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Riparian trees and aridland streams of the southwestern United States: An assessment of the past, present, and future

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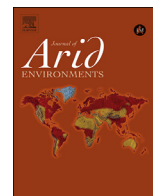D. Max Smith[*], Deborah M. Finch

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ABSTRACT

Riparian ecosystems are vital components of aridlands within the southwestern United States. Historically, surface flows influenced population dynamics of native riparian trees. Many southwestern streams has been altered by regulation, however, and will be further affected by greenhouse warming. Our analysis of stream gage data revealed that decreases in volume of annual discharge and mean peak discharge and a shift to earlier peak discharge will occur in the Southern Rockies region of Colorado, New Mexico, and Utah. These changes will likely decrease rates of reproduction and survival of cottonwood (*Populus fremontii* and *Populus deltoides* ssp. *wislizenii*), Goodding's willow (*Salix gooddingii*), and box-elder (*Acer negundo*), which rely on surface flows to stimulate germination and recharge groundwater aquifers. Streams in the Central Highlands of Arizona and New Mexico will likely see reductions in annual discharge volume, which could limit reproduction and survival of the above taxa and Arizona sycamore (*Platanus wrightii*). These effects may be exacerbated by demands of expanding urban areas and agricultural operations, but could also be ameliorated by increasing water use efficiency and environmental mitigation. These factors must be considered, along with climate projections, when planning for conservation of riparian trees and the animal communities they support.

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1. Introduction

Riparian ecosystems are uncommon and highly-valued components of aridlands in the western United States. Much of this value comes from woody plants that grow along the alluvial reaches of many streams, forming green avenues on the desert landscape. Riparian trees in particular are essential components of wildlife habitat. While living, as standing snags, and as fallen woody debris, these trees provide animals with shade, shelter, and foraging opportunities that are often absent in adjacent plant communities (Carothers et al., 1974; Bock and Bock, 1984; Brown, 2002; Smith et al., 2012; Smith and Finch, 2014). For centuries southwestern streams and their riparian trees have been favored by human communities as sources of material goods and for their aesthetic value (Bock and Bock, 1989; Weber and Stewart, 2009).

Hydrological patterns have deviated substantially from historical conditions at many streams in the southwestern United States. Changes have occurred in large part due to regulation of streams for

agricultural, industrial, and municipal purposes. Water has been diverted in the Southwest since the establishment of pre-Columbian societies, but changes accelerated during the 20th century when demand for irrigation and municipal water increased with the rapid expansion of agricultural and urban areas (Phillips et al., 2011; Summitt, 2013). To meet these demands, federal agencies and local irrigation districts conducted a series of large-scale water projects from the early 1900s to the 1970s. These projects included the construction of increasingly large dams and reservoirs and transbasin diversions. Because of these projects, discharge is now reduced from historical levels at many streams and some sections that once had perennial flows now run dry, apart from periods of heavy runoff (White and Stromberg, 2009). Other sections are inundated by dams while, below dams, magnitude and timing of peak discharges are altered when releases are scheduled for irrigation and power generation (Finch et al., 2014).

Southwestern streams and their riparian ecosystems are also vulnerable to alterations resulting from anthropogenic climate change, the effects of which are expected to be especially severe in the American Southwest (Seager et al., 2007; Garfin et al., 2014). Climatologists predict that, under current and projected levels of CO_2 emissions, higher temperatures and smaller snowpacks will

reduce the amount of runoff that enters streams (Pierce et al., 2008; Seager and Vecchi, 2010; Seager et al., 2013). Droughts, which have been a regular feature in recent years, will continue to occur, but with increasing severity, resulting in further reductions in discharge volume (Cayan et al., 2010; Woodhouse et al., 2010; Gutzler and Robbins, 2011). Summer monsoons also cause flood events in many of the region's streams (Stromberg et al., 2010). Changes in patterns of these storms are more difficult to model than other types of precipitation, but there is evidence that greenhouse warming will force monsoons to occur later in the year and with greater severity, further changing stream dynamics (Cook and Seager, 2013; Serrat-Capdevila et al., 2013). These projected changes will undoubtedly affect riparian ecosystems by limiting germination and increasing mortality of species dependent on floods and groundwater, to the benefit of generalist species, including nonnative trees and shrubs (Stromberg et al., 2010; Perry et al., 2012).

Current and projected hydrological patterns are not uniform among southwestern streams (Dixon et al., 2009), and an understanding of this variation is needed to forecast the effects of climate change on riparian trees. Sources of runoff vary from snowfields in the Southern Rockies to rain in the mountains near the U.S.-Mexico border to combinations of snow and rain in the areas between (Blakemore et al., 1994). Surface flow and groundwater dynamics are also influenced by variables including geology, climate, and extent of regulation (Merritt and Poff, 2010). Consequences of future changes in temperature and precipitation will therefore vary across the American Southwest (Dixon et al., 2009; Perry et al., 2012). In addition to response of streams to climate change, response of woody species will likely vary as well, given their differing requirements for reproduction, growth, and survival. Woody riparian plants also vary in their ecological relationships to other plants and animals. Climate change effects on riparian ecosystems may therefore be affected by interactions between floristic and hydrological characteristics.

Streams in the Colorado River and Rio Grande basins have been extensively studied for over a century, first to develop an understanding of hydrological patterns, which was essential to the development of infrastructure, and later to understand the ecological consequences of regulation (Phillips et al., 2011). Hydrological projections have also been made for many of these streams to help water users plan for future needs in a changing climate (Miller et al., 2011). By combining these sources of information, we (1) describe characteristics of surface flows measured at stream gage sites distributed across the southwestern U.S., (2) compare projected changes in these characteristics, (3) review hydrological requirements and ecological function of four taxa of riparian trees, and (4) discuss the likely effects of hydrological change on aridland riparian forests. This information can be used to prioritize research and management actions necessary to protect imperiled riparian species and their habitats.

2. Methods

2.1. Stream sites

We compiled information for 11 stream gage sites in the Colorado River and Rio Grande basins (Supplemental map). We chose gage sites that were located on alluvial reaches with woody vegetation. At each site, measurable surface flows occur during most months of the year, at least 40 years of hydrological data have been recorded by the U.S. Geological Survey (USGS), and future discharge patterns have been modeled by the U.S. Bureau of Reclamation (USBOR). For the purposes of this analysis, we classified the streams into two geographical groups. Six of the streams, referred to

hereafter as Southern Rockies streams, are headwatered in the Rocky Mountains of Wyoming and Colorado. Five streams, referred to as Central Highland streams, are headwatered in the Central Highland ranges of Arizona and New Mexico. The Southern Rockies stream sites are on the Colorado River, the Green River, the Gunnison River, the San Juan River, the Rio Chama, and the Rio Grande. The Central Highland stream sites are on the Gila River, the Salt River, the San Francisco River, Tonto Creek, and the Verde River. Gage sites are between 600 and 2000 m in elevation, and are located in the states of Arizona, Colorado, New Mexico, and Utah (Table 1).

2.2. Tree species

We visited stream gage sites and reviewed published information to describe the distribution and biology of four native tree taxa that are important components of aridland riparian ecosystems and whose reproduction and survival are closely tied to surface flows (Fig. 1). Two superficially similar cottonwood tree species: Fremont cottonwood (*Populus fremontii*) and Rio Grande cottonwood (*Populus deltoides* ssp. *wislizenii*), are referred to hereafter as cottonwood. The remaining taxa are Goodding's willow (*Salix gooddingii*), boxelder (*Acer negundo*), and Arizona sycamore (*Platanus wrightii*). These taxa are distributed across several southwestern stream systems and have been identified by multiple sources as important components of riparian wildlife habitat. We obtained information about the distribution of each species from the Global Biodiversity Information Facility website (www.gbif.org). We reviewed peer-reviewed publications to summarize hydrological effects on their reproduction, survival, and use by animal communities.

