 4), and higher stream power favored *P. deltoides* < 30 yr old over *Elaeagnus* in the CI tree differentiating their abundance (Fig. 5). Although the association of higher *Tamarix* abundance with lower stream power in the *Tamarix* CI abundance tree contrasted with this hypothesis (Fig. 4), this finding likely reflected increasing abundance of *Tamarix* at more downstream reaches.

Hypothesis 4: Populus deltoides *is more sensitive than* Tamarix *or* Elaeagnus *to flood timing and is favored by earlier peak flows*

Models of plant abundance supported this hypothesis, but occurrence models did not. As predicted, *P. deltoides* occurred at sites with earlier flooding than those where *Tamarix* was present (Table 2). In CI abundance trees (Fig. 4), peak flow timing provided the primary split for younger and older *P. deltoides*, but not for *Tamarix* or *Elaeagnus*. Similarly, in CI abundance forests (Table 4), peak flow timing was the most important variable for both age-classes of *P. deltoides*, but not for *Elaeagnus* or *Tamarix*. However, in CI forests and trees for occurrence, peak flow timing was not more important for *P. deltoides* than for *Tamarix* and *Elaeagnus* (Table 3; Fig. 3). Climatic variables superseded peak flow timing in all models of pairwise relative abundance (Fig. 5). However, peak flow timing was the third most important variable in CI forest models for the proportion of younger and older *P. deltoides* relative to *Tamarix* (Table 4).

Hypothesis 5: occurrence of introduced Elaeagnus *and* Tamarix *is strongly associated with intentional planting*

Occurrence of *Elaeagnus*, but not *Tamarix*, was dominated by patterns of introduction. The frequency of *Elaeagnus* planting was high (> 28% of the 456 sites; Table 1), and intentional planting was the strongest descriptor of *Elaeagnus* occurrence when included in a CI tree model (Fig. 3). Planted *Tamarix*, however, was found at < 2% of sites, indicating that planting is no longer strongly contributing to dispersal.

Discussion

Climate, hydrogeomorphology and introduction history are all strongly associated with the distribution of native and non-native riparian woody plants at the sub-continental scale. At this broad extent, temperature had the strongest relationships with vegetation, followed by precipitation. Among hydrogeomorphic variables, we found stream power, peak flow timing and 10-yr flood magnitude explained patterns of occurrence and abundance better than did peak flow predictability, low-flow magnitude, mean annual flow and channel confinement. Observed intentional introduction dominated the model of *Elaeagnus* occurrence, but not that of *Tamarix*. These results support the theory that simultaneous hierarchical filters define realized niches in river ecosystems (Poff 1997).

Because of the strong relationships between vegetation, hydrogeomorphic factors and patterns of introduction, projections of temperature and precipitation are not sufficient to predict the distribution of riparian plants even at the sub-continental scale. Climate envelope models of habitat quality can alert managers to a possible risk (Morisette et al. 2006), but models accounting for fluvial dynamics and biological processes of spread and decline are needed to support regulatory or resource allocation decisions (Brown et al. 2008, Kearney and Porter 2009). Our results support the expectation that functional traits (e.g. timing of seed release) will govern plant responses to changing hydrologic regimes (e.g. earlier peak flows) within a future zone of tolerable thermal and moisture conditions (Stewart et al. 2005, Merritt and Poff 2010, Perry et al. 2012). Results for *Tamarix* and *P. deltoides*, but not *Elaeagnus*, support the hypothesis that climate acts at the coarse scale to limit occurrence, while hydrogeomorphic variables operating at finer scales exert stronger effects on abundance.

Rivers within the study area are characterized by a composite gradient from higher-elevation reaches with cooler temperatures, greater precipitation, higher stream power, and earlier and more predictable snowmelt flood peaks to lower-elevation (higher-order) reaches that are warmer and locally drier, have lower power, greater peak flow variability, and later flood peaks (Patten 1998) (Fig. 2). The two most widespread invasive woody taxa in the region, *Tamarix* and *Elaeagnus*, occupy the warmer downstream end of this gradient. In contrast, the seven most widespread native taxa, excepting *Populus deltoides*, are found at the cooler upstream end of this gradient. This trend is consistent with observations of Ringold et al. (2008) that several invasive plants, including *Tamarix* and *Elaeagnus*, are more abundant in larger streams with greater human disturbance.

The dominance of this composite gradient complicates distinguishing the effects of individual environmental variables. For example, the variable producing the single best partition of the sites at each split in a CI tree may mask closely related and ecologically significant variables measuring other features of the gradient. More generally, this multicollinearity suggests that any postulated relationship between riparian vegetation and environmental factors across the interior western USA is susceptible to misattribution of causality, particularly when potentially significant factors go unmeasured. In our analysis, the variable rankings generated from CI forests provided valuable, complementary insight into the relative significance of confounded environmental factors.

Our finding that high temperature and low moisture are associated with high abundance of *Tamarix* relative to *Populus* agrees with physiological studies (Busch and Smith 1995, Glenn and Nagler 2005, Friedman et al. 2011) and climate envelope models (Evangelista et al. 2008, Jarnevich et al. 2011). This result suggests that increased temperatures and aridity associated with climate change will favor *Tamarix* (Stromberg et al. 2010, Perry et al. 2012). However, because warm temperatures favor *P. deltoides* over *Elaeagnus*, increased temperatures could reduce competitiveness of *Elaeagnus*, especially near the southern limit of its current distribution (Katz and Shafroth 2003, Guilbault et al. 2012). For most taxa, temperature was more strongly related to occurrence and abundance than was precipitation. Because of the moisture subsidy provided by the river, local precipitation is a less precise indicator of moisture conditions in riparian zones than in uplands.

