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Riparian vegetation in the face of environmental variability

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RIPARIAN VEGETATION IN THE FACE OF ENVIRONMENTAL VARIABILITY

by

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B.S., BIOLOGY, UNIVERSITY OF NEW MEXICO, 2013

THESIS

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ABSTTRACT

Riparian ecosystems are among the most highly disturbed ecosystems globally, over the past century dryland riparian forests have become less likely to flood, removing the largest historical disturbance. Yet these provide many essential ecosystem services. Climate change adds further change and uncertainty to the future of these ecosystems. In the southwestern United States, climate models predict changes in the mean and variance of temperature and precipitation. Determining the ecological consequences of interactions between slow changes in long-term climate means and amplified variability in climate is an important research frontier in plant ecology. We used long-term plant cover, groundwater and precipitation datasets from the Middle Rio Grande Valley in New Mexico to explore the relationships between riparian plants and environmental variability

We explored the relationships between the riparian plant community and climate factors (temperature, precipitation, water availability and variability) The sensitivity of riparian vegetation to climate and other abiotic factors will depend on the interaction between properties of the ecosystem, such as flood regime, and characteristics of plant species, like structure, and provenance. We found that the strength and direction of the relationships between diversity or plant cover and abiotic factors changed with flood regime.

To understand environmental variability on individual species, we combined the recent approach of climate sensitivity functions with the revised ‘bucket model’ to improve predictions on how plant species will respond to future changes in both the mean and variance of groundwater resources. We built the first *groundwater sensitivity function*s (GSFs) for common plant species of dryland riparian corridors. Riparian plant species differed in sensitivity to both the mean and variance in groundwater levels. Rio Grande cottonwood (*Populus deltoides* ssp. *wislizeni*) cover was predicted to decline with greater interannual variance in groundwater, especially during warmer periods, while coyote willow (*Salix exigua*) was predicted to benefit from greater variance. Non-native species, including Russian olive (*Elaeagnus angustifolia*) and tamarisk (*Tamarix*) were insensitive to groundwater variability. Altogether, our results indicate that changes in groundwater variability as well as mean may alter riparian plant communities.

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Chapter 1: Flood regime alters the abiotic correlates of riparian vegetation

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Abstract

Questions Predicting the influence of climate change on riparian plant communities improves management and restoration strategies. The sensitivity of riparian vegetation to climate and other abiotic factors will depend on the interaction between properties of the ecosystem, such as flood regime, and characteristics of plans, like structure, and provenance. To explore these interactions, we addressed three questions: How much does the composition and diversity of riparian vegetation vary with the flooding regime? Do abiotic correlates of vegetation, including climate and groundwater, differ between flooding and non-flooding sites? Which plant groups account for differential plant community sensitivity to abiotic factors between flood regimes?

Methods We used long-term observational datasets of plant community composition, groundwater depth, precipitation and interpolated temperature data from 24 sites spanning 210 km of the Rio Grande riparian corridor to explore the relative importance of abiotic correlates of riparian vegetation diversity and composition.

Results Riparian plant diversity was higher at flooding site than non-flooding. Plant diversity was related to groundwater depth at flooding sites, but was related to intra-annual groundwater variability at non-flooding sites. Plant community composition was correlated with groundwater depth and temperature at all sites, but at non-flooding sites intra-annual groundwater variability and precipitation also correlated with differences in community composition. Although the relationships between native plant cover and potential abiotic drivers diverged strongly between the two flood regimes, cover of non-native plants had weak relationships with most abiotic predictors at both flooding and non-flooding sites.

Conclusions The current flood regime of a site plays a role in what abiotic factors correlate with the plant community. The relationships between plant diversity or cover and groundwater, temperature, precipitation, and intra-annual groundwater variability can change strength or direction depending on whether or not a site still floods.

Introduction

Riparian ecosystems are some of the mostly highly disturbed ecosystems globally (Perry et al. 2012a; Klove et al. 2014), yet they provide essential ecosystem services, particularly in dryland regions (Capon & Pettit 2018) such as promoting biodiversity (Selwood et al. 2017; Rolls et al. 2018), carbon storage (Matzek et al. 2018), and flood protection (Brauman et al. 2007). A century of flood control, water diversion and non-native species invasions has changed the plant communities and hydrology of many riparian corridors (Naumburg et al. 2005; Osterkamp & Hupp 2010; Gurnell et al. 2012). Improved understanding of ongoing changes to riparian plant species composition is important to conservation, management, and restoration of the ecological functions and services provided by these ecosystems (Capon & Pettit 2018).

Many riparian corridors have become disconnected from river flows, and flooding is now rare to non-existent due to incised banks and river regulation (Crawford et al. 1993;

Gurnell et al. 2012; Hayes et al. 2018). Changes in the duration, magnitude, and timing of peak river flow affect the probability of floods (Gurnell et al. 2012). Floods, which promote recruitment of many riparian plants (Kehr et al. 2014), can increase plant species richness and diversity relative to adjacent forests that do not flood (Stromberg et al. 2012; Muldavin et al. 2017). However, additional biotic and abiotic factors also influence riparian plant species composition (Stromberg et al. 1996; Hingee et al. 2017). Here, we investigated whether the flood regime altered which abiotic factors best correlated with riparian plant community composition and diversity, and determined how the importance of abiotic correlates varied among plant groups that differed in life history and provenance.

