

Divergent effects of land-use, propagule pressure, and climate on woody riparian invasion

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Abstract Landscape-scale analyses of biological invasion are needed to understand the relative importance of environmental drivers that vary at larger scales, such as climate, propagule pressure, resource availability, and human disturbance. One poorly understood landscape-scale question is, how does human land-use influence riparian plant invasion? To evaluate the relative importance of land-use, climate, propagule pressure, and water availability in riparian invasion, we examined tamarisk (*Tamarix ramosissima*, *T. chinensis*, hybrids), Russian olive (*Elaeagnus angustifolia*), and Siberian elm (*Ulmus pumila*) occurrence, abundance, and dominance in 238 riparian sites in developed, cultivated, and undeveloped areas of four western USA river basins (281,946 km²).

The datasets generated or analyzed during the current study are available in the USGS ScienceBase repository, <https://doi.org/10.5066/f7tx3dpf> (Perry et al. 2018).

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Temperature and propagule pressure from individuals planted nearby largely drove invasive species occurrence, whereas factors likely to affect resource availability (e.g., land-use, precipitation, streamflow intermittency) were more important to abundance and dominance, supporting the argument that species distribution models based on occurrence alone may fail to identify conditions where invasive species have the greatest impact. The role of land-use varied among taxa: urban and suburban land-use increased Siberian elm occurrence, abundance, and dominance, and urban land-use increased Russian olive occurrence, whereas suburban land-use reduced tamarisk dominance. Surprisingly, Siberian elm, which has received scant prior scientific and management attention, occurred as or more frequently than tamarisk and Russian olive (except in undeveloped areas of the Colorado River headwaters) and had higher density and dominance than tamarisk and Russian olive in developed areas. More research is needed to understand the impacts of this largely unrecognized invader on riparian ecosystem services, particularly in urban and suburban areas.

Keywords Climate · Disturbance · Land-use · Propagule pressure · Saltcedar · Streamflow

Introduction

Landscape-scale analyses of biological invasion are necessary for understanding the role of environmental drivers that vary at larger scales (Pauchard and Shea 2006) and for informing management decisions on where and how best to control invasive species (Guisan et al. 2013), but such studies are relatively rare. Climate is often assumed to be the primary driver of large-scale invasive species distributions (Elith 2015), but the relative importance of other landscape characteristics that influence invasion, such as human land-use, propagule pressure, and resource availability, remains unclear (Catford et al. 2009; Theoharides and Dukes 2007). Further, invasive species abundance and dominance, which determine their impact (Parker et al. 1999), are rarely examined at landscape-scales (Bradley 2013; Seabloom et al. 2013). Consequently, we have little understanding of the roles of land-use, propagule pressure, and resource availability in shaping invasive species abundance and dominance, and hence impact, across the landscape.

Riparian ecosystems are a useful system for this scale of research because they occur wherever there is streamflow, under widely varying conditions of climate, propagule pressure, resource availability, and human disturbance. Riparian ecosystems tend to be heavily invaded, because they are rich in water and nutrients relative to the surrounding landscape, experience frequent fluvial and anthropogenic disturbance, and are natural corridors for hydrologic and animal dispersal (Hood and Naiman 2000; Pysek et al. 2010; Richardson et al. 2007). Riparian invaders can have large impacts on the unique flora and wildlife habitat supported by riparian ecosystems, as well as on other ecosystem services, including flood mitigation, erosion control, and water quality (Collette and Pither 2015b; Holmes et al. 2005; Shafroth et al. 2005; Tickner et al. 2001).

Tamarisk (saltcedar; *Tamarix ramosissima* Ledeb., *T. chinensis* Lour., and *T. ramosissima* × *chinensis* hybrids), Russian olive (*Elaeagnus angustifolia* L.), and Siberian elm (*Ulmus pumila* L.) are three woody riparian plants that are native to Asia, have been introduced repeatedly to North America, and have become naturalized in western USA riparian ecosystems (Christensen 1964; Nagler et al. 2011). Tamarisk and Russian olive are widely recognized as invasive species, and have been the subject of considerable

study and debate (Chew 2009; Collette and Pither 2015b; Glenn and Nagler 2005; Katz and Shafroth 2003; Nagler et al. 2011). A 1997–2001 plant survey identified tamarisk and Russian olive as among the five most common and abundant woody riparian taxa across the western USA (Friedman et al. 2005). Major efforts are underway to control their abundance and spread (Gaddis and Sher 2012; Hultine et al. 2010). Siberian elm has received little scientific attention or management, but occurs in 45 states of the conterminous USA (www.plants.usda.gov, accessed February 16, 2017) and is listed as a noxious weed in New Mexico (NM Department of Agriculture Noxious Weed List, updated 2009).

Landscape-scale variation in climate, propagule pressure from intentional planting, water availability, and human disturbance associated with water management and land-use all have potential to influence tamarisk, Russian olive, and Siberian elm distributions in their introduced ranges. Effects of climate, propagule pressure, streamflow, and streamflow regulation have been studied for tamarisk and Russian olive (Collette and Pither 2015b; McShane et al. 2015; Nagler et al. 2011), but not for Siberian elm. Climate limits large-scale distributions of invasive species, like all species, as a function of species-specific cold- and heat-tolerances and phenological requirements (Chaine 2010; Woodward 1987). Temperature is a key predictor of tamarisk and Russian olive distributions in the western USA (Collette and Pither 2015a; Jarnevich et al. 2011; Jarnevich and Reynolds 2011; McShane et al. 2015), with tamarisk's northern range limited by insufficient cold tolerance and Russian olive's southern range limited by unmet chilling requirements (Friedman et al. 2008; Guilbault et al. 2012). At the same time, propagule pressure can influence invasive species distributions by increasing dispersal, reducing the likelihood of random local extinction, and increasing genetic variation (Simberloff 2009). Spatial variation in propagule pressure due to intentional planting is an important predictor of Russian olive but not tamarisk occurrence across the western USA (McShane et al. 2015). Variation in resource availability can affect invasive species recruitment, growth, competition, and survival both within sites and across the landscape (Davis et al. 2000; Shea and Chesson 2002). Water availability is particularly likely to influence invasion in the arid and semiarid western USA, where water is a primary

limiting resource even in riparian ecosystems (Adair and Binkley 2002; Smith et al. 1998). While many invasive species have traits that allow for rapid resource acquisition and growth, and therefore thrive under resource-rich conditions (Daehler 2003; Rejmanek and Richardson 1996; van Kleunen et al. 2010), some occupy resource-poor environments and have relatively high resource-use-efficiency (Funk and Vitousek 2007). Tamarisk and Russian olive are more drought-tolerant than many native riparian species, and drier riparian conditions often favor their invasion (Glenn and Nagler 2005; Katz and Shafroth 2003; Nagler et al. 2011). Finally, streamflow regulation and other means of hydrologic alteration are among the most common, large-scale, and influential forms of human disturbance in riparian ecosystems (Graf 2006; Poff et al. 1997). Flow regulation favors tamarisk and Russian olive invasion by altering natural fluvial dynamics and the timing and quantity of moisture availability, and by increasing soil salinity and fire frequency (Merritt and Poff 2010; Mortenson and Weisberg 2010; Nagler et al. 2011; Stromberg et al. 2007).

In contrast, effects of human land-use on tamarisk, Russian olive, and Siberian elm distributions remain largely unexamined (Ringold et al. 2008). Nearby land-use can contribute to invasion by increasing both disturbance and propagule pressure from human introductions (Vila and Ibanez 2011). Human disturbance often creates conditions that favor invasive over native species, by increasing resource availability, removing competitors, and altering natural disturbance regimes (D'Antonio et al. 1999; Hobbs and Huenneke 1992; Jauni et al. 2015). Different human activities associated with different types of land-use may have distinct effects on riparian invasion (Meek et al. 2010; Moffatt et al. 2004; Pennington et al. 2010) due to differences in the nature and magnitude of effects on native riparian vegetation, floodplain topography, soil disturbance, and channel mobility. For example, urban, suburban, and transportation land-uses may entail streambank stabilization to protect human infrastructure, resulting in concrete and rock in the floodplain, reduced channel mobility, channel incision, and lower water tables (Groffman et al. 2003). Agricultural land-use may lead to clearing or grazing of floodplain vegetation and associated soil disturbance (Fleischner 1994; Zaimes et al. 2004), while urban, suburban, and recreational land-uses may

lead to horticultural landscaping and mowing in the floodplain (Kenwick et al. 2009). Agricultural, suburban, and recreational land-use may increase nutrient inputs to the floodplain from crop, pasture and lawn fertilizer, and animal waste (Carpenter et al. 1998). Despite the potential for land-use to be one of the primary drivers of riparian invasion, its importance remains unclear, especially in relation to other environmental drivers (Liendo et al. 2016; Menuz and Kettenring 2013).

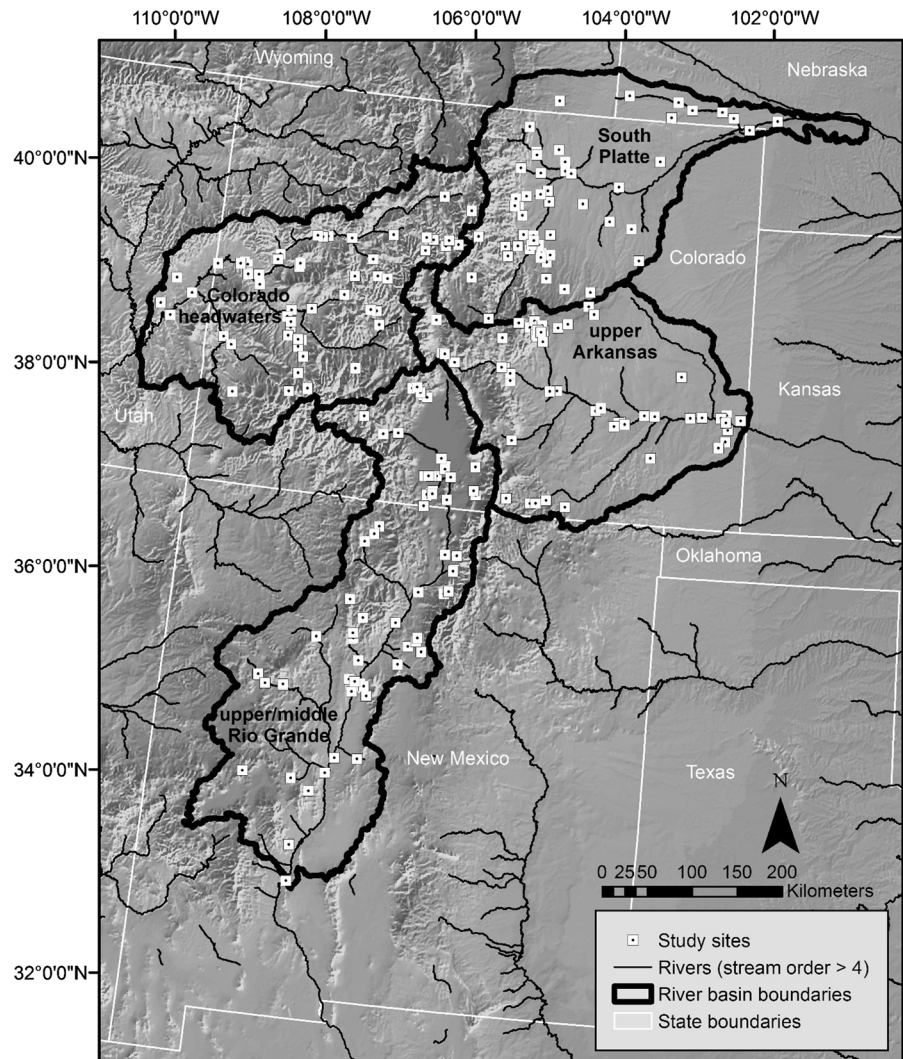
We measured tamarisk, Russian olive, and Siberian elm occurrence, abundance, and dominance along streams and rivers across a $\sim 282,000$ km² area composed of four major river basins that drain the southern Rocky Mountains (Fig. 1). Our objectives were (1) to examine the relative importance of land-use, climate, propagule pressure, and water availability in determining riparian invasive species' distributions, (2) to inform tamarisk, Russian olive, and Siberian elm management decisions by identifying specific environmental conditions that drive occurrence, abundance, and dominance of each invader, and (3) to compare the potential impact of Siberian elm invasion to tamarisk and Russian olive invasions. We hypothesized that climate, propagule pressure, water availability, and streamflow regulation would be critical drivers of the invasive species' distributions. We expected land-use to contribute meaningfully to their distributions within the context of suitable climate and moisture regimes, with distinct drivers for the different taxa reflecting their specific environmental requirements. Finally, we expected that environmental drivers that affect resource availability (e.g., land-use, streamflow, precipitation), and hence growth and reproduction, would be more important to abundance than occurrence.