2.3. Hydrological analyses

We analyzed historical and projected patterns of hydrological variables that affect survival and reproduction of riparian trees. These variables, defined here, were *annual discharge* (in million cubic meters): the total volume of water measured at a stream gage site each year; *mean daily discharge* (in cubic meters per second): the mean discharge volume for each day of the year; *peak discharge volume* (in cubic meters per second): the maximum mean daily discharge value recorded each year; and *peak discharge date* (in water year ordinal date): the day of each year when the peak discharge occurred. We selected these variables because large fluctuations in annual discharge and mean daily discharge affect survival of riparian trees through drought and flood mortality. In addition, peak discharge magnitude and date determine whether or not riparian trees will successfully reproduce during a given year (Lytle and Merritt, 2004).

We obtained mean daily discharge data for the longest complete historical period (no gaps in data exceeding 1 month) ending in 2013 at each of the 11 stream gage sites (Table 1). Data were collected by USGS and made available online by the National Water Information System Database (http://waterdata.usgs.gov/nwis). We calculated the total annual discharge for each site for each year of its historical period. To describe characteristics of peak discharges, we determined peak discharge volume and date for each year of the historical period as well. We calculated the mean, maximum, and coefficient of variation (CV) across years for annual discharge and peak discharge volume. We also calculated the mean and CV of peak discharge date across years.

We tested for trends in annual discharge, peak discharge volume, and peak discharge date using the Mann-Kendall statistic. This nonparametric, rank-based test has used to detect positive or negative trends in hydrologic time series data in numerous studies because it does not assume normality and is robust to missing

Table 1
Stream gage sites examined in this study.

| Gage site	Gage #	Gage record	Elevation (m)	State	Basin	Headwaters
Colorado River at Cameo	09095500	1934–2013	1467	Colorado	Colorado River	Rocky Mountains
Gunnison River at Grand Junction	09152500	1917–2013	1411	Colorado	Colorado River	Rocky Mountains
San Juan River at Bluff	09379500	1929–2013	1234	Utah	Colorado River	Rocky Mountains
Green River at Greendale	09234500	1951–2013	1705	Utah	Colorado River	Rocky Mountains
Rio Grande at Otowi	08313000	1919–2013	1673	New Mexico	Rio Grande	Rocky Mountains
Rio Chama near Abiquiu	08286500	1962–2013	1914	New Mexico	Rio Grande	Rocky Mountains
Salt River at Roosevelt	09498500	1914–2013	664	Arizona	Colorado River	Central Highlands
Verde River above Horseshoe Dam	09508500	1946–2013	618	Arizona	Colorado River	Central Highlands
San Francisco at Clifton	09444500	1936–2013	1047	Arizona	Colorado River	Central Highlands
Gila River at Gila	09430500	1928–2013	1419	New Mexico	Colorado River	Central Highlands
Tonto Creek at Roosevelt	09499000	1941–2013	769	Arizona	Colorado River	Central Highlands
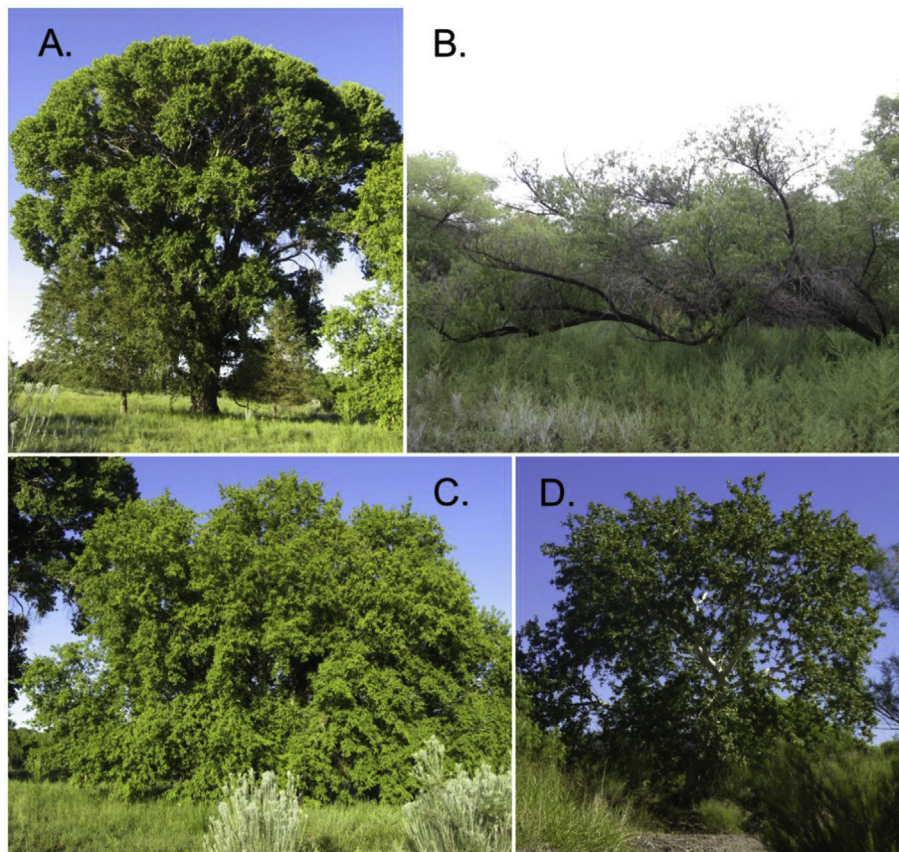
Fig. 1. Native trees of aridland riparian ecosystems in the American Southwest. (A) Fremont cottonwood, (B) Goodding's willow, (C) boxelder, and (D) Arizona sycamore.

values in the data (Hirsch and Slack, 1984; Yue et al., 2002). We used the "zyp" package in R to apply the Trend-Free Pre-Whitening procedure (Yue et al., 2002), which removes serial correlation from the data prior to conducting the Mann-Kendall test. Positive Z scores indicate positive trends in the data and negative Z scores indicate negative trends.

We obtained projections of mean daily discharge for each stream gage site from 1960 to 2099. Projections were made to forecast unregulated inflow to reservoirs (Miller et al., 2011) and are available from the USBOR (http://gis.usbr.gov/Streamflow_Projections/). The projections use bias-corrected spatial downscaled precipitation and temperature data from the World Climate Research Programme Coupled Model Intercomparison Project phase 3 (CMIP3). The precipitation and temperature data were incorporated into a National Weather Service River Forecasting System (NWS RFS) model, along with evapotranspiration demand,

which was estimated using the Variable Infiltration and Capacity (VIC) model, to produce hydrological projections (Miller et al., 2011). The projections, produced by the NWS RFS model, were bias-corrected by ensuring that means from the NWS RFS models, forced with observed temperature and precipitation data, had the same average as models forced with projected data across the same period. We examined output from 36 projections by 15 global climate models (GCMs) run under the A2 emissions scenario (Appendix) for each of the 11 stream sites. We focused on changes to the volume of annual discharge, magnitude of peak discharge, and timing of peak discharge. We projected estimates of these variables for each year from 1980 to 2099. We examined projected changes in hydrological variables by calculating their means and CVs across the 36 model runs for the periods of 1980–2009, 2010–2039, 2040–2069, and 2070–2099. We then calculated the departure from the 1980–2009 mean for each of the three future

periods and multiplied this figure by the historical mean for the period of 1980—2013. We also evaluated model agreement among sites by analyzing projections from each model run with the Kendall-Mann test, as with the hydrological data. We determined the percentage of model runs predicting increases, decreases, or no change in each hydrological variable, using a p value of 0.10 as the level of significance (Yue et al., 2003). If output from ≥50% of model runs fell into one of the above categories, we interpreted results as reflecting moderate to high model agreement for change or no change at that stream site. If output from ≥50% of the model runs did not fall into any of the categories, we interpreted the level of uncertainty as too high to draw conclusions.