During the last several decades, potential abiotic drivers of plant composition in riparian corridors may have switched from the key historical driver of the flood regime to modern drivers that include groundwater, climate, and both land and water management (Osterkamp & Hupp 2010; Palmquist et al. 2018). First, several studies have linked groundwater supply to riparian vegetation (Stromberg et al. 1996; Sommer & Froend 2014; Yin et al. 2015). Groundwater influences 20-30% of global land area (Fan et al. 2013), and the groundwater table has declined in many regions due to river regulation and groundwater use (Margat & Van Der Gun 2013).

Second, a few studies suggest that in addition to average groundwater supply, the seasonal fluctuation in groundwater levels may influence riparian vegetation. Seasonal fluctuations in the groundwater table may favor bimodal plant root distributions (Fan et al. 2017; Xi et al. 2018), perhaps promoting plant diversity as suggested by theory and data from other ecosystems (Kremer & Klausmeier 2017). However, relatively few studies have looked for patterns of association between intra-annual variability and vegetation composition. In a Mediterranean ecosystem, two dominant riparian plant species differed in their degree of dependence on intra-annual fluctuations in the water supply (Sargeant & Singer 2016). In Australia plant functional diversity increased in concert with greater variability in river flow, and surprisingly, was not related to average river flow (Lawson et al. 2015). Similarly, studies on arid rivers in Arizona (Katz et al. 2012) and South Africa (Naiman et al. 2008) revealed that plant diversity increased in sites where water was the most variable due either to flooding or stream intermittency.

Third, climate change adds additional stressors to riparian ecosystems (Wang et al. 2012; Capon & Pettit 2018), and the importance of changes to the climate may vary with the riparian flood regime (Death et al. 2015). In drylands of the southwestern US, both warming temperatures and changing precipitation regimes (Gutzler & Robbins 2011; Cook et al. 2015) may affect riparian plant species composition and diversity, although how these changes interact with flood regime are unresolved. For example, the importance of rainfall for riparian ecosystems may be stronger for sites that are disconnected from flooding than for sites that receive inputs to groundwater from flooding events (Thibault et al. 2017). To effectively predict the future of riparian plant communities and improve restoration and management strategies, it is important to understand how climate factors interact with the flood regime. Riparian ecosystems that consist of a mosaic of isolated, non-flooding and flooding sites may provide insight into how the composition and diversity of riparian vegetation changes under modern drivers.

To explore potential interactions between modern abiotic drivers and the flood regime, we leveraged environmental variability over time and space and investigated abiotic correlates of riparian vegetation. We chose a representative corridor ecosystem of the southwestern US, along the Rio Grande, which stretches for 2900 km from southern Colorado, USA to the Gulf of Mexico. Specifically, we used a 16-year observational dataset from 24 sites along a 210 km stretch of the Middle Rio Grande Valley in central New Mexico to evaluate the relative importance of flooding, groundwater depth and its intra-annual variability, and climate (temperature, precipitation) as correlates of riparian plant species composition and diversity. We addressed three specific questions: (1) How much does the composition and diversity of riparian vegetation vary with the flooding regime? We hypothesized that sites that flood would have greater plant diversity than sites that no longer flood. Because plant communities differed between flooding and non-flooding sites, we then asked (2) Do abiotic correlates of vegetation differ between flooding and non-flooding sites? We predicted that the flood regime would define which abiotic drivers were most strongly correlated with riparian vegetation, evidence of an interaction between the flood regime and modern drivers. Lastly, we asked (3) Do certain plant groups account for differences between flood regimes in plant community sensitivity to abiotic factors? We specifically compared native versus non-native plant species and canopy versus understory species.

Methods

Study Sites. We collected vegetation cover, groundwater and precipitation data as part of the Bosque Ecosystem Monitoring Program (BEMP) in the Middle Rio Grande Valley of New Mexico. BEMP conducts vegetation monitoring on county, state, federal and tribal land along 420 km of the Rio Grande. We focused on 24 sites (Fig. 1) in Rio Arriba, Sandoval, Bernalillo, Valencia and Socorro Counties that had comparable time series but differed in flood regime (Table 1). We compared six flooding sites against 18 non-flooding sites.

Study Design. Each BEMP site (Fig. 2) is 100 m X 200 m, the 200 m side runs north-south in parallel with the Rio Grande. Each site is divided into ten equal 20 X 100 m sections and one 30 m vegetation transect is randomly placed within each section running east to west. Each BEMP site also has two rain gauges and five groundwater wells (described below).

Vegetation Monitoring. Vegetation monitoring began in 2000 with seven sites and has continued to the present; new sites were included in monitoring as they were established (Table 1). We monitored vegetation transects once annually during peak biomass production (August-September). Plants were monitored using line-intercept sampling. For each plant species that crossed a transect, we recorded the length of the transect covered (cm). If individual plants of the same species overlapped, the cover was recorded as continuous, such that total cover for a single species never exceeded 3000 cm per transect. For plants < 1 m tall, we excluded gaps < 1 cm between individuals of the same

Table 1. Location of BEMP monitoring sites. Geographic coordinates, years of data used in the analysis, county location, designated flood regime.