Methods

Study species

Tamarisk (*Tamarix ramosissima*, *T. chinensis*, *T. ramosissima* \times *chinensis*) and Russian olive (*Elaeagnus angustifolia*) are small, deciduous trees or shrubs that typically grow to 8 and 12 m tall, respectively (Ackerfield 2015). Siberian elm (*Ulmus pumila*) is a deciduous tree that typically grows to 15 m tall (Ackerfield 2015). Tamarisk spreads primarily by

Fig. 1 Map of the study region, with locations of the four river basins and 238 riparian sites



seed, but has the capacity to reproduce vegetatively from abscised shoots, whereas Russian olive and Siberian elm reproduce only by seed, although they can resprout if injured or buried. All three taxa can be prolific seed producers (Brock 2003; Glenn and Nagler 2005; Tang et al. 2014), but tamarisk and Siberian elm have poor seed longevity (~ 5 weeks and < 1.5 years, respectively) (Di Tomaso 1998; Heit 1967) and Russian olive and Siberian elm can be subject to intense granivory (Dulamsuren et al. 2009b; Katz et al. 2001). Tamarisk and Siberian elm seeds are primarily wind-dispersed and have no dormancy. In contrast, Russian olive fruits are primarily animal-dispersed, require cold temperatures and/or scarification to break

dormancy, and remain viable for 1–3 years under moist conditions (Katz and Shaforth 2003).

The three taxa have similar native distributions (NPGS-ARS, <http://npgsweb.ars-grin.gov>, accessed February 16, 2017). Tamarisk's progenitor species are native to temperate central and western Asia and eastern Europe, including Korea, northern China, Mongolia, Pakistan, Afghanistan, Kyrgyzstan, Tajikistan, Uzbekistan, Turkmenistan, Kazakhstan, Iran, Iraq, the Caucasus, and Ukraine. Russian olive's native distribution extends farther northwest and south, including western Siberia, European Russia, Belarus, Turkey, and India, as well as most of tamarisk's native range. Siberian elm's native distribution is farther to the northeast, including far eastern Russia,

eastern Siberia, Korea, northern China, Mongolia, Kyrgyzstan, Uzbekistan, Turkmenistan, and Kazakhstan.

All three taxa were introduced to the USA as ornamental trees and have been planted extensively. Tamarisk was introduced in the early 1800s, sold as a horticultural plant beginning in the mid-1800s, and planted for hedges, windbreaks, and streambank stabilization in the southwestern USA in the early 1900s (Chew 2009). Russian olive was introduced in the late 1800s (Tellman 1997), and planted as a hedgerow, shelterbelt, and shade tree in the Great Plains and southwestern USA in the early 1900s (Christensen 1963; Hansen 1901; Read 1958). Siberian elm was introduced in the early 1900s (Leopold 1980), planted as a shelterbelt and shade tree in the Great Plains and southwestern USA in the early 1900s (Read 1958; Webb 1948; Werkhoven 1966), and marketed nationally as a landscaping species in the 1950s (Klingaman 1999).

Since being introduced, the three taxa have each escaped cultivation and spread to riparian ecosystems and other relatively moist areas primarily in the non-mountainous western USA (Nagler et al. 2011). Naturalized specimens were first recorded in the late 1800s for tamarisk (Chew 2009), the 1920s for Russian olive (Brock 1998; Christensen 1963), and the 1930s for Siberian elm (Christensen 1964). Today, tamarisk occurs in much of the southwestern USA and parts of the northwestern, central, and southeastern USA, Russian olive occurs in much of the western USA and parts of the midwestern and northeastern USA, and Siberian elm occurs in much of the western and midwestern USA and parts of the eastern USA (www.plants.usda.gov).

Study region

The study region was 281,946 km², composed of the Colorado River headwaters, the upper/middle Rio Grande, the upper Arkansas River, and the South Platte River basins, and spanning much of Colorado and portions of New Mexico, Utah, Wyoming, and Nebraska (Fig. 1). River basin boundaries were defined by 6-digit US Geological Survey hydrologic units (101900, 110200, 130100, 130201, 130202, 140100, 140200, and 140300), with the Colorado headwaters and upper/middle Rio Grande basins composed of multiple units. Hence, for this study,

the Colorado headwaters was defined as upstream of the confluence with the Green River, the upper/middle Rio Grande was defined as upstream of Elephant Butte Dam, the upper Arkansas was defined as upstream of the Colorado-Kansas border, and the South Platte was the entire South Platte River basin.

Elevation above sea level varies considerably across the study region, from ~ 4300 m at the headwaters in the Rocky Mountains to ~ 800 m on the Great Plains. The climate is temperate, with temperature regimes ranging from alpine to continental and moisture ranging from humid to semiarid. Temperatures are cooler and precipitation is higher in the mountains than on the plains. Across the region, maximum temperatures range from 11.3 to 37.6 °C (mean = 28.5 °C), minimum temperatures range from - 21.4 to - 0.6 °C (mean = - 10.9 °C), and annual precipitation ranges from 18 to 155 cm (mean = 44 cm) (www.climatesource.com, downloaded May 8, 2012). In the mountains, much precipitation falls as snow, leading to snowmelt-dominated streamflow hydrology in rivers with high-elevation headwaters. Part of the region is also influenced by the North American monsoon, which brings intense rainstorm events and associated high streamflow in late summer, particularly in the upper/middle Rio Grande basin (Adams and Comrie 1997).

Predominant land-uses include major cities, small cities and towns, manufacturing, service, and trade industries, cropland, rangeland, and oil and gas development, all mainly at lower elevations. In the 2010 census, the South Platte River basin contained 14 cities with populations > 50,000, while the upper/middle Rio Grande basin contained three, the upper Arkansas River basin contained two, and the Colorado headwaters basin contained one. The South Platte River basin also contains the most agricultural land, with cropland and pasture occupying 25% of the basin area, compared to 7, 3, and 3% of the upper Arkansas, Colorado headwaters, and upper/middle Rio Grande basins, respectively (National Land Cover Database (NLCD) 2006 classes 81–82; www.mrlc.gov/nlcd06_data.php, downloaded August 29, 2012).

Study sites

We selected study sites as a stratified random sample of all bridge crossings over streams in the study region, to allow us to observe widespread riparian sites

without entering private land. We identified bridge crossings from the 2011 National Bridge Inventory (<https://www.bts.gov>, downloaded May 31, 2012), excluding bridges > 100 m from streams in the National Hydrography Dataset (NHD flowlines, nhd.usgs.gov/index.html, downloaded August 20, 2008). To avoid data collection on major highways for safety, we also excluded bridges < 100 m from “primary roads” (TIGER 2010, road class S1100; <https://www.census.gov>).

We stratified the sites by river basin and predominant land-use using generalized random tessellation stratified sampling (GRTS) (Stevens and Olsen 2004) in R statistical software with the *spsurvey* package (R Development Core Team; www.r-project.org). We selected sites in each of the four river basins in proportion to total basin area, which was roughly proportional to total stream length within the basins. Then, within each basin, we selected equal numbers of sites for each of three land-use strata determined from predominant land-use within a 0.5-km radius of the bridge, using NLCD 2006 cover classes: (1) Developed (NLCD classes 22–24; constructed materials, sometimes mixed with vegetation, with > 20% cover by impervious surfaces), (2) Cultivated (NLCD classes 81–82; pasture and cropland), and (3) Undeveloped (NLCD classes 11–12, 31, 41–43, 52, 71, 90, 95; water, barren land, forest, shrubland, herbaceous communities, wetlands). We sampled equal numbers of sites for the three land-use strata because we were interested in analyzing effects of land-use on invasion. However, most stream segments in the study region flowed through predominantly Undeveloped areas. Across all bridge crossings in the region, 63% had predominantly Undeveloped land-use within a 0.5-km radius, whereas 22% were in predominantly Developed areas and 15% were in predominantly Cultivated areas. Further, bridge crossings were more likely than other stream segments to be in Developed and Cultivated areas. Across approximately two million points arrayed at 100-m intervals along all rivers and streams in the region, 93% were in predominantly Undeveloped areas.

In addition to the stratified random sample, we revisited 32 sites within the study region from an earlier, larger-scale riparian plant survey (Friedman et al. 2005; McShane et al. 2015). Woody riparian species at these sites were recorded for the earlier survey between 1997 and 2001. Total N = 238 in the

present study, with 56, 77, 52, and 53 sites in the Colorado headwaters, upper/middle Rio Grande, upper Arkansas, and South Platte River basins, respectively.