3. Results and discussion

3.1. Observed hydrological variables

The historical stream gage records revealed generalities about the Southern Rockies and Central Highland sites. Five of the Southern Rockies sites had greater mean and maximum annual discharge than any of the Central Highlands sites (Table 2, Fig. 2). The range of mean peak discharge volume was similar between the two site types, but three of the Central Highland sites had greater maximum peak discharge volume than any of the Southern Rockies sites. Timing of peak flows were more consistent at Southern Rockies sites, with peaks that generally occurred in May or June (Fig. 3). On average, peak flows at Central Highland sites occurred in February or March, but annual peaks regularly occurred during other times of the year (Figs. 3 and 4). The Central Highland sites had greater variability in all three hydrological variables, as measured by CV, than any of the Southern Rockies sites.

The differences between Central Highland and Southern Rockies sites result from a number of geophysical factors. With their high elevation (>3000 m) and latitudinal position, the Rocky Mountains accumulate considerable snowpack during the winter months, which contributes to high flows in the spring and summer. The Central Highland ranges are lower in elevation and latitude than the Rocky Mountains, so snowmelt, rain, or a combination of the two can produce high flows (Webb et al., 2007; Neary et al., 2012). The Central Highlands intercept extremely large amounts of rainfall from Pacific frontal storms in winter, tropical storms in the fall, and monsoon storms in the summer (Stromberg et al., 2007; Serrat-Capdevila et al., 2013). Flows of exceptionally high magnitude can therefore occur at different times of year at these sites. The localized nature of many storms and annual variation in their occurrence produce the substantial variation in peak discharge events at Central Highland streams relative to the snowpack-fed Southern Rockies sites.

Observed trends in the three hydrological variables differed between Southern Rockies and Central Highland streams (Table 2). Considerable decreases ($Z < -0.10$) in annual discharge occurred at the San Juan River and Green River sites, which were located downstream of major dams and reservoirs (each exceeding 1 million acre feet capacity) and, in the case of the San Juan site, the San Juan-Chama Project transbasin diversion. The Rio Chama was the only Southern Rockies site showing a positive trend in annual discharge, likely resulting from the water delivered by this diversion (Flanigan and Haas, 2008). The Salt River was the only Central Highlands site showing a negative trend in annual discharge. The river above this station is largely unregulated, so reasons for this trend are unclear. Considerable decreases in peak discharge volume occurred at the four of the Southern Rockies sites (Table 2), all of which have dams and diversions upstream from the sites, including the Colorado-Big Thompson Project, which transports water from the upper Colorado to the east side of the Continental Divide (Phillips et al., 2011; Summitt, 2013). Peak discharge volume considerably increased at the Gila River site, likely due to several heavy precipitation events that occurred in recent decades (Soles, 2008). There were considerable trends for earlier peak discharges at the Gunnison River site and at the Gila River site, but weak trends in this variable at the other sites. Earlier peak discharge at the Gunnison River site could be attributed to accelerated runoff due to warming or to hydrological changes that have occurred following construction of several upstream dams (Friedman and Auble, 1999).

Table 2
Characteristics of hydrological variables measured during the stream gage record at each site. The annual mean, maximum, and coefficient of variation are reported, as well as trend in annual mean, measured with Mann-Kendal tests.

Gage site	Headwaters	Annual discharge (million cubic meters)				Peak discharge volume (cubic meters per second)				Peak discharge timing (ordinal water date)		
		Mean (CV)	Max	Z[a]	p	Mean (CV)	Max	Z	p	Mean (CV)	Z	p
Colorado River at Cameo	Southern Rockies	3416.9 (31.9)	7002.4	−0.10	0.21	514.9 (41.3)	1076.0	−0.18	0.02	248 (4.5)	−0.07	0.35
Gunnison River at Grand Junction	Southern Rockies	2240.8 (40.8)	4718.5	−0.09	0.19	336.2 (59.9)	996.7	−0.30	<0.001	226 (20.7)	−0.15	0.03
San Juan River at Bluff	Southern Rockies	1918.3 (52.1)	6042.0	−0.15	0.04	319.5 (65.8)	1203.4	−0.27	<0.001	241 (37.0)	0.06	0.43
Green River at Greendale	Southern Rockies	1760.0 (39.9)	3741.0	−0.12	0.16	177.5 (62.2)	543.7	−0.07	0.40	218 (33.8)	−0.02	0.81
Rio Grande at Otowi	Southern Rockies	1288.1 (46.1)	3198.1	−0.07	0.34	175.8 (68.0)	628.6	−0.16	0.02	228 (23.2)	0.05	0.49
Rio Chama at Abiquiu	Southern Rockies	414.3 (37.9)	745.8	0.08	0.40	80.3 (55.7)	183.5	−0.02	0.84	225 (23.0)	0.03	0.74
Salt River at Roosevelt	Central Highlands	772.9 (70.7)	2995.2	−0.09	0.18	508.1 (110.6)	2576.8	−0.10	0.15	184 (49.3)	−0.02	0872
Verde River above Horseshoe Dam	Central Highlands	494.5 (73.2)	1937.3	<0.001	1.0	446.5 (124.8)	3114.8	0.05	0.54	168 (62.0)	−0.02	0.83
San Francisco River at Clifton	Central Highlands	185.6 (76.9)	749.1	0.08	0.29	174.5 (141.7)	1478.1	0.02	0.77	191 (65.8)	−0.09	0.23
Gila River at Gila	Central Highlands	140.0 (58.9)	369.4	0.11	0.15	87.7 (137.5)	662.6	0.15	0.04	197 (61.0)	−0.12	0.10
Tonto Creek at Roosevelt	Central Highlands	136.3 (97.3)	578.9	0.001	1.0	216.1 (112.4)	1039.2	0.03	0.73	166 (61.6)	0.02	0.98