Site number	Years of data available	Longitude	Latitude	County	Flood regime
1	16	35.188	-106.647	Bernalillo	non- flooding
2	16	35.127	-106.688	Bernalillo	non- flooding
3	16	34.812	-106.714	Valencia	flooding
4	16	34.648	-106.738	Valencia	flooding
5	15	35.3428361	-106.54585	Sandoval	non- flooding
6	16	35.143	-106.682	Bernalillo	non- flooding
8	14	35.069	-106.658	Bernalillo	non- flooding
9	13	--	--	Rio Arriba	flooding
10	13	35.192	-106.644	Bernalillo	non- flooding
11	12	35.191	-106.649	Bernalillo	non- flooding
12	10	35.193	-106.647	Bernalillo	non- flooding
13	12	35.015	-106.674	Bernalillo	flooding
14	13	34.258	-106.883	Socorro	non- flooding
15	13	34.649	-106.739	Valencia	non- flooding
16	13	34.647	-106.738	Valencia	non- flooding
17	12	35.145	-106.680	Bernalillo	non- flooding
18	12	34.660	-106.742	Valencia	non- flooding
19	11	34.661	-106.743	Valencia	non- flooding
20	11	35.101	-106.692	Bernalillo	flooding
21	10	35.196	-106.642	Bernalillo	non- flooding
22	10	35.197	-106.644	Bernalillo	non- flooding
23	9	35.079	-106.668	Bernalillo	non- flooding
24	8	35.5098917	-106.38961	Sandoval	non- flooding
25	8	34.640	-106.742	Valencia	flooding

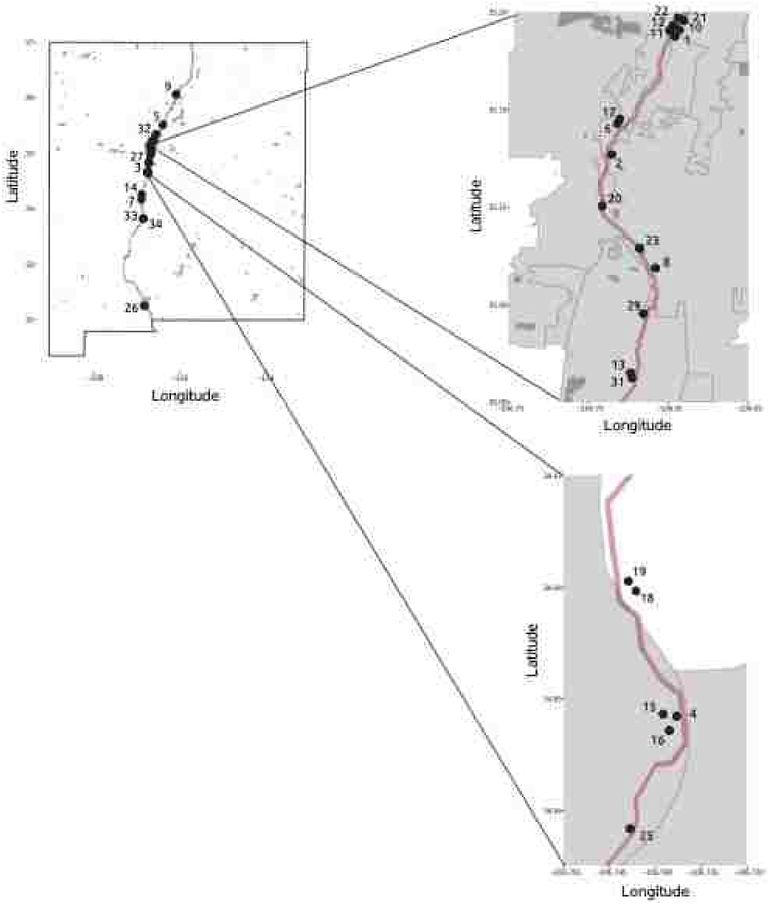

Figure 1. BEMP monitoring sites. Sites used in this analysis cover 210 km of the Rio Grande in central New Mexico. Once established, sites were monitored annually, this analysis used data from 24 sites monitored for 8-16 years between 2000 and 2015.

Figure 2. Layout of a BEMP monitoring site. Sites include five groundwater wells and two precipitation gauges which are measured monthly. Vegetation cover is measured by species annually along 10 vegetation transects that run east to west.

species, and recorded plant cover as continuous. For plants 1-3 m tall, we excluded gaps of < 10 cm between individuals of the same species. For plants taller than 3 m, we excluded gaps of < 1 m. We then summed the transect length covered by each individual plant species over the 30 m transect. Transect identity was our smallest unit of observation; thus, we had 10 samples per site per year monitored, which enabled our analyses to estimate year-to-year variability and between-site variability in vegetation.

Groundwater. At each BEMP site, there were five groundwater wells, one located in the center of the site, the other 4 wells installed 40 m from the center in each of the four cardinal directions. We measured depth to groundwater (cm) at each well monthly using a Solinst water level meter (Georgetown, Ontario, Canada), subtracting the above-ground height of the well from the total measurement. Wells were constructed and installed using published methods (Martinet et al. 2009). We averaged data from each of the five wells at a BEMP site to obtain arithmetic mean depth to groundwater per site for each month of observation. Monthly groundwater levels were averaged to estimate mean annual groundwater level. To estimate intra-annual variability in groundwater depth, we calculated the coefficient of variation (*CV*) for groundwater across months within each year, hereafter referred to as intra-annual groundwater variability.

Precipitation. At each site, two rain gauges were used to monitor precipitation. One gauge was located in an open area and the other under forest canopy, which allowed canopy cover to intercept precipitation before it hit the ground. Each Tru-Chek rain gauge (Edwards Manufacturing Company, St. Albert Lea, MN, USA) was accurate to < 1mm and mounted to a metal bracket on a wooden post at approximately 1.2 m above the ground surface. Any gaps in the precipitation data for a site were filled with values from the Parameter-elevation Regressions on Independent Slopes Model (PRISM, see next section) (PRISM Climate Group 2018).