Site measurements

We visited all sites in June–August 2012. At each site, we observed the riparian corridor from the bridge and measured the maximum viewable distance along each bank, upstream and downstream, with a rangefinder (Bushnell Yardage Pro 400). We counted tamarisk, Russian olive, and Siberian elm individuals in the viewable riparian corridor in each of four size-classes to determine occurrence, estimate population density (number of individuals per longitudinal river-km), and assess percent composition by different size-classes. Because the study taxa differ in growth form and stature, size-classes differed for each: < 1-m tall or < 1, 1–3, and > 3-m crown diameter for tamarisk, < 1-m tall or < 2, 2–5, and > 5-m crown diameter for Russian olive, and < 5, 5–15, 15–30, and > 30-cm diameter at breast height (1.37 m; DBH) for Siberian elm. We used leaf size to distinguish Siberian elm from American elm (*U. americana*) and slippery elm (*U. rubra*), and leaf arrangement to distinguish Russian olive from silver buffaloberry (*Shepherdia argentea*), using binoculars (Nikon Travelite V, 8× magnification) and a spotting scope (Bushnell Spacemaster 78–1800, 60 mm, 15–45× magnification) for species identification as needed. To evaluate rank dominance, we ranked the five woody taxa with the greatest cover in the viewable riparian corridor. We lumped species that were difficult to distinguish reliably at a distance, including (1) plains, Rio Grande, and Fremont cottonwood; (2) narrowleaf, sandbar, and dusky willow; (3) other shrub willows; (4) green and velvet ash; and (5) junipers (see Table S1 in Online Resource 1 for scientific nomenclature). We also lumped related species that occurred infrequently across sites, including (1) spruces and firs, (2) pines, and (3) roses.

To understand effects of environmental conditions on tamarisk, Russian olive, and Siberian elm invasion, we obtained measures of 16 environmental variables that we hypothesized could influence their distributions or abundance (Online Resource 1: Table S2). First, in addition to stratifying our study sites by dominant NLCD land-use, we measured land-use at

each site in more detail using aerial photographs in Google Earth Pro. We examined images from 2012 or, when 2012 images were unavailable, using images from both before and after 2012 to confirm that conditions were consistent through time. We recorded five types of human land-use directly adjacent to or within the riparian corridor in the aerial images as binary data (presence/absence): (1) urban (i.e., factories, businesses, high-rises, parking lots, urban brown fields), (2) suburban (i.e., houses with yards), (3) recreational (i.e., parks, golf courses, campgrounds), (4) transportation (i.e., roads, paved trails, railroad tracks, aligned parallel to the stream), and (5) agricultural (i.e., cropland, pasture). A single site could have all five adjacent land-uses.

The remaining 11 environmental variables included measures of climate, propagule pressure, floodplain grazing, streambank stabilization, riparian forest cover, streamflow hydrology, and water management. For each site, we obtained mean annual temperature and precipitation from 1971 to 2000 at a 400-m spatial resolution from PRISM (Bio₁ and Bio₁₂; www.climatesource.com, downloaded May 8, 2012). To evaluate the importance of local propagule pressure, we noted in the field whether planted tamarisk, Russian olive, or Siberian elm occurred within 5 km along the route to and from the site, as binary data (presence/absence). We also recorded in the field any evidence of domestic grazing in the riparian corridor, including livestock presence, access, dung, or hoof prints, as a single binary variable (presence/absence). We estimated percent of the viewable streambank length stabilized by rip-rap, placed rock, or walls in the field, and then confirmed or corrected those estimates using aerial photographs in Google Earth Pro. We also estimated forest cover along the riparian corridor in aerial photographs and placed the sites into four ordinal forest cover classes: < 10, 10–50, 50–90, or > 90% of the viewable distance (midpoints = 5, 30, 70, 95%). We measured upstream watershed drainage area at each site as a proxy measure of annual streamflow, using the ArcMap flow accumulation hydrology tool and 2009 National Elevation Dataset data at a 1 arc-second resolution (<http://seamless.usgs.gov>, downloaded September 14, 2010). We obtained binary data for streamflow intermittency (intermittent/ephemeral vs. perennial) for each site from NHD flowline data. Although NHD flow intermittency data are not always based on complete information, they

were the best available for our sites. Twenty-four of the 91 streams labelled intermittent were dry when we visited them. Finally, to assess streamflow regulation, we calculated total upstream reservoir normal storage volume per mean annual flow at each site using the National Inventory of Dams database (http://nid.usace.army.mil/cm_apex/f?p=838:12, downloaded June 23, 2016). We removed duplicate records for reservoirs with multiple dams and corrected erroneous dam locations. Our final database included 317 reservoirs with normal storage > 0 within the study region. We assigned the storage volume for each reservoir to all sites downstream of the water source for that reservoir. For 23 reservoirs that stored water from multiple watersheds due to transbasin diversions, we assigned the storage volume to all affected watersheds.

Statistical analysis

To correct non-normality, we log-transformed population densities, watershed drainage area, reservoir storage, and percent streambank stabilization, and square-root-transformed precipitation. For invasive taxa rank dominance, we assigned the appropriate rank value between 1 and 5 if the taxon was among the five most abundant woody taxa at the site, and assigned the value 6 if the taxon was present but not among the five most abundant taxa.

We used conditional inference (CI) binary recursive partitioning and CI forests (Hothorn et al. 2006) to evaluate the relative importance of the 16 environmental variables as predictors of tamarisk, Russian olive, and Siberian elm invasion, with separate analyses for occurrence, density, and dominance of each taxon. This statistical approach allowed us to explore potentially non-linear main effects, interactions, and thresholds of our mix of binary, ordinal, and continuous environmental variables. In analyses for each taxon, we included nearby planting for only that taxon, resulting in 14 environmental variables per analysis. We performed the analyses in R statistical software with the *party* package using the *ctree* and *cforest* functions (R Development Core Team; www.r-project.org). To evaluate effects of environmental variables on density and dominance independently from effects on occurrence, we treated invasive taxon absences as missing data, not zeros, in analyses of density and dominance.

To understand the results more completely, we also tested univariate effects of each environmental variable on tamarisk, Russian olive, and Siberian elm occurrence, density, and dominance. Each model included a single environmental variable, with land-use stratum, basin, and land-use \times basin as additional fixed effects, and site as a random effect. We examined effects on occurrence and dominance using generalized linear mixed models with PROC GLIMMIX in SAS 9.3, with binomial logit models with the residual subject-specific pseudolikelihood method and Kenward–Roger degrees of freedom for occurrence and cumulative logit models with the residual marginal pseudolikelihood method and standard degrees of freedom for dominance. We examined effects on density using linear mixed models with PROC MIXED in SAS 9.3, with the residual maximum likelihood method and Kenward–Roger degrees of freedom. We evaluated spatial autocorrelation in the data by constructing variograms for each taxon from the residuals of models that included no environmental variable, using PROC VARIOGRAM in SAS 9.3. Variograms for density and dominance did not indicate spatial autocorrelation (Moran's I , $p > 0.05$), so we used a variance components covariance structure for those analyses. However, variograms of the Pearson residuals for occurrence indicated significant spatial autocorrelation, so we estimated the G-side covariance matrices for those analyses using a spherical spatial covariance structure, with starting points for the parameters derived from the variograms.

In addition, we examined pairwise correlations between the environmental variables, ordinated the environmental variables using nonmetric multidimensional scaling (NMDS), and examined correlations between the ordination axes and tamarisk, Russian olive, and Siberian elm occurrence, density, and dominance. Further, we tested univariate effects of the environmental variables on rank dominance of other common woody taxa at the sites, and examined correlations between other common woody taxa and tamarisk, Russian olive, and Siberian elm occurrence. Detailed methods for these analyses are provided in Online Resource 1.

To evaluate the importance of Siberian elm invasion relative to tamarisk and Russian olive in the study region, we compared the frequency, density, and dominance of the three taxa in the three land-use strata and four river basins. Statistical methods were

identical to the univariate analyses described above, except that taxon and all interactions with taxon were included as fixed effects, taxon was included as a repeated measure within sites, and environmental variables were not included. To address problems with model convergence, we did not include the taxon \times land-use stratum \times basin interaction in the models for occurrence or dominance. As above, to evaluate differences among taxa in density and dominance independently from differences in frequency, we treated invasive taxon absences as missing data, not zeros, for these analyses.

To evaluate population size-class structure, we compared percent composition by the different size-classes for each taxon among land-use strata and river basins using multivariate analysis of variance with PROC MIXED in SAS 9.3, with size-class, land-use stratum, basin, and all interactions as fixed effects, the residual maximum likelihood method, and Kenward–Roger degrees of freedom. We used a repeated statement to treat percent composition by the four size-classes and the total number of stems at the site as separate dependent variables with an unstructured covariance structure. We square-root-transformed tamarisk and log-transformed Russian olive and Siberian elm data to meet model assumptions. Variograms of the residuals for each size-class of each taxon did not indicate spatial autocorrelation (Moran's I , $p > 0.05$).

Results

Tamarisk, Russian olive, and Siberian elm occurred in 32, 40, and 54% of sites, respectively, and were among the five dominant woody taxa in 25, 30, and 46% of sites, making them the seventh, fourth, and third most commonly dominant woody riparian taxa across the sites (Fig. 2; Online Resource 1: Table S1). Tamarisk and Siberian elm were ranked the top-most dominant woody taxon in 7 and 14% of sites, respectively, more than any other taxa but narrowleaf/sandbar/dusky willow, plains/Rio Grande/Fremont cottonwood, and narrowleaf cottonwood. A fourth non-native tree, hybrid crack willow, an important riparian invader in Australia and South America (Datri et al. 2017; Greenwood et al. 2004), ranked among the five dominant woody taxa in 13% of sites and was the top-most dominant taxon at 4% of sites.