[a] Positive values of the Mann-Kendal Z statistic indicates increasing trends, negative values indicate decreasing trends.
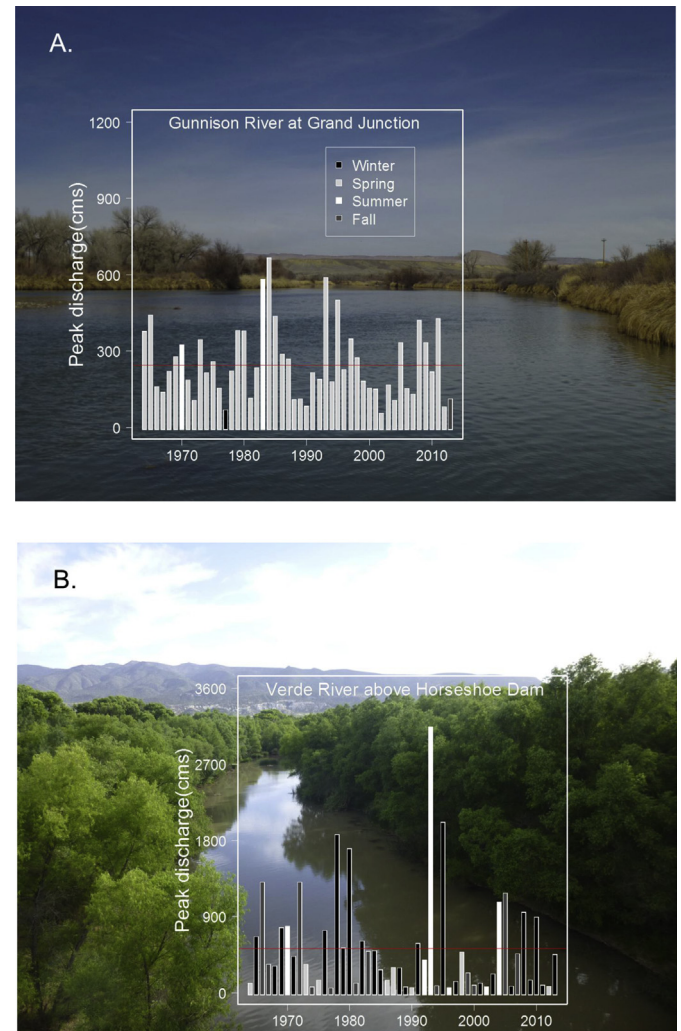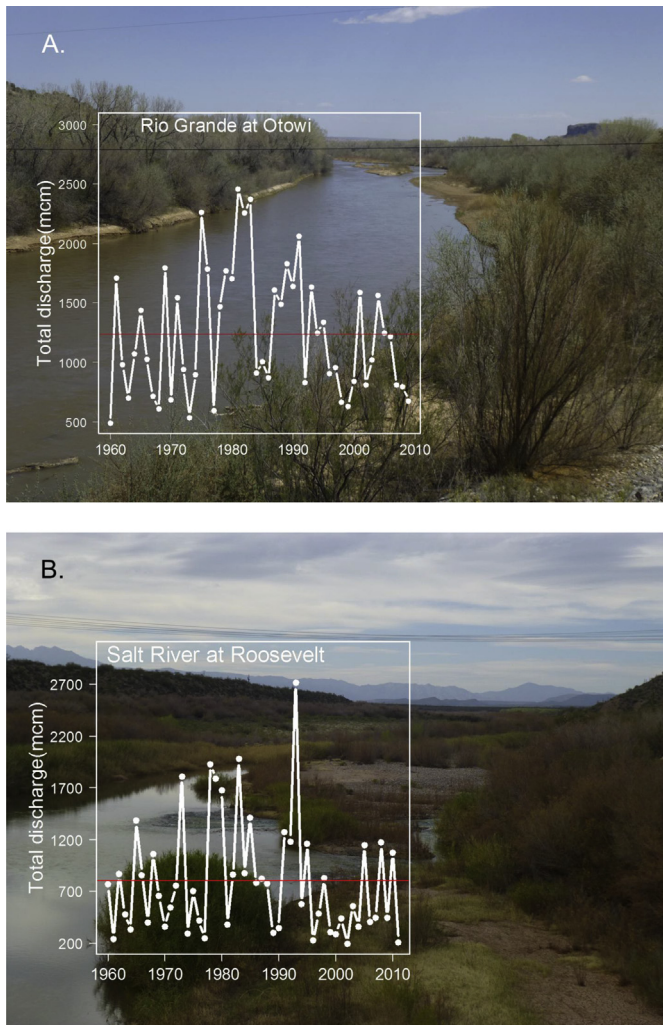
Fig. 2. Examples of variation in total annual discharge, in million cubic meters, at a Southern Rockies stream (A) and a Central Highland stream (B). Red lines indicate long-term means (1960–2011). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 3. Examples of variation in magnitude and timing of peak discharge at a Southern Rockies stream (A) and a Central Highland stream (B). Red lines indicate long-term means (1960–2011). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Earlier peaks at the Gila River site were likely attributable to the recent heavy precipitation events that occurred during winter months.

3.2. Hydrological projections

Decreases in annual discharge were projected at each site except for the Green River, based on means from 15 GCMs (Table 3). Model agreement for decreasing trends was greatest for sites on the Gunnison River, the San Juan River, the Rio Grande, the Rio Chama, and the San Francisco River, at which ≥50% of the model runs predicted negative trends. Decreases in peak discharge volume were projected at each Southern Rockies site except for the Green River and the Rio Chama. Decreases were also projected at the Salt River and Tonto Creek Central Highlands sites (Table 3). The Rio Grande site, however, was the only one in which these decreases were projected by ≥50% of the model runs (Table 3). Earlier peak discharge date was projected for all of Southern Rockies sites and there was high agreement among model runs (>80%) for trends of earlier peak discharge at each of these sites. Later peak discharge date was projected for the Central Highland sites, but there was high agreement among model runs (≥80%) for no change in this variable (Table 3).

The projected decreases in annual discharge at many of the sites we examined fit with climate change projections from other studies in the American Southwest. There is high model agreement for a continued increase in temperature and evaporation in this region (Garfin et al., 2014), which will reduce the amount of precipitation that falls as snow and decrease the amount of rainfall that enters streams (Das et al., 2011; Wi et al., 2012; Vano et al., 2014). This warming will reduce discharge volume in several southwestern streams, even if amount of precipitation is unaffected (Christensen et al., 2004; Seager et al., 2013). Similar reductions in total discharge have been modeled at the Verde River and Salt River by Ellis et al. (2008). Because the climate models we examined do not adequately forecast droughts, which may occur with greater frequency and severity in the Colorado and Rio Grande basins, future decreases in discharge will likely be greater than those projected (Serrat-Capdevila et al., 2013; Gutzler, 2013).

The projected changes in characteristics of peak discharge have been anticipated as a result of climate change. Peak discharges in Southern Rockies streams typically result from snowpack runoff, which is strongly influenced by temperature. The predicted increase in temperatures would shrink the snowpack and accelerate snowmelt (Pierce et al., 2008; Garfin et al., 2014). As a result, peak
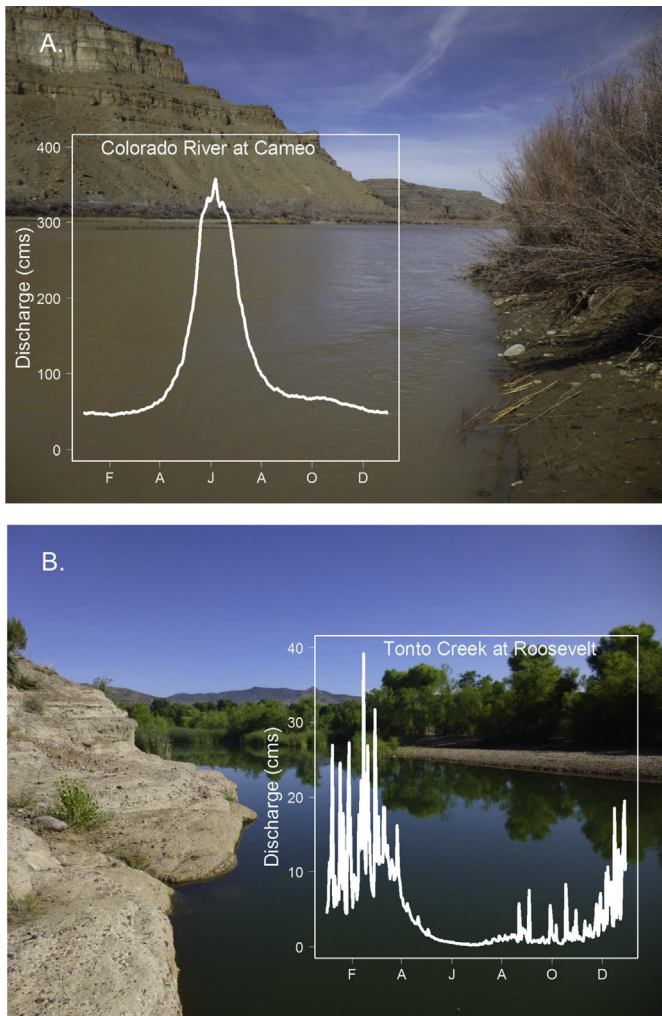
Fig. 4. Examples of mean daily discharge hydrographs at a Southern Rockies stream (A) and a Central Highland stream (B). Line values represent mean daily streamflow for each day of the year between 1960 and 2011.