Climate. We also obtained annual and monthly temperature and precipitation data at the 4 km spatial resolution from the PRISM database (PRISM Climate Group 2018). Annual values were used for minimum, maximum, and average daily temperatures and cumulative precipitation at each site. For summer data, we averaged monthly average, minimum, and maximum daily temperatures over the months of June, July and August to calculate summer temperatures for each site.

Data Analysis. (1) How much does the composition and diversity of riparian vegetation vary with the flooding regime? Community composition analysis included 24 plant species that appeared in 10% or more of the transects, 2556 transect-years remained after removing transects that only included rare species (258 individual transects sampled across 16 years). Using PRIMER (Clarke & Gorley 2015), we calculated Bray-Curtis distances between each pair of transects across the dataset. We tested for significant differences in community composition between flooding and non-flooding sites using PERMANOVA, including the random effects of site and year to account for the non-independence of transects within a site and observations across sites within the same year. Using the centroid values from each of the 10 transects per site per year, we created NMDS plots to visualize differences among flood regimes in plant community composition. We also compared dispersion in community composition among sites that flooded or did not using PERMDISP (Clarke & Gorley 2015); this analysis tested for differences in the spread of community composition across the sites representing each flood regime.

Our resolution on abiotic correlates came through variation in both space (e.g., sites that differed in climate) and time (years that differed in climate). We examined the relative importance of abiotic drivers (continuous variables) on the distance matrix of community composition using distance-based linear models (Dist-LM) in PRIMER (Clarke & Gorley 2015). We then used Akaike's Information Criterion (*AIC*) in model selection procedures (Burnham & Anderson 2002) to identify the abiotic variables that explained the most variation in community composition across the full dataset. Sites 5, 9, and 24 were omitted from this analysis because groundwater depth data was unavailable.

Abiotic drivers considered in model selection procedures were depth to groundwater, intra-annual groundwater variability, maximum, minimum, average and average daily summer (June – August) temperature, annual precipitation, monsoon precipitation (Jun - Oct), and a drought index that was integrated over the water year (Oct – Sept): *SPEI*, standardized precipitation-evapotranspiration index (Vicente-Serrano et al. 2010). All abiotic variables were scaled to mean = 0 standard deviation = 1 so that their effect sizes (as estimated by the slope) could be compared on similar scales. In addition to analysis of individual abiotic correlates, we constructed a multivariate model using forward model selection; we did not include minimum, average or summer temperature, or monsoon precipitation, in the multivariate model due to multi-collinearity with maximum summer temperature and annual precipitation. We plotted vectors for abiotic variables onto the NMDS plots to visualize their relative importance (Clarke & Gorley 2015).

We calculated Simpson diversity index, richness and evenness for each transect in the vegan package (Oksanen et al. 2018) in R (R Core Team 2018). Differences in diversity metrics between flooding and non-flooding sites were examined with general linear mixed effects models that included the fixed effect of flood regime and the random effects of site and year (Bates et al. 2015; R Core Team 2018).

(2) Do abiotic correlates of riparian vegetation differ between flooding and non-flooding sites? We separated flooding (N=6) and non-flooding (N=18) sites and recalculated the Bray-Curtis distances among pairs of transects within each group. Current methods available for PERMANOVA and Dist-LM do not allow the inclusion of categorical and continuous variables in the same model; therefore, it was not possible to statistically evaluate interactions between abiotic variables and flood regime type in the analysis of community composition. We followed the same steps as in question 1 to conduct Dist-LM analysis with *AIC*-based model selection separately for each flood regime group. We also created NMDS plots onto which we mapped the vectors for the abiotic variables to visually depict their relative importance for each subset of flooding and non-flooding sites.

For the plant diversity metrics described above, we examined relationships with abiotic correlates using general linear mixed effects models that included the random effects of site and year as well as one of the following abiotic correlates: groundwater, groundwater variability, precipitation, maximum annual temperature(Bates et al. 2015; R Core Team 2018). Models also included the fixed effect of flood regime (as described for question (1)) and the interaction term between flood regime (flooding/non-flooding) and the abiotic variable, which tested explicitly whether allowing abiotic correlates of diversity to differ among flood regimes improved model fit based on the *AIC* criterion. An improvement of model fit with the inclusion of the flood regime × abiotic factor interaction term would indicate *that drivers of diversity significantly differed between the two flood regimes*. *AIC*-based model selection (Burnham & Anderson 2002) was used to rank the relative importance of the candidate abiotic variables for explaining variation in plant diversity metrics.

(3) Do certain plant groups account for differential sensitivity of vegetation to abiotic factors? We classified each plant species into categories for *life history*: canopy versus understory and *provenance*: native versus non-native. Canopy plants were defined as trees and shrubs, understory included all the herbaceous plant species. Provenance was determined using The Plants Database (USDA & NRCS 2018). We divided sites by flood regime and for each plant group, we used general linear mixed effects models that included the random effects of site and year one of the 4 abiotic variables used above to determine the slope of the relationship between total plant cover and each abiotic variable (e.g., Fig 5) (Bates et al. 2015).