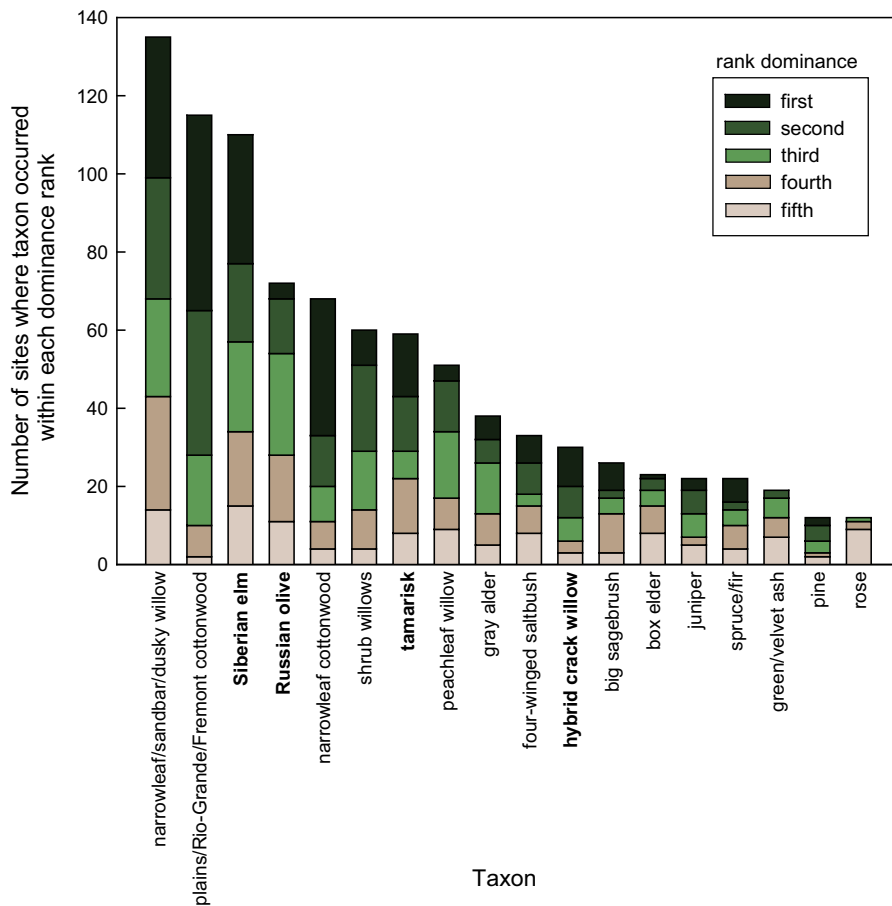


Fig. 2 Rank dominance of tamarisk, Russian olive, Siberian elm, and other common riparian woody taxa in sites where they were one of the five most abundant woody taxa. Non-native taxa

are listed in bold. Results are shown only for taxa recorded as one of the five most abundant woody taxa in at least 5% of sites. See Table S1 in Online Resource 1 for scientific nomenclature

Environmental conditions associated with tamarisk

Tamarisk occurred more frequently in sites with warmer temperatures, lower precipitation, and higher watershed area. Mean temperature and annual precipitation were the most important predictors in the CI forest and produced the primary, secondary, and tertiary splits in the CI tree (Figs. 3a, 4a). Watershed area was a moderately important predictor in the CI forest. Accordingly, in univariate analyses, tamarisk frequency was significantly higher with warmer temperatures, lower precipitation, and higher watershed area (Table 1).

The primary split of the CI tree for tamarisk density was not significant, suggesting that none of the

measured environmental variables were strong predictors of tamarisk density.

Tamarisk dominance was higher in sites that lacked adjacent suburban land-use. Suburban land-use was the most important predictor in the CI forest and produced the only split in the CI tree (Figs. 3b, 4b). Mean temperature was also important in the CI forest. Accordingly, in univariate analyses, tamarisk dominance was significantly higher without adjacent suburban land-use (Table 1).

Environmental conditions associated with Russian olive

Russian olive occurred more frequently in sites with warmer temperatures, Russian olive planted nearby, adjacent urban land-use, and higher forest cover.

Mean temperature was the most important predictor in the CI forest and produced the primary split in the CI tree (Figs. 3c, 4c). Nearby planting and forest cover were also important predictors in the CI forest, and forest cover produced a secondary split in the CI tree. Adjacent urban land-use was a moderately important predictor in the CI forest. Accordingly, in univariate analyses, Russian olive frequency was significantly higher with warmer temperatures, nearby planted Russian olive, and adjacent urban land-use (Table 1). Further, in NMDS ordination analyses, Russian olive occurrence was correlated with two ordination axes, both linked to Russian olive planted nearby and one linked to adjacent urban land-use and warmer temperatures, (Online Resource 1: Table S3, Fig. S1).

Russian olive density was higher in sites with higher forest cover and lower precipitation. Forest cover and annual precipitation were the first and second most important predictors in the CI forest and produced the primary and secondary splits in the CI tree (Figs. 3d, 4d). In univariate analyses, Russian olive density was significantly higher with higher forest cover (Table 1), but not with lower precipitation, perhaps because the effect of precipitation was limited to sites with high forest cover (Fig. 3d).

The primary split of the CI tree for Russian olive dominance was not significant, suggesting that none of the measured environmental variables were strong predictors of Russian olive dominance.

Environmental conditions associated with Siberian elm

Siberian elm occurred more frequently in sites with Siberian elm planted nearby, warmer temperatures, adjacent urban land-use, and higher watershed area and reservoir storage. Mean temperature was the most important predictor in the CI forest, although it produced only a tertiary split in the CI tree (Figs. 3e, 4e). Nearby planting produced the primary split in the CI tree and was the second most important predictor in the CI forest. Adjacent urban land-use, reservoir storage, and streambank stabilization were moderately important predictors in the CI forest. Adjacent urban land-use and watershed area produced secondary splits in the CI tree. Accordingly, in univariate analyses, Siberian elm frequency was significantly higher with nearby planted Siberian elm, warmer temperatures, adjacent urban land-use, and higher watershed area

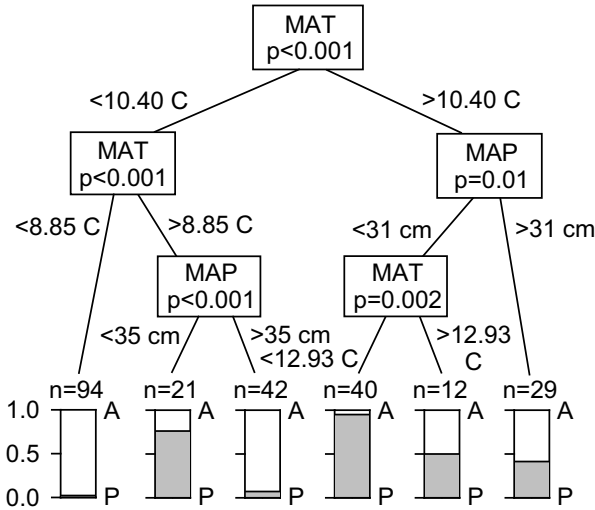
Fig. 3 Conditional inference tree models for tamarisk **a** occurrence and **b** dominance, Russian olive **c** occurrence and **d** density, and Siberian elm **e** occurrence, **f** density, and **g** dominance, as a function of 14 environmental variables. MAT = mean annual temperature and MAP = mean annual precipitation. Boxes indicate the environmental variable producing the most significant data partition at each intermediate node. Values immediately below each box indicate the threshold value of the environmental variable for which the split produces the most homogenous groups. Threshold values were back-transformed for MAP and watershed area splits. n = the number of sites within each terminal node. For occurrence (panels a, c, and e), bar plots indicate the % presence (gray) and % absence (white) of the taxon at each terminal node. For density (panels d and f), box plots indicate the mean (dotted line), median (solid line), 25th and 75th percentiles (gray box), 10th and 90th percentiles (error bars), and values < 10th percentile or > 90th percentile (open circles) for log-transformed density (individuals per longitudinal river-km) of the taxon at each terminal node. For dominance, (panels b and g), stacked bars indicate the percent of sites in which the taxon was the first, second, third, fourth, fifth, or > fifth most abundant woody taxon within each terminal node. Conditional inference trees for tamarisk density and Russian olive dominance are not shown because the first split was not significant ($p > 0.05$)

and reservoir storage (Table 1). Further, Siberian elm occurrence was correlated with two NMDS ordination axes, both linked to Siberian elm planted nearby, one linked to warmer temperatures and adjacent urban land-use, and the other linked to higher watershed area and reservoir storage (Online Resource 1: Table S3, Fig. S1).

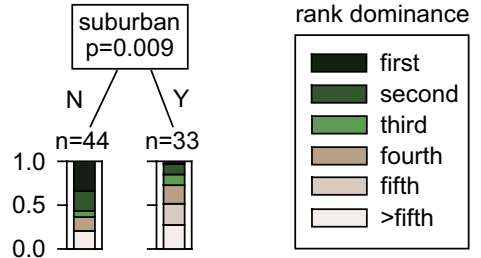
Siberian elm density was higher at sites with adjacent urban and suburban land-use and higher streambank stabilization and forest cover. Adjacent urban land-use was the most important predictor in the CI forest and produced the primary split in the CI tree (Figs. 3f, 4f). Adjacent suburban land-use, streambank stabilization, forest cover, and watershed area were also relatively important predictors in the CI forest. Adjacent suburban land-use produced a secondary split in the CI tree. Accordingly, in univariate analyses, Siberian elm density was significantly higher with adjacent suburban land-use, streambank stabilization, and forest cover (Table 1). Further, Siberian elm density was correlated with two NMDS ordination axes, both linked to higher streambank stabilization, one linked to adjacent urban land-use, and the other linked to suburban land-use and higher forest cover (Online Resource 1: Table S3, Fig. S1).

Although Siberian elm was more likely to occur at sites with higher watershed area and reservoir storage, Siberian elm dominance at those sites where it