discharges will on average occur earlier and with lower magnitude (Stewart et al., 2005; Hurd and Coonrod, 2008). We only found moderate model agreement for decreases in future peak discharge volume at one of our sites, the Rio Grande at Otowi, but there was strong agreement on changes to earlier peak discharge date at all of the Southern Rockies sites. Managers should therefore anticipate greater change in timing than magnitude for southwestern streams with snowmelt-driven high flows. Among climate change studies, there is less model agreement on changes in amount of rainfall, which has a greater impact on timing and magnitude of peak discharge at the Central Highland streams (Ellis et al., 2008). Greenhouse warming may result in heavier storms occurring during the summer, fall, and winter periods, which would increase variability of peak discharges from year to year, especially at Central Highland streams, which flood readily when heavy rainfall occurs (Hawkins et al., 2015). There was high agreement among models we examined for no change to volume or timing of peak discharge at Central Highland streams. Decreases in annual discharge may be a greater concern for management of riparian ecosystems along these streams.

As with any model output, there are caveats to the projections we examined. We found disagreement among models with regard to discharge characteristics within stream gage sites. Also, the

projections do not account for current or future regulation of streams (Miller et al., 2011), so much of the future variation in hydrological variables is not included. The relative magnitude of changes, however, is useful for this analysis, assuming that changes in water use will be consistent across the region. Development of site-specific, alternative water use scenarios, similar to those of carbon emission scenarios, is needed to improve projections (Palmer et al., 2009). Finally, we used CMIP3 projections, which are older and less complex than CMIP5 projections because streamflow projections, derived from these models, were not yet available. Though CMIP5 projections do not differ substantially from CMIP3 projections for the western United States (Baker and Huang, 2014), output from CMIP5 models should be incorporated into projections at our stream gage sites as soon as possible to test the validity of our results.

3.3. Biology of focal trees

Based on distribution data from the Global Biodiversity Information Facility, three of the four taxa we examined (cottonwood, Goodding's willow, and boxelder) occur throughout much of the southwestern United States. The fourth taxa, Arizona sycamore, is limited to southern Arizona and southwestern New Mexico. We found cottonwood and Goodding's willows at each of the 11 stream gage sites we examined. These often co-occurring taxa usually grow in alluvial reaches below 2000 m. Their presence along each of the streams indicates that they have adapted to a variety of flow regimes in regulated and unregulated reaches. Boxelders are present in the upper reaches of Southern Rockies and Central Highland streams and are often the dominant trees in canyon-bound segments (Friedman and Auble, 1999). Boxelder can also be a component of mixed deciduous montane riparian communities in alluvial reaches (Stoleson and Finch, 2003). Arizona sycamores are present along Central Highland streams, often occupying higher reaches of streams than Fremont cottonwood and Goodding's willow, though the three species can co-occur in middle reaches (Smith and Finch, 2014).

Reproduction and survival of each of the four tree taxa are influenced and/or determined by hydrological events (Table 4). Each year, reproductive cottonwoods and willows release tiny seeds that are carried by wind or water to potential germination sites. Germination and seedling establishment occurs only if the seeds settle on damp, exposed soil during their month-long viability period (Braatne et al., 1996; Stromberg, 1997). At Southern Rockies streams, cottonwoods release seeds from June through August following the typical peak of snowmelt-driven floods (Molles et al., 1998; Cooper et al., 1999). In the wake of these floods lie sites, devoid of competing vegetation, that are ideal germination spaces for woody pioneer species (Auble and Scott, 1998). As flood waters recede, they leave behind soil moisture that is required for seedling survival (Bhattacharjee et al., 2008). At Central Highland streams cottonwood and willow seed dispersal can occur from February to May, when high flows subside (Beauchamp and Stromberg, 2007). Though high flows regularly occur at other times of the year, especially at Central Highland streams, it is the flows coinciding with cottonwood and willow seed dispersal that are necessary for their reproduction. At Central Highland streams, floods resulting from fall or winter storms provide the scouring and deposition that create germination sites. Subsequent high flows from precipitation or snowmelt in the spring provide moisture that induces germination (Stromberg, 1997). Following floods in the Central Highland or Southern Rockies streams, drawdowns of water tables must not exceed the rates of seedling root growth until taproots gain contact with the capillary fringe above the saturated groundwater table (Mahoney and Rood, 1998; Horton and Clark, 2001; Bhattacharjee

Table 3
Projected characteristics at the stream gage sites used in this analysis. "% of model runs" indicates the percentage of 36 model runs that projected decreasing or increasing trends, as indicated by Mann-Kendal tests, with a significance level of 0.10. Bold values indicate that >= 50% of models predicted decreases or increases.

Gage site	Headwaters	Variable[a]	% Of model runs		Projected means		
			Decrease	Increase	2010—2039	2040—2069	2070—2099
Colorado River at Cameo	Southern Rockies	Annual discharge (mcm)	36	8	3369.8	3267.3	3216.7
		Peak discharge volume (cms)	25	17	492.6	490.7	485.4
		Peak discharge timing (owd)	**100**	0	2423	237	230
Gunnison River at Grand Junction	Southern Rockies	Annual discharge (mcm)	**50**	3	2202.7	2062.1	1965.1
		Peak discharge volume (cms)	31	6	253.3	241.7	228.4
		Peak discharge timing (owd)	**100**	0	212	205	197.5
San Juan River at Bluff	Southern Rockies	Annual discharge (mcm)	**67**	0	1703.1	1525.1	1388.3
		Peak discharge volume (cms)	44	0	238.7	218.8	197.0
		Peak discharge timing (owd)	**100**	0	240	232	223
Green River at Greendale	Southern Rockies	Annual discharge (mcm)	30	17	1679.7	1653.3	1679.3
		Peak discharge volume (cms)	8	28	163.1	168.9	174.9
		Peak discharge timing (owd)	**97**	0	216	211	205
Rio Grande at Otowi	Southern Rockies	Annual discharge (mcm)	**64**	3	1262.3	1106.4	997.9
		Peak discharge volume (cms)	**53**	0	149.1	131.5	117.1
		Peak discharge timing (owd)	**86**	0	229	219	209
Rio Chama at Abiquiu	Southern Rockies	Annual discharge (mcm)	**50**	3	462.1	418.5	392.0
		Peak discharge volume (cms)	36	0	91.1	84.3	79.2
		Peak discharge timing (owd)	**86**	0	226	219	205
Salt River at Roosevelt	Central Highlands	Annual discharge (mcm)	44	3	779.5	708.7	631.0
		Peak discharge volume (cms)	14	8	596.7	573.9	565.9
		Peak discharge timing (owd)	11	0	184	186	178
Verde River above Horseshoe Dam	Central Highlands	Annual discharge (mcm)	36	3	549.8	498.5	444.1
		Peak discharge volume (cms)	14	11	590.8	577.2	575.6
		Peak discharge timing (owd)	14	6	156	160	164
San Francisco River at Clifton	Central Highlands	Annual discharge (mcm)	**50**	3	207.1	191.1	176.2
		Peak discharge volume (cms)	11	17	208.8	214.2	218.0
		Peak discharge timing (owd)	14	0	185	187	176
Gila River at Gila	Central Highlands	Annual discharge (mcm)	47	3	160.8	148.8	139.3
		Peak discharge volume (cms)	14	11	134.7	138.9	142.1
		Peak discharge timing (owd)	8	3	180	174	175
Tonto Creek near Roosevelt	Central Highlands	Annual discharge (mcm)	33	3	153.8	138.4	121.5
		Peak discharge volume (cms)	14	8	293.5	291.1	282.7
		Peak discharge timing (owd)	8	6	166	172	173