Results

(1) How much does the composition and diversity of riparian vegetation vary with the flooding regime? Riparian plant community composition and diversity differed between flooding and non-flooding sites (PERMANOVA, flood regime, *pseudo-F* =34.9, P = 0.0001). Across all sites combined, plant community composition was most strongly correlated with groundwater depth ($r^2 = 0.08$, $P = 0.0001$), average maximum temperature ($r^2 = 0.06$, $P = 0.0001$) and intra-annual groundwater variability ($r^2 = 0.04$, $P = 0.0001$), although no correlate explained substantial variation in composition. Flooding and non-flooding sites significantly differed in some of these abiotic correlates. Flooding sites had shallower depth to groundwater (mean = 118 cm ± 0.69 s.e.) than non-flooding sites (mean = 161 cm ± 1.2 s.e.) ($P < 0.001$). Groundwater levels at flooding sites were also significantly more variable throughout the year (mean = 0.23 ± 0.039 s.e.) than levels at non-flooding sites (mean = 0.03 ± 0.006, $P < 0.001$). Other abiotic variables did not significantly differ between flooding and non-flooding sites.

Plant community composition was more similar among sites that flooded than among non-flooding sites (PERMDISP, $P = 0.001$). Flooding sites tended to have more similarity in understory cover, than non-flooding sites (see question 3), which may explain this convergence in community composition. However, this result should be interpreted cautiously because the sample sizes for each flood regime were uneven. The group of 18 non-flooded sites had more potential for divergence in plant composition among sites than the group of six flooded sites.

Sites that flooded had nearly 40% greater plant diversity (Simpson index, mean = 0.73 ± 0.005 s.e.) than non-flooding sites (mean = 0.53 ± 0.005 s.e.) (log-likelihood $X^2 = 51.4$, $P < 0.0001$). Differences between the flood regimes in plant species diversity were due primarily to differences in species richness, which was 63% greater at flooding sites (mean = 10.9 ± 0.19 s.e.) than at non-flooding sites (mean = 6.7 ± 0.08 s.e., $X^2 = 56.9$, $P < 0.0001$). Species evenness was ~17% greater at flooding sites (mean = 0.69 ± 0.004 s.e.) than non-flooding sites (mean = 0.59 ± 0.004 s.e.; $X^2 = 23.7$, $P < 0.0001$). Non-flooding sites spanned a larger range in plant diversity, with an inter-quartile range from 0.42 to 0.70 across sites, compared to flooding sites which ranged from 0.69 to 0.81. As with community divergence among sites, the greater range of diversity among non-flooding sites may be due to the larger sample size (180 transect × year combinations) than flooding sites (60 transect × year combinations).

(2) Do abiotic correlates of vegetation differ between flooding and non-flooding sites?

The best abiotic correlates of plant community composition differed with flood regime, and non-flooding sites had a greater number of abiotic variables that correlated with community composition than did flooding sites. At flooding sites (Fig. 3A), average

annual maximum daily temperature ($r^2 = 0.22$, $P = 0.0001$) and depth to groundwater ($r^2 = 0.12$, $P = 0.0001$) explained variation in plant community composition. At non-flooding sites (Fig. 3B), groundwater variability ($r^2 = 0.05$, $P = 0.0001$) and mean annual precipitation ($r^2 = 0.01$, $P = 0.023$) were additional significant correlates of community