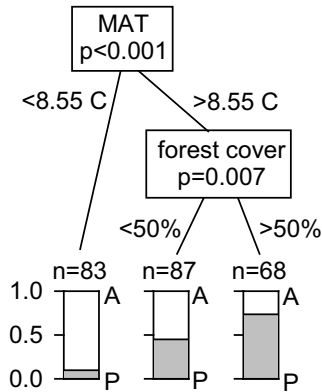
(a) tamarisk occurrence



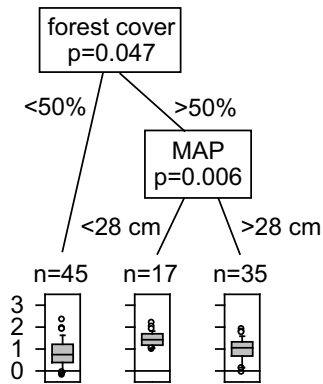
(b) tamarisk dominance



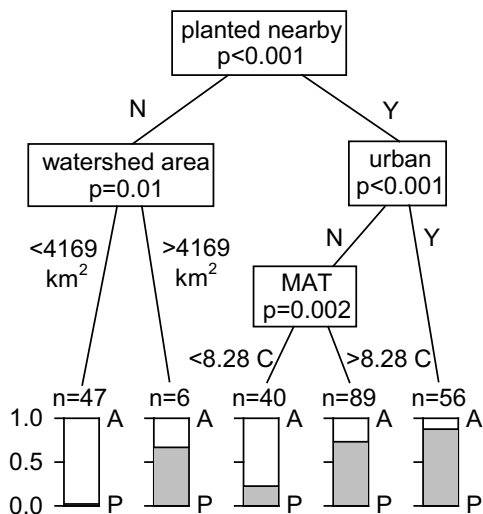
(c) Russian olive occurrence



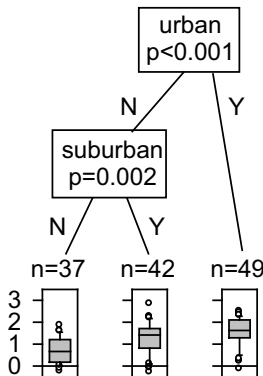
(d) Russian olive density



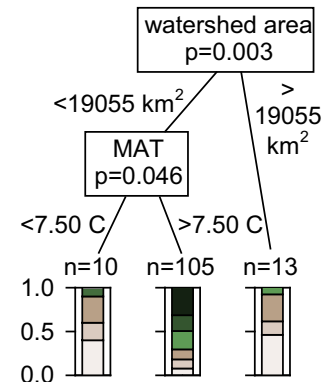
(e) Siberian elm occurrence



(f) Siberian elm density



(g) Siberian elm dominance



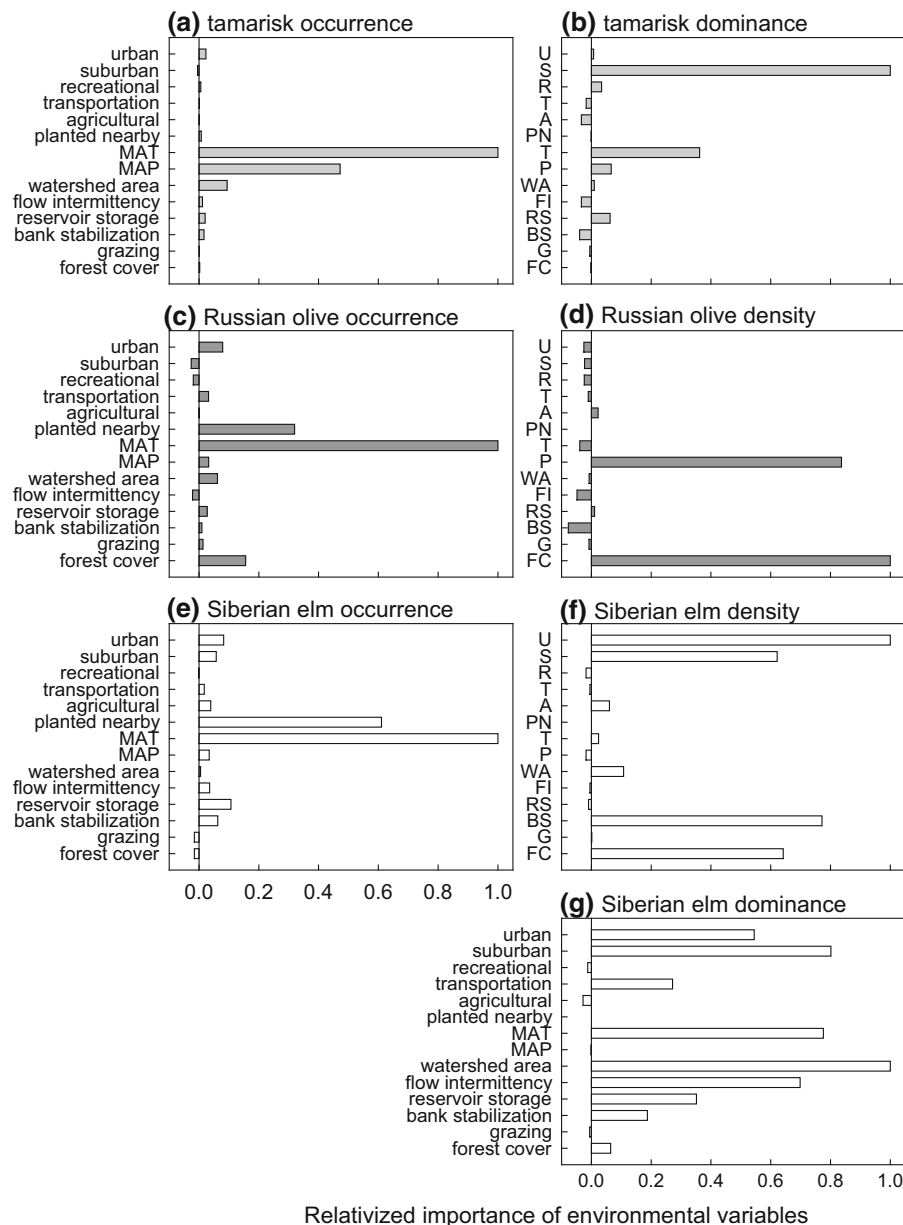


Fig. 4 Relativized importance of environmental variables, from conditional inference forests for tamarisk **a** occurrence and **b** dominance, Russian olive **c** occurrence and **d** density, and Siberian elm **e** occurrence, **f** density, and **g** dominance, as a function of 14 environmental variables. MAT = mean annual temperature and MAP = mean annual precipitation. In **b**, **d**, and

f, brief abbreviations are used for all environmental variables, in the same order as in the other panels. Results of conditional inference forests for tamarisk density and Russian olive dominance are not shown because their conditional inference trees from the full dataset were not significant ($p > 0.05$)

occurred was higher with lower watershed area and reservoir storage, as well as with intermittent streamflow, warmer temperatures, and adjacent suburban land-use. Watershed area was the most important predictor in the CI forest and produced the primary

split in the CI tree (Figs. 3g, 4g). Streamflow intermittency, mean annual temperature, adjacent suburban, urban, and transportation land-use, reservoir storage, and streambank stabilization were also relatively important predictors in the CI forest. Mean

Table 1 Univariate effects of environmental variables on tamarisk, Russian olive, and Siberian elm occurrence, density, and dominance, from generalized linear mixed models

	Occurrence				Density				Dominance							
	Tamarisk		Siberian elm		Tamarisk		Russian olive		Siberian elm		Tamarisk		Russian olive		Siberian elm	
	Odds	d^b	Odds	d^b	β	d	β	d	Odds	d^b	Odds	d^b	Odds	d^b	Odds	d^b
Adjacent land-use																
Urban	3.66	6.61**	5.35**	d^b	-0.12	-0.17	0.79	1.69	0.56	2.43						
Suburban	0.75	0.69	1.97	d	-0.39	0.25	0.57*	Odds	0.23**	2.20*						
Recreational	0.58	1.49	2.78	d	-0.43	0.21	0.38	Odds	0.18*	0.44						
Transportation	2.98	2.79*	2.24	d	0.23	0.02	0.12	Odds	0.78	0.29**						
Agricultural	1.51	0.73	0.61	d	-0.30	0.14	-0.53	Odds	4.03*	1.47						
Planted nearby																
Tamarisk	4.08			d	-0.07			Odds	8.11*							
Russian olive		9.45****		d	0.59			Odds	0.99							
Siberian elm			35.38****	d			1.33	Odds		6.84						
MAT	2.46****	1.95****	1.55**	β	0.16	0.10*	-0.05	Odds	1.04	1.21						
MAP	0.47****	0.69**	0.69**	β	- 0.18**	-0.05	0.01	Odds	0.72	1.09						
Watershed area	3.37****	1.80****	1.79**	β	0.19*	0.06	0.01	Odds	1.03	0.64**						
Flow intermittency	0.28*	0.56	0.95	d	0.01	-0.07	-0.09	Odds	1.23	3.45**						
Reservoir storage	2.29**	1.58**	1.70**	β	0.09	0.06	0.07	Odds	0.91	0.73*						
Bank stabilization	0.75	1.36	1.32	β	-0.08	-0.09	0.17*	Odds	1.08	1.18						
Floodplain grazing	2.03	0.60	0.50	d	-0.53	-0.11	-0.46	Odds	1.38	0.83						
Forest cover	1.01	1.00	1.00	β	0.01*	0.01*	0.01****	Odds	0.99	0.99						

Significant effects are shown in bold (**** $p < 0.0001$, *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$)

^aOdds ratios are shown for occurrence and dominance (> 1 indicates positive relationship)

^bFor density analyses, Cohen's d effect sizes ($(\text{mean}(y_{\text{yes}}) - \text{mean}(y_{\text{no}}))/\text{standard deviation}(y)$) are shown for binary environmental variables, and estimated slopes (β) are shown for continuous and ordinal environmental variables (> 0 indicates positive relationship)

annual temperature produced a secondary split in the CI tree. Accordingly, in univariate analyses, Siberian elm dominance was significantly higher with lower watershed area and reservoir storage, intermittent streamflow, and adjacent suburban land-use (Table 1). Further, in NMDS ordination analyses, Siberian elm dominance was correlated with an ordination axis linked to lower watershed area and reservoir storage and intermittent streamflow (Online Resource 1: Table S3, Fig. S1).

Land-use cover in the proximate, surrounding landscape

Our binary measures of land-use provided detailed information on specific types of human development directly adjacent to the floodplain. However, continuous measures of land-use cover in the surrounding landscape might have revealed stronger or different effects of land-use on riparian invasion. To explore this possibility, we also constructed CI trees and forests that instead included three continuous land-use metrics calculated from NLCD 2006 land cover data: arcsin, square-root transformed percent cover by Developed-NLCD (NLCD classes 22–24), Cultivated-NLCD (NLCD classes 81–82), and Undeveloped-NLCD (NLCD classes 11–12, 31, 41–43, 52, 71, 90, 95) classes within a 0.5-km radius of each site. Developed-NLCD, Cultivated-NLCD, and Undeveloped-NLCD mean cover across sites was 23 ± 31 (median = 5), 22 ± 28 (median = 1), and $46 \pm 33\%$ (median = 37), respectively. Developed-NLCD cover

was strongly correlated with adjacent urban land-use and Cultivated-NLCD cover was strongly correlated with adjacent agricultural land-use (Online Resource 1: Table S4). Accordingly, Developed-NLCD cover had similar importance to adjacent urban land-use in CI trees and forests for Russian olive and Siberian elm (Online Resource 1: Figs. S2, S3). Cultivated-NLCD and Undeveloped-NLCD cover were negatively correlated with adjacent urban land-use and Developed-NLCD cover, and therefore were also sometimes important in the CI forests, reflecting effects in the opposite direction from adjacent urban land-use. The similarity of these different land-use metrics and analyses indicates that the effects of land-use were robust to different methods and scales of land-use measurement.