Although response to climatic variables in our analysis strongly reflected the superior drought tolerance of *Tamarix* relative to *P. deltoides*, we did not find the expected advantage of *Tamarix* over *P. deltoides* in streams where seasonal low flow is far below the mean. The detrimental physiological effects of extreme low flows on *P. deltoides* have been observed in Arizona, which includes the most arid portions of our study area (Stromberg et al. 2007), but apparently are less prevalent in cooler regions, and do not manifest a clear distributional response at the sub-continental scale. In addition, a moderately strong negative correlation between growing degree-days and seasonal low flow ($r_s = -0.4$; Supplementary material Appendix 1, Table A1) may have led climatic variables to obscure low-flow effects in our analysis.

The occurrence of large floods distinguishes sites occupied by *P. deltoides* and *Tamarix* from those occupied by *Elaeagnus,* supporting the hypothesis that *Populus* and *Tamarix* are better adapted to flood disturbance (Katz and Shafroth 2003). Larger seed size, smaller seed number and limited dispersal of *Elaeagnus* reduce its ability to take advantage of flood disturbance. Larger seed size, however, also gives *Elaeagnus* an energetic advantage over *Populus* and *Tamarix* when germinating in drier, shaded sites in the presence of competing vegetation (Katz et al. 2001, Reynolds and Cooper 2011). Therefore, our results support the expectation that reduced flood disturbance resulting from flow regulation should favor *Elaeagnus* over *Populus*.

Our results also support the argument that changes to peak flow timing caused by climate change and reservoir construction are playing an important role in shaping the community composition of western USA floodplains (Rood and Mahoney 1990). *Populus deltoides*, because of its short period of seed release, is especially susceptible to delays or advances in timing of peak flows (Fenner et al. 1985). Our finding that abundance of *P. deltoides* was more strongly related to flow timing than was that of *Tamarix* or *Elaeagnus* supports the contention that delayed peak flows resulting from flow regulation should favor *Tamarix* and *Elaeagnus* over *P. deltoides* (Katz and Shafroth 2003, Merritt and Poff 2010). We also found an age-based shift in abundance of *P. deltoides* that may be caused by earlier snowmelt runoff induced by warming along undammed streams (Stewart et al. 2005). Flood timing best explained the west-wide abundance of both younger (< 30 yr old) and older (> 30 yr old) *P. deltoides* (Fig. 4), but higher abundance of younger stands was associated with sites where flooding occurred later relative to the last day of frost. This result accords with the hypothesis that earlier spring runoff during recent decades (Stewart et al. 2005, Moore et al. 2007) has outpaced advancement in the timing of seed release in *P. deltoides* (Stella et al. 2006, Rood et al. 2008, Perry et al. 2012).

Distribution of *Elaeagnus* in the western USA is strongly influenced by patterns of introduction. This is demonstrated by the high frequency of *Elaeagnus* planting and the fact that observation of nearby intentional planting was the strongest descriptor of *Elaeagnus* occurrence when included in a CI tree model (Fig. 3). This result implies that *Elaeagnus* has not reached all suitable areas, and thus classification of *Elaeagnus* as a noxious weed in many western states may help slow its further spread (Nagler et al. 2011). In contrast, we found that planting of *Tamarix* is now uncommon. Although

Tamarix and *Elaeagnus* were introduced at roughly the same time, the abundant widely dispersed seeds of *Tamarix* likely enabled it to spread rapidly and gain greater dominance by the time of our survey (Friedman et al. 2005). Yet, our results support the idea that the ability of *Elaeagnus* to reproduce in the absence of disturbance may allow it to benefit from flow regulation and maintain greater long-term population growth (Reynolds and Cooper 2010) where temperature is not too high.

There are biases in the location of stream gages that could affect the patterns we observed. Gages tend to be located close to population centers, a bias we countered by favoring relatively isolated gages in our site selection process (Auble et al. 2012). Gages are usually located at sites accessible by road, which could increase opportunities for establishment of introduced plants. Gages are also typically located where the channel is narrow and stable, a tendency we partly countered by sampling a large area near each gage. Finally, small and ephemeral streams are under-represented in the gage network because they are relatively unimportant as water sources. This bias reduced the number of sites where competitors of *Tamarix* were likely limited by dry conditions.

Although livestock grazing can have a strong influence on channel morphology and vegetation at the reach to watershed scale (Green and Kauffman 1995, Trimble and Mendel 1995), it was not strongly associated with occurrence or abundance of woody riparian vegetation at the sub-continental scale. Grazing was strongly associated with occurrence of only one of nine taxa, and was among the five strongest predictors in only one of eight abundance models of focal taxa. This modest effect reflects generally low levels of grazing on our subjectively defined index and low variability in grazing among sites (Table 1, 2).

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Supplementary material (Appendix ECOG-01285 at <www.ecography.org/appendix/ecog-01285>). Appendix 1.