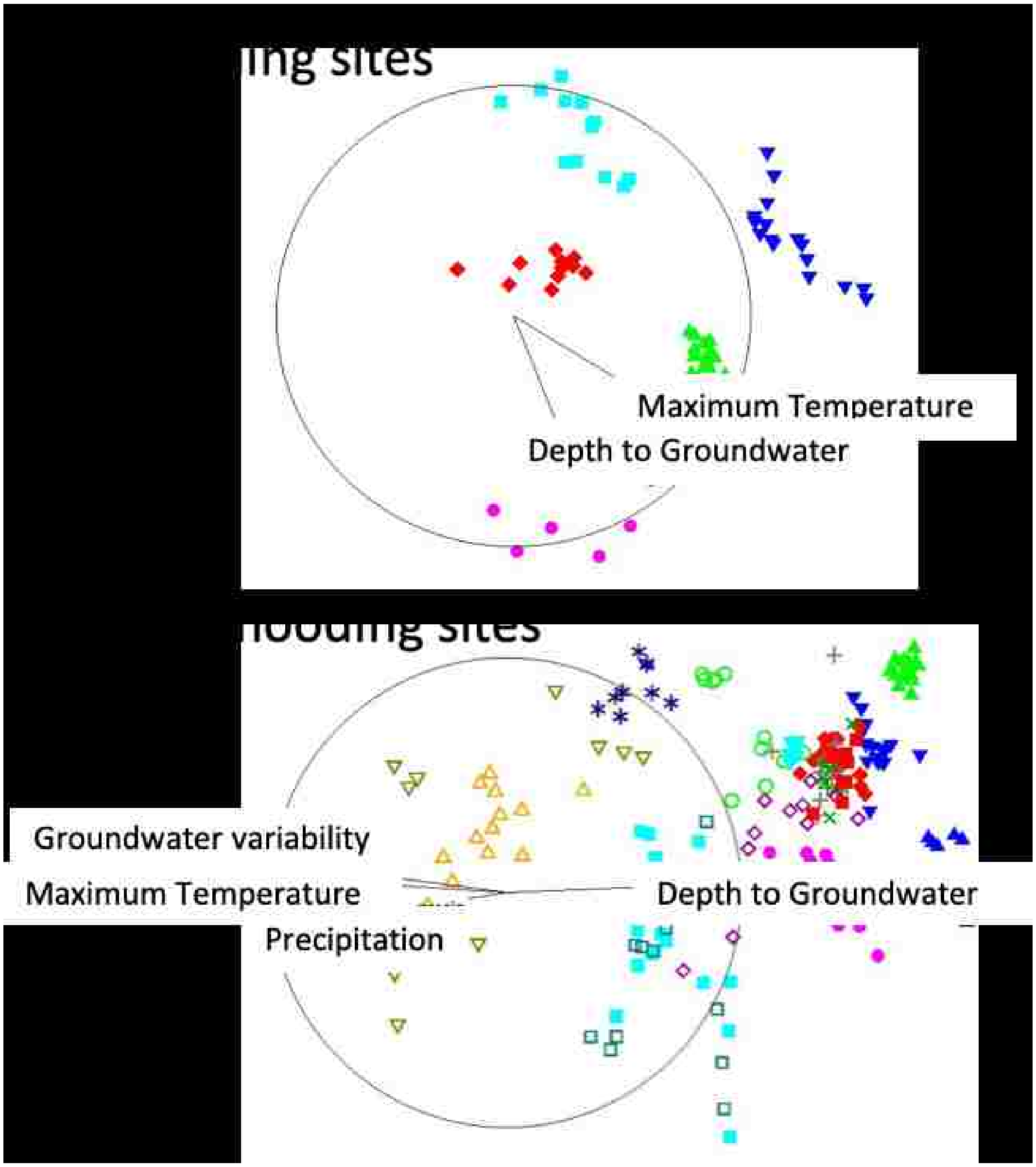

Figure 3. Community composition at (a) flooding sites and (b) non-flooding sites. Each symbol x color combination represents one of 21 BEMP sites. Plots are results of non-metric multidimensional scaling analysis (NMDS, Primer v. 6, Plymouth, United Kingdom). Each plot shows statistically significant abiotic factors as vectors that correlated with the distance matrix of vegetation composition. NMDS stress was 0.12 for flooding sites and 0.16 for non-flooding sites, indicating an adequate 2-dimensional solution. R^2 values for each abiotic correlate analysis were 0.29 for flooding sites and 0.16 for non-flooding sites.

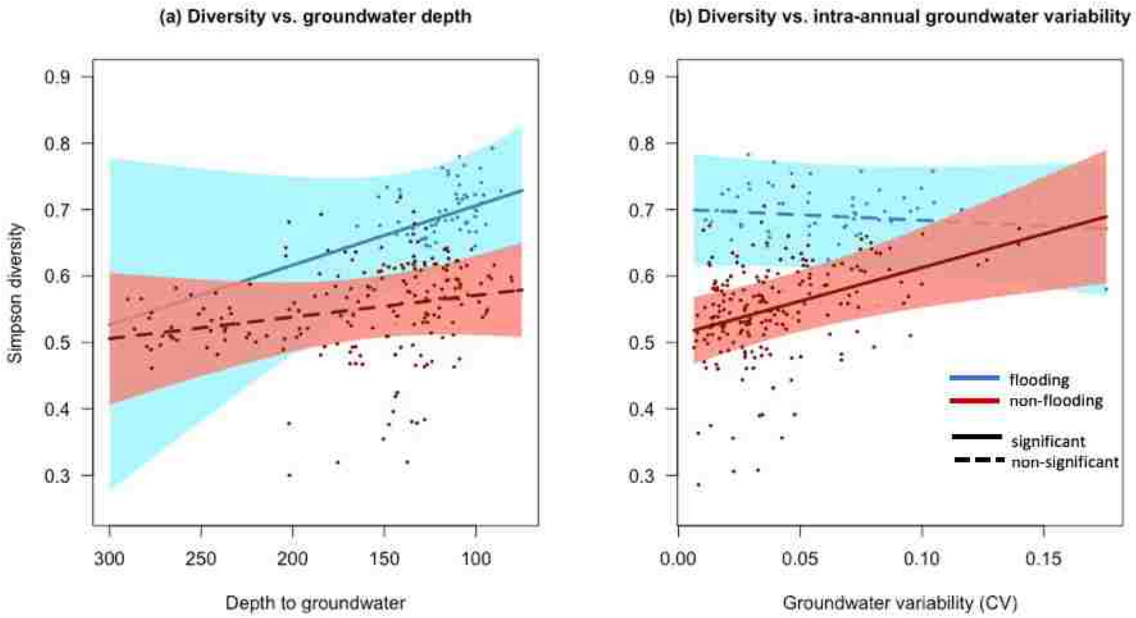

Figure 4. Relationships between plant diversity and water availability differ at based on flood regime. The relationships between plant diversity and (a) depth to groundwater and (b) intra-annual groundwater variability at flooding sites and non-flooding sites. Lines show best fit model with 95% confidence bands, plotted using visreg (Breheny & Burchett 2017). Each graph represents a separate linear regression of plant cover by the environmental variable interacting with flood regime.

composition, along with depth to groundwater (r^2 = 0.10, P = 0.0001) and annual maximum temperature (r^2 = 0.07, P = 0.0001), both of which explained less variation in community composition at non-flooding sites than flooding sites. For non-flooding sites, a multivariate model, including all four abiotic correlates, explained 15% of the variation in plant community composition (r^2 = 0.15, P = 0.0001). For flooding sites, two abiotic variables (depth to groundwater, annual maximum temperature) explained 29% of the variation in plant composition despite the smaller total number of sites (r^2 = 0.29, P = 0.0001).