Comparing frequency, density, and dominance among invasive taxa

Differences in frequency, density, and dominance among the three invasive taxa depended on both land-use stratum and river basin (taxon \times basin and taxon \times land-use, Table 2; Fig. 5). For frequency, model convergence issues prevented us from testing for a taxon \times land-use stratum \times basin interaction, but post hoc analyses suggested that differences among taxa depended on interacting effects of land-use stratum and basin. In predominantly-Developed sites, Siberian elm occurred more frequently than tamarisk and Russian olive (post hoc taxon, $F_{2,169} = 14.9$, $p < 0.0001$). This difference was most pronounced in

Table 2 Statistical comparisons of frequency, density, and dominance among the three invasive taxa (tamarisk, Russian olive, Siberian elm), three land-use strata (Developed,

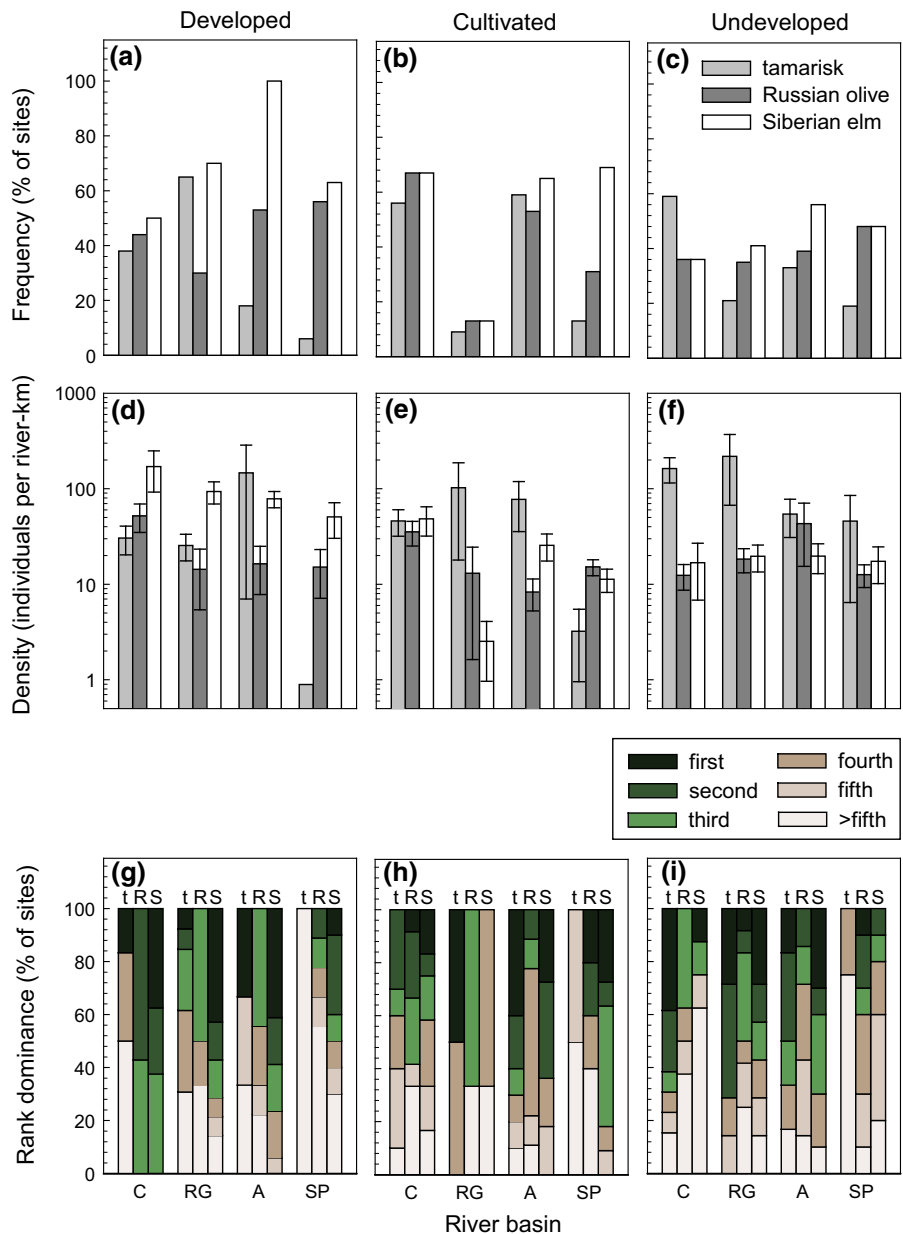
Cultivated, Undeveloped), and four river basins (Colorado headwaters, upper/middle Rio Grande, upper Arkansas, South Platte), from linear and generalized linear mixed models

	ndf	Frequency			Density			Dominance		
		ddf	F	<i>p</i> *	ddf	F	<i>p</i>	ddf	F	<i>p</i>
Taxon	2	522	20.0	< 0.0001	213	2.6	0.08	123	7.1	0.001
Land-use strata	2	277	1.5	0.2	150	2.2	0.1	151	1.1	0.3
Taxon \times land-use strata	4	521	2.3	0.05	211	7.7	< 0.0001	123	6.5	< 0.0001
Basin	3	42	0.8	0.5	137	5.7	0.001	151	5.6	0.001
Taxon \times basin	6	520	4.6	0.0002	205	2.4	0.03	123	3.0	0.009
Land-use strata \times basin	6	274	0.9	0.5	134	1.7	0.1	151	2.6	0.02
Taxon \times land-use strata \times basin ^a	12	–	–	–	203	1.4	0.2	–	–	–

*Significant effects ($\alpha = 0.05$) are shown in bold

^aTo address problems with model convergence, the three-way interaction was not included in models for frequency and dominance

Fig. 5 a–c Frequency, d–f mean density (individuals per longitudinal river-km), and g–i rank dominance of tamarisk, Russian olive, and Siberian elm in each of the three land-use strata (Developed, Cultivated, and Undeveloped) and four river basins [Colorado headwaters (C), upper/middle Rio Grande (RG), upper Arkansas (A), and South Platte (SP)]. For density and dominance, only sites where the taxon was present are included in the values shown. Density was log-transformed for analysis; in panels d–f, means of untransformed densities are shown on a log scale. Error bars are one standard error of the mean (S.E.M.). In panels g–i, letters above the bars indicate the taxon (t = tamarisk, R = Russian olive, S = Siberian elm)



the upper Arkansas River basin, where Siberian elm was present in all predominantly-Developed sites, whereas Siberian elm and tamarisk frequency were higher than Russian olive frequency in the upper/middle Rio Grande basin, Siberian elm and Russian olive frequency were higher than tamarisk frequency in the South Platte River basin, and there was little difference in frequency among taxa in the Colorado headwaters basin. In predominantly-Cultivated sites, Siberian elm occurred more frequently than tamarisk,

but not than Russian olive (post hoc taxon, $F_{2,148} = 7.3$, $p = 0.0009$). This difference was most pronounced in the South Platte River basin, but the post hoc taxon \times basin interaction was not significant with a Bonferroni-adjusted α ($F_{2,148} = 2.4$, $p = 0.03$). In predominantly-Undeveloped sites, Siberian elm occurred more frequently than tamarisk in the upper/middle Rio Grande basin, and both Siberian elm and Russian olive occurred more frequently than tamarisk in the South Platte River basin, but tamarisk occurred more

frequently than Siberian elm and Russian olive in the Colorado headwaters basin (post hoc taxon \times basin, $F_{6,192} = 3.4$, $p = 0.003$).

Similarly, Siberian elm density was higher than tamarisk and Russian olive density in predominantly-Developed sites (post hoc taxon, $F_{2,91} = 15.9$, $p < 0.0001$). In contrast, in predominantly-Undeveloped sites, tamarisk density was higher than Siberian elm and Russian olive density (post hoc taxon, $F_{2,74} = 5.9$, $p = 0.004$). Densities did not differ significantly among taxa in predominantly-Cultivated sites. In addition, tamarisk density was higher in the Colorado headwaters, upper/middle Rio Grande, and upper Arkansas River basins than in the South Platte River basin (post hoc basin, $F_{3,65} = 3.7$, $p = 0.016$).

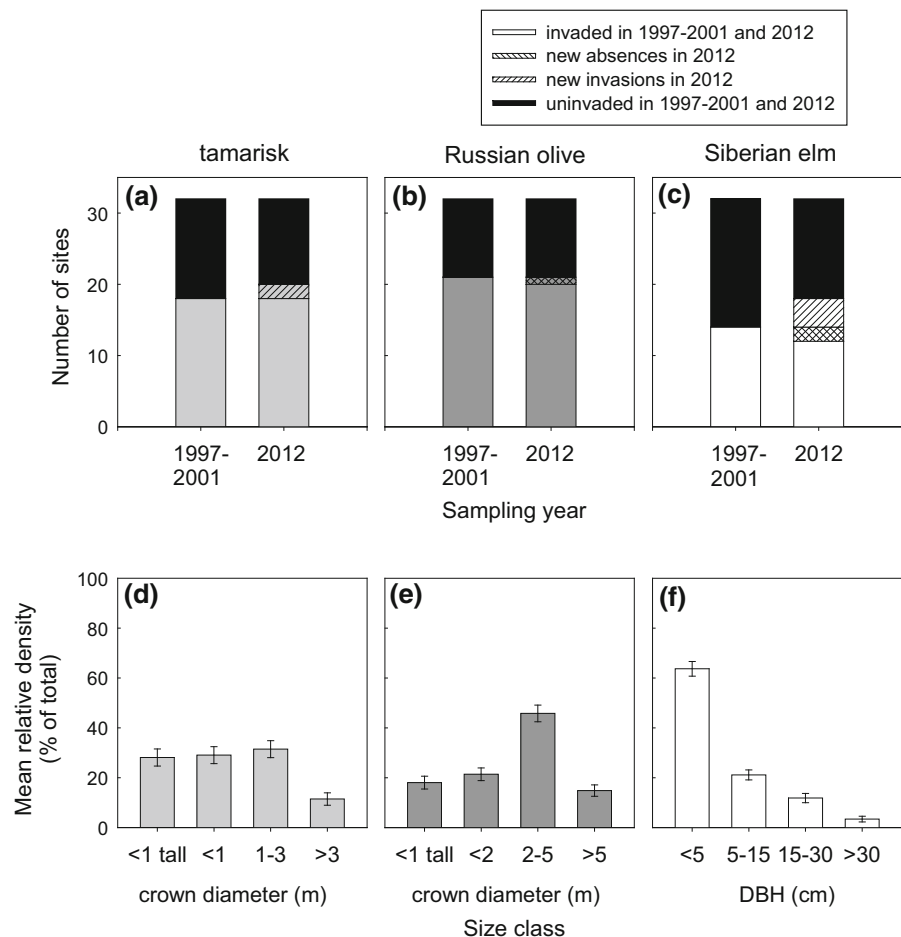
For dominance, like frequency, model convergence issues prevented us from testing for a taxon \times land-use stratum \times basin interaction, but post hoc analyses suggested that differences among taxa depended on

interacting effects of land-use stratum and basin. Siberian elm dominance was higher than tamarisk and Russian olive dominance in predominantly-Developed sites (post hoc taxon, $F_{2,40} = 11.0$, $p = 0.0002$). In contrast, in predominantly-Undeveloped sites in the Colorado headwaters basin, tamarisk dominance was higher than Siberian elm dominance (post hoc taxon \times land-use, $F_{4,40} = 4.8$, $p = 0.003$). Dominance did not differ significantly among taxa in predominantly-Cultivated sites. In addition, Siberian elm dominance was higher than Russian olive dominance in the upper Arkansas River basin (post hoc taxon, $F_{2,27} = 5.9$, $p = 0.007$).