[a] Units are mcm = million cubic meters; cms = cubic meters per second, owd = ordinal water date.

Table 4
Characteristics of four native riparian trees examined at Southern Rockies (SR) and Central Highland (CH) streams in this study. The distribution information is based on literature review and our field observations.

Species	Seed longevity	Seed dispersal period	Shade tolerance	Drought tolerance	Distribution
Fremont cottonwood	<2 months	Winter-spring (CH streams), spring-summer (SR streams)	Low	Low-intermediate	SR and CH streams
Goodding's willow	<3 months	Winter-spring (CH streams), spring-summer (SR streams)	Low	Low	SR and CH streams
Boxelder	>5 months	Summer-fall-winter	High	Intermediate	SR and CH streams
Arizona sycamore	>5 months	Fall-winter-spring	Low	Low	CH streams

et al., 2006). Cottonwood seedlings can survive up to four weeks in saturated soils, but mortality occurs if shoots are submerged for over one week (Auchincloss et al., 2013). Willow saplings can survive in saturated soils as long as the shoots are not submerged (Tallent-Halstell and Walker, 2002). High flows that occur in the late summer or fall cause mortality of cottonwood and willow seedlings through flood scour or inundation (Gladwin and Roelle, 1998; Mahoney and Rood, 1998). Likewise, extremely low flows will cause seedling or sapling mortality by lowering the water table too rapidly, causing desiccation (Shafroth et al., 2000). These requirements make cottonwood and willow reproduction sensitive fluctuations in surface flow.

Boxelder and Arizona sycamore have different seed structures than cottonwoods and willows, but their reproduction is also dependent on high surface flows. Boxelders and sycamores produce relatively large seeds that develop during the growing season, unlike cottonwoods and willows, which release seeds at the start of the growing season. Boxelder seeds are released in the summer or fall, become viable the following spring, and will germinate if induced by high flows (Dewine and Cooper, 2007). Sycamore seeds

mature within spherical fruits that are retained on the tree until they fall to the ground during the fall, winter, and spring (Bock and Bock, 1989). The seeds separate from the fruits upon or after hitting the ground, so they are typically not dispersed as far as those of other species. For sycamore germination to occur at streams in Arizona, heavy winter floods must expose sites prior to seed deposition. As with cottonwoods and willows, high flows are needed to stimulate springtime germination (Stromberg, 2002). Sycamore seedlings require additional moisture from surface flows or precipitation to survive their first summer, but are also vulnerable to flood mortality during the summer monsoon (Bock and Bock, 1989). Sycamore establishment is therefore limited by timing and intensity of precipitation and discharge during the winter, spring, and summer seasons. Boxelders differ from cottonwood, willow, and sycamore, in their ability to germinate on top of litter and grow beneath established woody plants (Dewine and Cooper, 2008, 2009). Floods need only dampen soil, not scour sites to encourage boxelder establishment. In fact, Galuska and Kolb (2002) noted that boxelder was one of only two species that did not establish following heavy winter and spring floods along a tributary

of the Verde River in Arizona.

Following establishment, riparian trees remain influenced by hydrological processes. C ottonwood, Goodding's willow, and Arizona sycamore are phreatophytic, hydroriparian trees that usually require a shallow groundwater connection for growth and survival (Snyder and Williams, 2000; Stromberg and Merritt, 2015). Low flows can increase depth to groundwater in the floodplain, causing dieback and mortality of cottonwoods and willows (Amlin and Rood, 2002; Stromberg et al., 2007; Tyree et al., 1994), giving drought-tolerant species a competitive advantage (Horton et al., 2001; Lite and Stromberg, 2005). Goodding's willow is more dependent on groundwater and more sensitive to fluctuations than is cottonwood (Snyder and Williams, 2000; Horton et al., 2001). Because of a later seed release period, Goodding's willow seedlings establish closer to stream channels during flood recession. This spatial arrangement likely helps Goodding's willows avoid drought stress and mortality (Stromberg et al., 2007). Boxelders are meso-riparian trees that are more drought-tolerant than other woody riparian species (Table 4) making them more likely to survive periods of low flows (Dewine and Cooper, 2008 Stromberg and Merritt, 2015). Growth and survival of established sycamores is dependent on shallow depths to groundwater, as with cottonwood and Goodding's willow. At depths greater than 2 m, sycamore growth rate and seedling density declines (Stromberg, 2001b). Where surface flows are ephemeral, sycamore populations rely on winter floods to replenish groundwater aquifers and deliver nutrients to the soil (Stromberg, 2001a). If depth to groundwater remains shallow and surface flow is perennial, high flows can slow the growth of sycamores, possibly through root hypoxia (Stromberg, 2001a). Late-season floods can also cause mortality through hypoxia, shear stress, and erosion (Stromberg, 1997; Tallent-Halstell and Walker, 2002; Katz and Shafroth, 2003).