Abiotic correlates of plant diversity strongly differed with flood regime (Fig. 4). At flooding sites, plant diversity increased with shallower mean groundwater depth

(Simpson index, slope = 0.07, $P < 0.0001$), but there was no significant relationship between plant diversity and depth to groundwater at non-flooding sites ($P = 0.9$) (Fig. 4A). This result was confirmed by a large increase in model fit when the interaction between flood regime and depth to groundwater was included in the model (delta *AIC* = 23). At non-flooding sites, plant diversity increased with greater intra-annual variability in groundwater (slope = 0.02, $P < 0.0001$) but there was no significant relationship at flooding sites (slope = 0.003, $P = 0.5$) (Fig. 4B). Again, inclusion of the interaction between groundwater variability and flood regime greatly improved model fit relative to a model lacking the interaction (delta *AIC* = 54), indicating that the best abiotic correlates of plant diversity strongly differed with flood regime. Analyses that included only native plant diversity revealed a similar pattern, where native plant species diversity increased with shallower groundwater at non-flooding sites (slope = 0.13, $P < 0.0001$), but not at non-flooding sites (slope = 0.01, $P = 0.12$). However, there was no significant relationship between native plant diversity and intra-annual groundwater variability for either flood regime ($P > 0.05$).

(3) Do certain plant groups account for differences in community sensitivity to abiotic factors between flood regimes? The abiotic correlates of native plant cover differed greatly between flood regimes (Fig. 5). Across all sites, native pants made up 76% of total plant cover. At flooded sites, native cover increased most strongly with warmer temperature (slope = 3.20, $P < 0.0001$), among the abiotic correlates we examined. Native plant cover was not significantly related to average groundwater depth at flooding sites, indicating that either individual plant species diverged in their