Invasive taxa size-class structure

Tamarisk individuals were evenly distributed among size-classes in most basins (Fig. 6d). However, small individuals (< 1 -m tall) made up a larger proportion of

Fig. 6 a–c Change in tamarisk, Russian olive, and Siberian elm occurrence between 1997–2001 and 2012, in 32 sites that were sampled in both the current study and a previous survey. **d–f** Mean percent of total density composed of each of four size-classes of tamarisk, Russian olive, and Siberian elm, averaged across river basins and land-use strata. Error bars are one standard error of the mean (SEM). Size-classes differed for each taxon, reflecting differences in growth form and stature; hence, comparisons among taxa may be misleading. For tamarisk and Siberian elm, differences in relative abundance among size-classes varied among river basins (see “Results” section); separate means for each river basin are shown in Fig. S4 in Online Resource 1



populations in the upper/middle Rio Grande than in the Colorado headwaters and South Platte River basins (size-class \times basin, $F_{12,104} = 2.5$, $p = 0.007$; post hoc basin, $F_{3,65} = 4.7$, $p = 0.005$) (Online Resource 1: Fig. S4).

Russian olive populations were mainly composed of mid-sized individuals with 2–5-m crown diameters in all four river basins (size-class, $F_{4,82} = 547.1$, $p < 0.0001$; Fig. 6e).

Siberian elm populations were mainly composed of small individuals < 5 -cm DBH, with few trees > 15 -cm DBH and very few trees > 30 -cm DBH in most river basins (Fig. 6f; Online Resource 1: Fig. S4). This pattern was less pronounced in the South Platte River basin (size-class \times basin, $F_{12,192} = 3.8$, $p < 0.0001$), where individuals < 5 -cm DBH made up only $45 \pm 7\%$ of the population and trees > 30 -cm DBH made up $12 \pm 4\%$ of the population (36 of 554 individuals) (post hoc basin; < 5 -cm DBH, $F_{3,115} = 6.6$, $p = 0.0004$; > 30 -cm DBH, $F_{3,115} = 6.1$, $p = 0.0007$).

Change in invasive taxa occurrence at revisited sites

In the 32 sites that we revisited 11–15 years after a previous survey, tamarisk had invaded 2 of the 14 sites (14%) where it was previously absent, Russian olive had invaded 1 of 11 sites (9%), and Siberian elm had invaded 6 of 18 sites (33%) (Fig. 6a–c). The rate of invasion did not differ significantly among taxa ($\chi^2 = 3.0$, $p = 0.3$). We also failed to find Russian olive in one site and Siberian elm in two sites where they were observed previously. New invasions occurred in the upper/middle Rio Grande and South Platte River basins for tamarisk, the upper/middle Rio Grande basin for Russian olive, and all four basins for Siberian elm. All but one of the previously uninvaded sites were in predominantly-Undeveloped areas; there was no change in occurrence in the one predominantly-Cultivated site.

Discussion

Landscape-scale drivers of riparian invasion

Occurrence versus abundance and dominance

The principal environmental drivers of invasive species occurrence differed markedly from the

principal drivers of abundance and dominance in this study. Tamarisk, Russian olive, and Siberian elm occurrence was driven primarily by climate and, for Russian olive and Siberian elm, secondarily by propagule pressure from nearby planting (Fig. 4). Mean annual temperature was the most important predictor of occurrence for all three invaders, with cooler temperatures at higher elevations apparently restricting colonization and survival. Nearby planted Russian olive and Siberian elm were the second most important predictors of Russian olive and Siberian elm occurrence, suggesting that seed production and dispersal from planted individuals increased propagule pressure and thus contributed to invasion. In contrast, environmental drivers likely to affect resource availability and disturbance, such as urban land-use, streambank stabilization, streamflow intermittency and forest cover, were the most important predictors of density and dominance for different taxa, and were considerably less important predictors of occurrence (Figs. 3, 4).

These results support the idea that successful invasion depends on the ability of non-native species to pass through a series of interacting filters (Milbau et al. 2009; Mortenson and Weisberg 2010; Theoharides and Dukes 2007). Propagule pressure and dispersal determine whether and how many potential invaders can reach a site within a novel continent or region (Simberloff 2009). Then, climate is often the primary environmental factor that determines whether and where potential invaders can survive, with secondary, interacting roles of resource availability, disturbance, and biotic interactions determining the likelihood of successful colonization (Menuz and Kettenring 2013; Theoharides and Dukes 2007; Wisz et al. 2013). At sites with adequate propagule pressure and abiotic and biotic conditions for colonization, the combined effects of resource availability, disturbance, and biotic interactions then determine whether the invader is able to increase in abundance and achieve dominance over native species (Catford et al. 2009; Theoharides and Dukes 2007). The differences in drivers of occurrence, density, and dominance in the present study underscore the importance of using abundance measures to understand and predict invasive species distributions (Bradley 2013; Truscott et al. 2008). Models based on occurrence alone will not necessarily identify conditions where invasive

species are most abundant and hence likely to have greatest impact.

The role of land-use

Human land-use in and surrounding the riparian corridor can lead to streambank stabilization and channelization, vegetation management or removal, domestic grazing, soil disturbance, and eutrophication, all of which may contribute to invasion (Aguilar et al. 2001; Liendo et al. 2015; Meek et al. 2010; Moffatt et al. 2004; Pennington et al. 2010). However, few studies have examined land-use effects on riparian invasion in the western USA (Ringold et al. 2008). Land-use was a critical factor for invasion in the present study, but its role and importance varied among taxa. Urban and suburban land-use adjacent to the floodplain were key predictors of higher Siberian elm density and dominance (Figs. 3, 4). Further, urban land-use, but not suburban land-use, moderately increased the likelihood of Siberian elm and Russian olive occurrence. In contrast, suburban land-use reduced tamarisk dominance, and none of the land-use types we examined were important predictors of tamarisk occurrence and density or Russian olive density and dominance. The distinct responses of the different taxa to different land-use types suggest that the importance of land-use in riparian invasion depends on specific characteristics of both the invasive species and the land-use.

Several aspects of urban and suburban land-use may have contributed to Siberian elm and Russian olive invasion. First, streambank stabilization by riprap, placed rock, and walls may have created more favorable habitat for Siberian elm. Streambank stabilization tended to be more extensive with urban land-use and, to a lesser degree, with suburban, transportation, and recreational land-use (Online Resource 1: Table S4), and was one of the strongest predictors of higher Siberian elm density (Fig. 4f). In the dry extremes of its native range, Siberian elm growing in montane steppe ecosystems tend to occupy stony soils on steep slopes, which may increase water availability by facilitating deeper root growth or capturing rainwater in rock crevices (Dulamsuren et al. 2009a). Riprap along riparian corridors may create similar habitat in its introduced range. Second, landscaping in the riparian corridor associated with suburban land-use may have reduced habitat suitability for thicket-

forming shrubs like tamarisk, and thus increased dominance by trees like Siberian elm. Among the common native taxa at the sites, suburban land-use was also associated with higher dominance by narrowleaf cottonwood trees and lower dominance by thicket-forming, narrowleaf/sandbar/dusky willow shrubs (Online Resource 1: Table S5). With regard to Siberian elm and Russian olive occurrence, propagule pressure was probably higher in urban areas due to higher frequency of nearby planted Siberian elm and Russian olive (Online Resource 1: Table S4). However, the CI tree for Siberian elm occurrence indicated that adjacent urban land-use was an important predictor even within sites with nearby planted Siberian elm (Fig. 3e). Siberian elm may have been planted more densely in urban areas, leading to even higher propagule pressure than in other areas with planted Siberian elm. In addition, anthropogenic floodplain disturbance in urban areas may increase opportunities for colonization by Siberian elm and Russian olive, as both also often occur in other disturbed habitats, such as roadsides, abandoned farmland, and vacant lots (Christensen 1964; Olsen and Knopf 1986). Alternatively, channel stabilization and reduced channel migration and fluvial disturbance in urban areas may favor Siberian elm and Russian olive because they are larger-seeded and shade tolerant, and therefore less dependent on fluvial disturbance for establishment than tamarisk, cottonwoods, and willows (Reynolds and Cooper 2010). Finally, impervious surfaces in urban areas increase surface water runoff and thus often reduce groundwater recharge and base flows (McGrane 2016), which might favor Siberian elm and Russian olive because their seedlings are relatively drought-tolerant (Reynolds and Cooper 2010; Su et al. 2014). Drain pipes associated with the bridges at our sites may have contributed further to this effect, but we lacked data on drain pipe abundance at our sites to test this hypothesis.

Despite apparent land and vegetation management associated with agricultural land-use in and adjacent to the floodplain, we observed little evidence of effects of agriculture on tamarisk, Russian olive, or Siberian elm invasion. Further, although domestic grazing can alter riparian geomorphology and vegetation (Belsky et al. 1999; Trimble and Mendel 1995), and threatens Siberian elm populations in parts of its native range (Li et al. 2003; Liu et al. 2012), there was little

evidence of grazing effects on invasion in the present study or in McShane et al. (2015).

Although tamarisk's high seed production and viability, rapid seedling growth, and early reproductive maturity make it well-adapted to fluvial disturbance (Glenn and Nagler 2005; Stromberg et al. 2007), our results suggest that human disturbance due to local land-use does not facilitate tamarisk colonization or spread. All land-use types we examined either reduced or were unimportant to tamarisk success. Similarly, in a study of 12 invasive riparian taxa across the western USA, Russian olive and most other invasive species occurred more frequently along river reaches with some form of human disturbance, but tamarisk did not (Ringold et al. 2008).

Additional differences in environmental drivers among taxa

The importance of environmental drivers other than land-use also differed considerably among tamarisk, Russian olive, and Siberian elm, suggesting that the different invaders may have greater impacts and require more intense management under different riparian conditions.

Tamarisk occurrence was associated with warmer temperatures than Russian olive and Siberian elm, based on CI tree thresholds (Fig. 3) and odds ratios (Table 1) and in accord with previous studies on tamarisk and Russian olive (McShane et al. 2015). Surveys outside our study region indicate that tamarisk also occurs frequently farther south and at lower elevations, where temperatures are warmer, whereas Russian olive does not (Guilbault et al. 2012; Nagler et al. 2011). Siberian elm occurrence had the coldest temperature CI tree thresholds and odds ratios of the three taxa, suggesting that Siberian elm may occur in even colder areas than Russian olive, in accord with its more northern native distribution in Eurasia. However, Siberian elm's susceptibility to frost damage in the USA (Klingaman 1999) may make it less competitive in the colder parts of its introduced range.