Because of the responses by woody riparian plants to high and low flows, hydrological changes can influence the composition of riparian ecosystems as well as the animal communities they support (Brand et al., 2008; Merritt and Bateman, 2012). Though the four tree taxa examined are conspicuous components of riparian ecosystems, mature cottonwoods and sycamores are perhaps the most significant because of their exceptional size (Whitham et al., 2006; Bock and Bock, 1984). Species richness of migrating and nesting birds has been linked to the presence of cottonwood and sycamore (Brand et al., 2008; Keller and Avery, 2014; Powell and Steidl, 2015). Under typical conditions, cottonwoods and sycamores are the tallest species in alluvial stretches, capable of forming a forest canopy where animals nest, roost, and forage. Birds in particular rely on cottonwoods and sycamores for nesting and foraging sites (Bock and Bock, 1984; Carothers et al., 1974; Knopf et al., 1988; Powell and Steidl, 2002). Cottonwoods and sycamores are used by more species of birds than other trees because their branches support large nests, they often have dead and decaying limbs that are excavated for nest sites, and their substantial canopies are foraging sites for foliage gleaners (Bock and Bock, 1984; Hunter et al., 1987; Sedgwick and Knopf, 1990; Sedgwick, 1997; Stoleson et al., 2000; Smith and Finch, 2014). Large native trees continue to contribute to forest function when they become snags and fallen woody debris. Snags of native trees are used as nest sites by breeding birds more frequently than snags of small, nonnative trees (Stoleson and Finch, 2001; Smith and Finch, 2014). Course woody debris is used as shelter, basking sites, and foraging areas for a variety of forest floor animals (Harmon et al., 1986). Abundant arthropods, such as the giant cicada (*Tibicen* spp.*) and the flood-plain cricket (*Gryllus alogus*), are dependent on cottonwoods as sources of food and moisture (Smith et al., 2006; Sabo et al., 2008), making cottonwoods an important link in the riparian food and water web. Large trees influence riparian habitat indirectly as well, by shading the soil and water. Increased temperatures impact the activity and survival of soil-dwelling organisms and their consumers (Smith et al., 2006). Water temperatures influence growth of aquatic producers, which affects food availability for consumers, including endangered fish species. Stream temperatures directly influence the physiology of these fishes as well (Finch et al., 2014). The leaves of cottonwoods, sycamores, and other deciduous riparian trees play key roles in biological and physical processes on the forest floor (Ellis et al., 1998).

Fewer species of birds are known to nest in Goodding's willow and boxelder, as compared to cottonwoods and sycamores, but these trees are important to certain species and the breeding bird community as a whole. Mature boxelder and Goodding's willow trees are excavated by woodpeckers and they are used as nest plants by the range-restricted, secondary cavity-nesting Lucy's warbler (*Oreothlypis luciae*; Stoleson et al., 2000). The trunks of Goodding's willows often grow horizontally, making them ideal nest sites for mourning doves (*Zenaida macroura*) and other large understory-nesters (Smith et al., 2012). Along with cottonwood, the presence of Goodding's willow has been shown to increase the abundance and diversity of bird, small mammal, and herpetofauna communities (Brand et al., 2008; Bateman and Ostoja, 2012). Boxelder has been identified as an important habitat component for birds because it is preferred as a nest plant over other trees by the federally endangered southwestern willow flycatcher (*Empidonax traillii extimus*; Stoleson and Finch, 2003). In addition, willow flycatcher nests in boxelder are less vulnerable to brown-headed cowbird (*Molothrus ater*) parasitism than nests in other tree species (Brodhead et al., 2007). Where it co-occurs with larger trees, boxelder forms a woody subcanopy layer that is absent in many western riparian forests, effectively increasing potential nesting opportunities (Knopf and Olson, 1984; Smith et al., 2014).

3.4. Consequences of hydrological change for riparian ecosystems

Though we did not measure response of native riparian trees to the changes in annual discharge, peak discharge magnitude, and peak discharge timing at the stream sites examined, we found examples from these and other streams in the scientific literature. Modification of peak flows was associated with decreased cottonwood and Willow cover at several streams (Cooper et al., 1999; Merritt and Poff, 2010; Mortenson and Weisberg, 2010). Decreases in peak discharge have limited the extent of recruitment of cottonwoods and Goodding's willow below dams at the Rio Grande, the Green River, and the Colorado River (Howe and Knopf, 1991; Birken and Cooper, 2006; Webb et al., 2007). Dams and diversions have also lowered the water table in areas away from the active channel, thereby causing mortality of established trees (Molles et al., 1998; Dewine and Cooper, 2007; Coble and Kolb, 2013). Conversely, increases in peak discharge, resulting from changing climate patterns, have led to increases in cottonwood and willow abundance at the Verde River, the Gila River, and other streams in the southern portion of our study area (Stromberg, 1998; Webb et al., 2007; Soles, 2008). Decreases in total discharge and peak discharge result in channel narrowing and stabilization, which has increased areas suitable for cottonwood and willow establishment at the San Juan River and other streams (Webb et al., 2007; Merritt and Poff, 2010; Mortenson et al., 2012; Coble and Kolb, 2013). This channel narrowing has, however, reduced the area suitable for boxelder establishment along regulated streams including the Green River (Dewine and Cooper, 2007; Coble and Kolb, 2013). Reduction in peak discharge following construction of dams reduced mortality of boxelder from shear stress along the Gunnison River (Friedman and Auble, 1999). We are unaware of studies showing response of Arizona sycamores to changes in discharge

variables, but we expect that they would be similar to those of cottonwood and Goodding's willow because of their similar requirements for growth, survival, and reproduction.

3.5. Potential response to future changes

Population dynamics of woody riparian plants are sensitive to even small changes in discharge (Merritt and Poff, 2010), so projected changes will no doubt affect riparian communities, but in ways that vary among the streams we examined. As a result of continued greenhouse warming, peak discharges may occur before the release of seeds at each of the Southern Rockies sites. Detailed information about seed release phenology is still needed, however, to determine the sensitivity of native and nonnative trees to these changes. Decreases in annual discharge volume may increase depth to groundwater at the Rio Grande and other sites, which would slow growth and increase mortality. Goodding's willow, Arizona sycamore, and cottonwoods are vulnerable to mortality resulting from decreased discharge because they are relatively drought-intolerant. Because of this vulnerability, a better understanding of the connections between surface flow and groundwater is needed to link decreases in discharge volume to increases in mortality. A decrease in peak discharge volume would prevent germination of cottonwoods and willows at streams such as the Rio Grande if occasional floods no longer have the magnitude needed to scour the floodplain and deposit silt. Of the four tree taxa examined, cottonwood and Goodding's willow are likely most vulnerable to changes in peak discharge timing because of their relatively short germination window. Decreased peak discharge volume could prevent germination of all species, though boxelder would perhaps be the least vulnerable because it does not require exposed sites for germination. Factors such as soil type and geological setting influence these dynamics, but additional information is needed for most streams in the Southwest. Following decreasing reproduction and increasing mortality of native trees, drought-tolerant species such as saltcedar (*Tamarisk* spp.) and Russian olive (*Elaeagnus angustifolia*) may be released from competition, increasing their invasive capacity (Cleverly et al., 1997; Katz and Shafroth, 2003). A combination of increased frequency of heavy rains and decreased magnitude of spring floods, predicted by other climate change studies, may benefit late-successional species such as Arizona Walnut (*Juglans major*), mesquites (*Prosopis* spp.), and Russian olive (Stromberg and Patten, 1990; Cook and Seager, 2013; Garfin et al., 2014).

Other climate change effects on riparian forest are possible, but have not been effectively included in climate and hydrology models. These include changes to the North American Monsoon, which has a large effect on southwestern streams, especially the Central Highland streams (Stromberg et al., 2007; Webb et al., 2007). Recent analysis of CMIP5 projections suggests that monsoon storms may increase and occur later in the year (Cook and Seager, 2013). Monsoons produce floods in late summer and fall, long after cottonwoods and willows have dispersed seeds, but within the window of saltcedar dispersal. These late-season floods are not only poorly times for cottonwood and willow germination, but they can also scour or drown newly established seedlings and saplings. A better understanding of the species, both native and nonnative, that can germinate in response to these late-season floods in needed to determine how a shift from runoff to monsoon-dominated flood regimes will affect riparian communities. Another factor affecting hydrology and forest composition is drought. Though occurrence of drought is difficult to model, there is widespread agreement that greenhouse warming will increase drought severity by overlaying high temperatures on drying conditions (Gutzler and Robbins, 2011). These hot droughts will result

in high rates of tree mortality and limit recruitment of many species (Dixon et al., 2009). Changes to the characteristics of monsoons and drought could therefore compound our projected effects of climate change on riparian trees.