Nearby planting was important to Russian olive and Siberian elm occurrence, but not to tamarisk, in accord with McShane et al. (2015), suggesting that elevated propagule pressure due to seed production from planted individuals is contributing to the spread of Russian olive and Siberian elm. Because Russian olive

and Siberian elm cannot spread vegetatively, seed availability is essential for their colonization and establishment. Planted Russian olive and Siberian elm were more common than planted tamarisk (68 and 77% compared to 5% of sites), perhaps because more Russian olive and Siberian elm have been recently planted and/or more planted tamarisk have been removed. In addition, propagule pressure from intentional planting may be more important to Russian olive and Siberian elm because they are more strongly dispersal-limited than tamarisk. Russian olive's ~ 90-mg fruits and Siberian elm's ~ 6-mg samaras almost certainly travel shorter average distances than tamarisk's 0.01-mg, plumed seeds (Schopmeyer 1974), although all three species may sometimes disperse long distances via hydrochory (Rood et al. 2010), Russian olive seeds sometimes disperse long distances via zoochory (Edwards et al. 2014), and Russian olive's longer seed longevity may give it more time to disperse. As a result of greater dispersal-limitation, more recent introduction, and slower maturation, Russian olive and Siberian elm may be at earlier phases of colonization and range expansion than tamarisk, when propagule pressure from external sources may contribute more to invasion (Lesica and Miles 2001; McShane et al. 2015).

Riparian plant communities in the arid and semiarid western USA are typically structured by water availability and fluvial processes, which are determined by both streamflow hydrology and local precipitation (Merritt et al. 2010; Patten 1998). Tamarisk, Russian olive, and Siberian elm are all thought to be relatively drought-tolerant (Glenn and Nagler 2005; Katz and Shafroth 2003; Nagler et al. 2011; Perry et al. 2013; Read 1958), but had distinct responses to variables related to water availability in this study. Surprisingly, intermittent streamflow was not an important predictor of tamarisk invasion, in contrast to previous studies conducted at smaller, river-scales (Lite et al. 2005; Stromberg et al. 2007). Instead, low annual precipitation was one of the most important predictors of tamarisk occurrence and Russian olive abundance both in the present study (Figs. 3, 4) and in McShane et al. (2015), suggesting that low surface soil moisture due to low precipitation may give tamarisk and Russian olive a competitive advantage over more mesic native riparian species. In contrast, intermittent streamflow was among the most important predictors of higher Siberian elm dominance (Figs. 3g, 4g),

suggesting that Siberian elm may be better adapted to deep groundwater due to low streamflow than other woody riparian species. In its native range, Siberian elm occupies dense, tall, phreatophytic riparian forests in humid river valleys, but also dominates open, upland woodlands of stunted, short-lived, sparsely distributed trees in semi-arid savanna, sandland, and montane steppe, relying on deep roots and high root allocation to access limited groundwater (Dulamsuren et al. 2009a; Jiang et al. 2014; Park et al. 2012; Schlutz et al. 2008; Su et al. 2014). Siberian elm also commonly colonizes uplands in its invaded range, unlike tamarisk and Russian olive. In the present study, Siberian elm may have achieved higher rank dominance in sites with intermittent streamflow in part because other riparian trees were less abundant or competitively inferior there. In a study of USA shelterbelts, plains cottonwood suppressed Siberian elm growth in moist lowlands, but Siberian elm reduced plains cottonwood survival in drier uplands (Read 1958).

Despite the widely recognized role of streamflow regulation in tamarisk and Russian olive invasion (Merritt and Poff 2010; Nagler et al. 2011; Ringold et al. 2008; Stromberg et al. 2007), upstream reservoir storage was not an important predictor of invasion in our study. More specific measures of flow regime and flow regulation (e.g., change in timing, frequency, duration, or magnitude of high and low flows) might have been more clearly related to invasion, but those data were not available for our wide array of sites. For example, McShane et al. (2015) found that late peak flows and low stream power, both of which are sometimes associated with flow regulation, were important predictors of tamarisk and Russian olive occurrence.

Higher riparian forest cover was associated with higher Russian olive frequency and density, and to a lesser extent Siberian elm density, but not with tamarisk. Russian olive seedlings can establish in deeper shade than tamarisk, perhaps because of their larger seed reserves (Reynolds and Cooper 2010). Siberian elm has been indexed as more shade-tolerant than both Russian olive and tamarisk (Niinemets and Valladares 2006). Forest shade may favor Russian olive and Siberian elm recruitment by reducing water stress, especially in sites with warmer temperatures or lower precipitation (Figs. 3c, 3d). However, causation in these associations is unclear, as higher Russian olive

and Siberian elm density also probably contributed to higher forest cover.

Implications for tamarisk, Russian olive, and Siberian elm management

Together, our results indicate specific environmental conditions where riparian managers are most likely to need to control dense populations of the three invasive taxa. In particular, Russian olive and Siberian elm are more likely to occur in urban areas near planted propagule sources. In addition, Russian olive is more likely to be abundant in forested sites, while Siberian elm is more likely to be abundant in urban and suburban sites with stabilized streambanks. The importance of propagule pressure suggests that reducing on-going planting of Russian olive and Siberian elm would slow their spread. Currently, sale of Russian olive and Siberian elm in the western USA is restricted only where they are listed as noxious weeds: Colorado, Montana, New Mexico, and Wyoming for Russian olive and New Mexico for Siberian elm. Also, the importance of streambank stabilization to Siberian elm suggests that reducing installation of bank-stabilizing structures could reduce Siberian elm abundance.

Siberian elm: An unrecognized important invader?

Current status of Siberian elm invasion

The frequency, abundance, and dominance of Siberian elm in this study suggests that Siberian elm invasion in riparian ecosystems of the western USA warrants greater attention from land managers and the scientific community. Siberian elm occurred as or more frequently than tamarisk and Russian olive in all river basins and land-use strata except for predominantly-Undeveloped sites in the Colorado headwaters. Further, in predominantly-Developed sites, Siberian elm had higher density and dominance than tamarisk and Russian olive. Across our study sites, Siberian elm was one of the five dominant taxa at more sites than any other taxa except narrowleaf/sandbar/dusky willow and plains/Rio Grande/Fremont cottonwood (Fig. 2).

Our stratified sampling design overestimated Siberian elm prevalence in the study region by sampling predominantly-Developed areas to a greater extent than they occurred in the region. However, even in

predominantly-Undeveloped areas, Siberian elm occurred as or more frequently than tamarisk and Russian olive in most river basins (Fig. 5c). Sampling at bridge-crossings also may have overestimated Siberian elm density because streambank stabilization is more common at bridge crossings. However, including streambank stabilization as a covariate did not alter the results of our density comparisons, indicating that Siberian elm density was higher than tamarisk and Russian olive density in predominantly-Developed areas regardless of variation in streambank stabilization. In addition, invasive species control efforts aimed at tamarisk and Russian olive could have contributed to the relatively high Siberian elm frequency and abundance in our study. However, we observed little evidence of mechanical, chemical, or biological control of any woody taxa across sites. Few sites contained cut stumps or standing dead trees. Tamarisk had yellow or brown foliage in 24 sites, which could have been due to chemical or biological control; however, we included those individuals in measures of frequency, density, and dominance as they appeared to be alive, so they did not contribute to lower tamarisk frequency or abundance. Further, tamarisk and Russian olive occurrence in the sites we revisited did not decline in the decade before this study (Fig. 6), suggesting that control efforts have not been sufficiently widespread to influence occurrence across the study region.

Are Siberian elm populations expanding?

Although Siberian elm was first introduced to North America over a century ago, it may still be expanding in range, frequency, or abundance. Many invasions exhibit lag times between initial colonization and subsequent population growth and range expansion, as a result of slow dispersal, exponential population growth, and/or genetic change (Crooks 2005; Simberloff 2009). For example, widespread Russian olive invasion in the western USA did not become apparent until 2–5 decades after introduction (Katz and Shafroth 2003). Riparian hybrid crack willow invasion in the western USA appears to be proceeding even more slowly, perhaps because it relies almost entirely on vegetative reproduction for dispersal (Shafroth et al. 1994). For Siberian elm, the high importance of nearby planting to occurrence suggests that Siberian elm's current distribution is dispersal-limited, and that

Siberian elm may continue to spread to additional suitable habitat. Among the sites we revisited, Siberian elm colonized previously uninvaded sites at two and three times the rates of tamarisk and Russian olive, respectively, in the decade before this study (Fig. 6a–c). Although this difference was not statistically significant, perhaps due to the small sample size, it suggests that Siberian elm may be spreading faster than the other taxa.

Whether Siberian elm is continuing to increase in abundance where it occurs is less clear. We did not observe extensive Siberian elm monocultures like those created by tamarisk and Russian olive in some settings. Unlike tamarisk and Russian olive, Siberian elm populations were dominated by small individuals and included very few large individuals (Fig. 6f), which could reflect recent invasion or poor recruitment to larger size-classes.

Environmental conditions associated with Siberian elm invasion suggest that continued environmental change also may influence the future spread of Siberian elm. New urban and suburban development, and associated streambank stabilization and planting of Siberian elm, may widen Siberian elm's distribution and increase its abundance where it invades. Further, predicted warming in the western USA with climate change may contribute to Siberian elm range expansion by increasing temperatures at higher elevations and northern latitudes (Christensen and Lettenmaier 2007), and to Siberian elm dominance by reducing summer streamflow and increasing streamflow intermittency (Perry et al. 2012; Seager et al. 2013).

Should riparian managers address Siberian elm invasion?

Control of Siberian elm invasion has rarely been considered to date (Ding et al. 2006; USDA 2014). Siberian elm's frequency, abundance, dominance, and potential for spread in the study region suggest that Siberian elm management should be given greater consideration. The breadth of its naturalized range, including most of the USA, Canada (Davis et al. 2013), Mexico (Todzia and Panero 1998), Argentina (Zalba and Villamil 2002), Spain (Gonzalez-Munoz et al. 2013), and Italy (Brunet et al. 2013), is also cause for concern.

A key unanswered question is whether and how Siberian elm invasion influences riparian ecosystem

services. Like Russian olive, Siberian elm is relatively large-seeded, drought-tolerant, and shade-tolerant, and so may have similar impacts, such as increasing the longevity of late-successional riparian forests and competing with native understory trees (Katz and Shafroth 2003). Mature Siberian elm are shorter than cottonwoods, but taller than tamarisk and Russian olive, and so may further increase intermediate-height forest canopy structure. Siberian elm is not susceptible to Dutch elm disease (DED; *Ophiostoma novo-ulmi*), and therefore may be particularly likely to invade areas where native elm populations have declined due to DED. However, Siberian elm is susceptible to many insect herbivores and pathogens, including the Eurasian elm leaf beetle (*Pyrrhalta luteola*) and elm leafminer (*Kaliopfenusa ulmi*), cankers, and wetwood flux (Bosu et al. 2007; Leopold 1980), which may reduce its competitive ability. Kominoski et al. (2013) posited that because Siberian elm is structurally similar to cottonwood it may serve as a better replacement than tamarisk and Russian olive for cottonwood in riparian ecosystems where changes in streamflow, land-use, or floodplain management have contributed to declines in native riparian vegetation. Future research should examine effects of Siberian elm invasion on plant community composition, wildlife habitat, flood mitigation, erosion, water quality, and recreational value of invaded riparian ecosystems.

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