Loss of native riparian trees, brought upon by climate change, would have wide-ranging ecological effects. Eradication of cottonwoods and sycamores would result in local extinction of animals that nest, forage, or roost exclusively in large trees (Hunter et al., 1987; Smith and Finch, 2014). Loss of these trees would influence riparian habitat indirectly as well, through loss of shade over soil and water. If drought-tolerant species such as saltcedar increase in relative abundance in response to native tree reductions, properties of litter will change, including factors such as soil chemistry and composition of fungal communities (Shafroth et al., 1998; Meinhardt and Gehring, 2012). Nonnative trees do not break down into pieces as large as native trees, so course woody debris would eventually be absent from the forest floor. Loss of habitat for imperiled riparian species including the southwestern willow flycatcher could occur in response to loss of Goodding's willow and boxelder, though additional research is needed to determine if they will successfully use other woody species as habitat throughout their range (Sogge et al., 2008).

3.6. The human element

In the coming decades, semiarid riparian ecosystems will be affected not only by changes in climate and hydrology but also by changes in human activity. Our actions in the 21st century will continue to influence streams and riparian communities, but in ways that have changed since the 20th century. A demographic shift is occurring in the Southwest as urban centers gain area and population size, applying pressure to a system of water laws that was primarily developed for agriculture (Summitt, 2013). Population growth will continue, increasing the demand for over-allocated water in the Colorado River, the Rio Grande, and other streams (Phillips et al., 2011; Georgescu et al., 2013). To meet municipal demands, programs such as water markets are being used to purchase water rights from agriculture. As water conservation and treatment improves in urban areas, an increasing amount of municipal water is returning to streams, resulting in smaller net losses than would have occurred from agriculture. Urban growth and the resulting shift in public values have changed the perception of a tenet of water law known as beneficial use. Once limited to the use of water primarily for agriculture and industry, beneficial use now includes to the role of water in maintaining ecosystems and recreational opportunities. Water markets and other programs have thus been employed to maintain surface flows for these purposes (Summitt, 2013). Transfers of water rights from agriculture to other uses could increase the amount of water being used to maintain survival and reproduction of riparian trees in some stream sections. The long-term viability and legality of these programs is in question, however, so their effects on future hydrology remain to be seen (Summitt, 2013).

Changes in demand for and use of water by agricultural communities are inevitable and will continue to influence the ecohydrology of the Southwest. Though the era of large-scale dams and diversion projects has ended, smaller projects are planned, including a transfer of water from the upper Gila Basin in New Mexico (Summitt, 2013; Gori et al., 2014). Such diversions would exacerbate the projected decreases in annual discharge at these streams, affecting the survival and reproduction of cottonwoods, willows, sycamores, and boxelders, potentially eliminating their contributions to riparian animal communities. In addition, groundwater removal is occurring at an accelerating rate in response to decreased availability of surface flows (Castle et al.,

2014). Unregulated groundwater withdrawals will likely contribute to decreases in surface flows, with legal and ecological repercussions. For riparian ecosystems to exist alongside agricultural operations in an increasingly arid environment, planners must look beyond diversion projects and consider efficiency improvements that maintain surface flows where possible.

Humans can also shape semiarid riparian ecosystems by mitigating the effects of regulation and climate change. At riparian forest sites below large reservoirs, managers can release pulsed flows at times that will encourage germination of native woody species (Shafroth et al., 2010). These environmental flows could ameliorate effects of earlier peak discharge at Southern Rockies streams, which might otherwise prevent germination of species such as cottonwoods and willows. Releases can also be scheduled to ensure that surface flows continue during periods of drought to minimize mortality of native trees. These programs will only work at select streams because allocation of ecological flows is complicated by water law and some streams are more over-allocated than others. If prolonged drought reduces the amount of water that can be stored along certain streams there will be fewer opportunities to use dams and reservoirs as management tools for riparian ecosystems. Modest decreases in demand, however, can mitigate risk of reservoir depletion (Rajagopalan et al., 2009). Climate change effects cannot be mitigated in this manner along unregulated reaches, such as the Central Highland sites, so different management strategies are needed. Unregulated reaches typically have higher rates of reproduction by native trees and less extensive invasion by nonnative trees including saltcedar and Russian olive (Merritt and Poff, 2010). The highest species richness and densities of riparian plants and animals in the region have been documented at unregulated Central Highland sites (Webb et al., 2007; Gori et al., 2014; Smith and Finch, 2014). Special protections from regulation and species invasions are necessary to keep these ecosystems resilient to future hydrological changes.

4. Summary and conclusions

The American Southwest is experiencing and will continue to experience increasing temperatures and changes to precipitation patterns as a result of greenhouse gas emissions. These departures from historical conditions will manifest themselves in changes to streams originating in the Southern Rockies and the Central Highlands, but in different ways. Changes in peak discharge timing or total annual discharge will likely occur at most of the Southern Rockies streams, with the potential to reduce the rates of survival and reproduction of cottonwood, Goodding's willow, and, to a lesser extent, boxelder. Additional research on reproductive phenology of these species is needed to prevent an ecological mismatch between peak discharge, seed dispersal, and seedling establishment. These effects can be dampened if environmental flows are released from dams to promote survival and reproduction of native vegetation. Discharge patterns of the unregulated reaches of Central Highland streams are more variable than at Southern Rockies streams. Characteristics of peak discharge may not be affected at these streams, but decreases in annual discharge volume may increase the mortality rates of cottonwood, willow, and Arizona sycamore. Loss of these species would significantly affect the ecological function and aesthetic value of these streams. Minimum discharge thresholds should be developed for the taxa found at each stream to prevent such losses. Future discharges will be largely determined by agricultural, municipal, and industrial sectors, which will undergo change in the future as well. Following the example of carbon emission scenarios, demographic research should be conducted to develop multiple water use scenarios for the Southwest. Management actions to maintain surface flows and occasional flooding should be developed under each scenario to protect riparian forests and the animal communities they support.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2016.08.016.

Appendix

Models used to project streamflow at gage sites.

Model name	Modeling center or group	Number of projections
bccr_bcm2	Bjerknes Centre for Climate Research, Norway	1
cccma_cgcm3	Canadian Centre for Climate Modeling & Analysis	5
cnrm_cm3	Météo-France/Centre National de Recherches Météorologiques	1
csiro_mk3	CSIRO Atmospheric Research, Australia	1
gfdl_cm2	US Dept. of Commerce/NOAA/Geophysical Fluid Dynamics Laboratory	2
giss_model_e_r	NASA/Goddard Institute for Space Studies	1
inmcm3_0.1	Institute for Numerical Mathematics, Russia	1
ipsl_cm4.1	Institut Pierre Simon Laplace, France	1
miroc3_2_medres	Center for Climate System Research (The University of Tokyo), National Institute for Environmental Studies, and Frontier Research Center for Global Change (JAMSTEC)	3
miub_echo_g	Meteorological Institute of the University of Bonn	3
mpi_echam5	Max Planck Institute for Meteorology, Germany	3
mri_cgcm2_3_2a.1	Meteorological Research Institute, Japan	5
ncar_ccsm3_0.1	National Center for Atmospheric Research	4
ncar_pcm1.1	National Center for Atmospheric Research	4
ukmo_hadcm3.1	Hadley Centre for Climate Prediction and Research/Met Office, UK	1

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