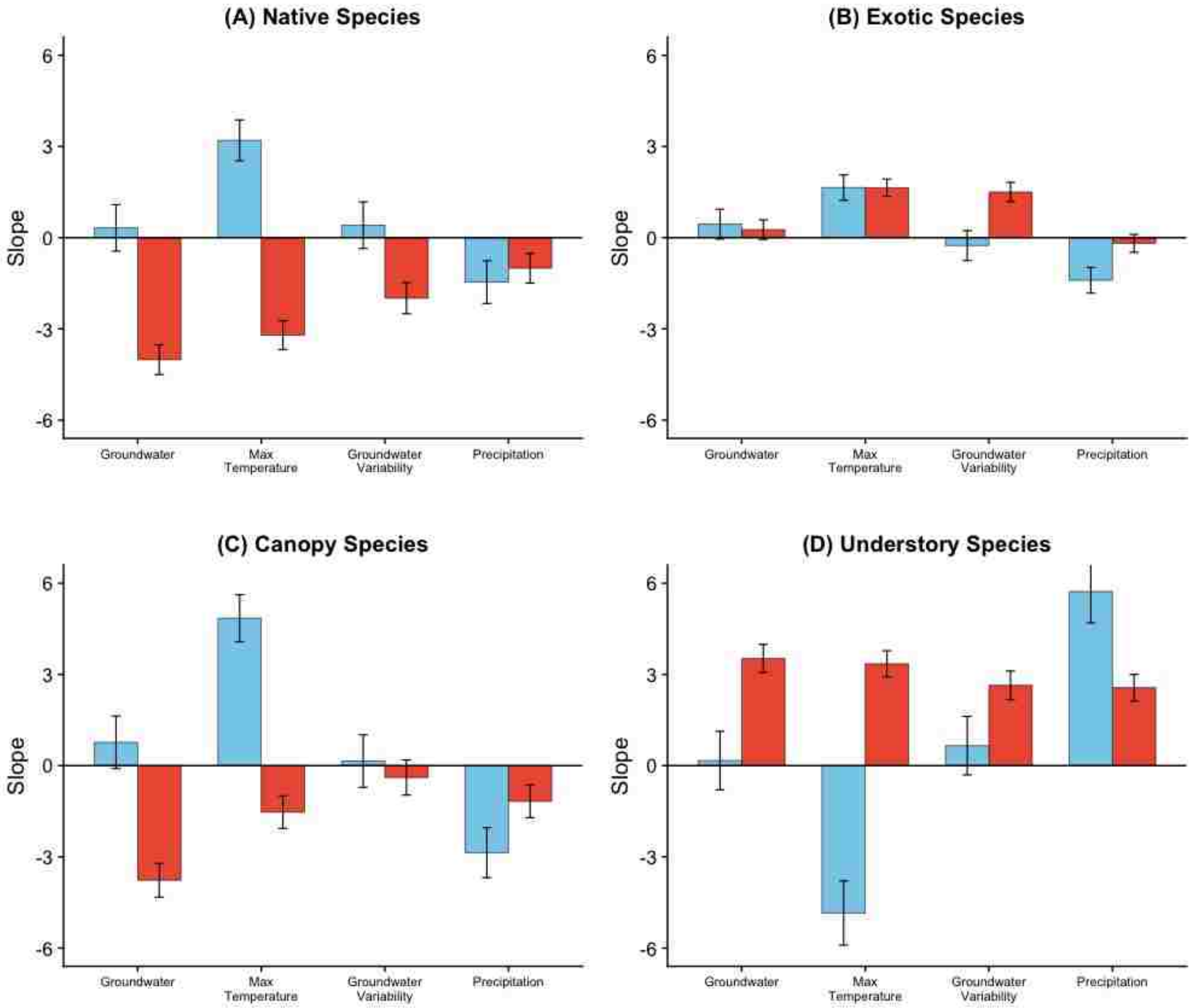

Figure 5. Relationships between plant cover and abiotic factors at flooding sites and non-flooding sites by plant groups. Total native plant species cover (A), non-native plant cover (B), woody plant cover (C), and herbaceous understory plant cover (D) differed in the strength and sometimes direction relationships to abiotic factors based on flood regime. Each bar represents the slope of a separate linear regression of plant cover by the environmental variable. In all cases, models that included an interaction between flood regime and the abiotic driver and thereby allowed the slopes to differ between flood regimes fit the data better than models that did not include the interaction term.

associations with groundwater levels such that total native cover showed no strong relationship or that where flooding is possible, groundwater is not the most limiting factor for native plants. In contrast, at non-flooding sites, native cover strongly decreased with shallower groundwater (depth to groundwater, slope = -4.01, $P < 0.0001$), decreased with warmer temperature (slope = -3.20, $P < 0.0001$), decreased with greater intra-annual groundwater variability (slope = -1.99, $P < 0.0001$) and decreased with higher precipitation (slope =-1.00, $P < 0.0001$).

Although the relationships between native plant cover and potential abiotic drivers diverged strongly between the two flood regimes, cover of non-native plants had similarly weak relationships with most abiotic predictors at both flooding and non-flooding sites. Non-native plants differed between flood regimes in their relationship with intra-annual groundwater variability, which was non-significant at flooding sites ($P = 0.30$), and strongly positive at non-flooding sites (slope = 1.50, $P < 0.0001$). Thus, for both native and non-native plant cover, intra-annual groundwater variability was important at the drier, non-flooding sites, than at the wetter, flooding sites. Non-native plants were also significant correlated with precipitation, but only at flooding sites (slope = -1.40, $P < 0.0001$). Responsiveness of total canopy cover and understory plant cover to abiotic variables diverges between flooding and non-flooding sites. Neither understory cover nor canopy cover co-varied with groundwater depth at flooding sites. However, cover of both groups varied with groundwater level at non-flooding sites, although in opposite directions. At non-flooding sites, understory cover increased with higher groundwater levels (slope = 3.52, $P < 0.0001$). Canopy cover at non-flooding sites had a similar magnitude of response to groundwater, but instead declined with higher groundwater levels (slope = -3.79, $P < 0.0001$). Understory plants were the only group positively correlated with precipitation. Regardless of flood regime, understory cover increased with greater precipitation (flooding slope = 2.30, $P < 0.0001$; non-flooding slope = 1.44, $P < 0.0001$). Canopy plants decreased with precipitation at both site types (flooding slope = -2.86, $P < 0.0001$; non-flooding slope = 1.17, $P < 0.0001$).

Discussion

The Middle Rio Grande Valley serves as a useful case study for understanding processes affecting riparian communities in many parts of the world. The legacy of past floods appears in the current dominance of mature Rio Grande cottonwood trees, which require floods to germinate and established in the valley prior to dam construction. Today, large regions of the Middle Rio Grande riparian corridor do not flood due to channelization, incised banks, and dams — changes that have occurred commonly in dryland riparian ecosystems worldwide (Gurnell et al. 2012; Capon & Pettit 2018; Hayes et al. 2018). Here, we documented substantial divergence in plant community composition between sites that had the capacity to flood and those that no longer flood, including more than 60% greater plant species richness in flooding sites. These results align with findings in other arid rivers [e.g., (Mata-Gonzalez, Martin, et al. 2012; Hingee et al. 2017; Palmquist et al. 2018)], but were larger in magnitude than prior reports. We also uncovered correlations between plant diversity and intra-annual variability in groundwater. Recent studies have similarly linked seasonal changes in river flow or intermittency with increased plant diversity in riparian ecosystems (Katz et al. 2012; Lawson et al. 2015b; Poff 2018), suggesting that the role of intra-annual variability in water availability in structuring vegetation composition deserves greater attention (Xi et al. 2018).

Most importantly, our results suggest that the contemporary flood regime alters the strength and the direction of abiotic correlates of plant community composition. Thus, the key environmental factors that may be most useful to monitor as harbingers of change in riparian ecosystems differed with the local flood regime. Our results suggest that where flooding does not occur, sites with highly variable groundwater levels will have not only greater total and native plant diversity but also more non-native plant cover. This result for non-flooding sites helps to explain the generally low explanatory power of depth to groundwater in prior studies of riparian vegetation in heavily regulated ecosystems (Mata-Gonzalez, McLendon, et al. 2012; Mata-Gonzalez, Martin, et al. 2012). In addition, at non-flooding sites where water is less readily available even during peak river flows, both mean annual precipitation and intra-annual groundwater variability were significant correlates of plant community composition, yet these variables were absent as predictors of composition at sites that had the capacity to flood. In contrast, average groundwater depth was the strongest predictor of total and native plant diversity at flooding sites. Finally, plant diversity and composition was more divergent among non-flooding sites than at flooding sites. Although this difference in range could arise due to the larger number of non-flooding than flooding sites in our study, it may also indicate that where floods are no longer occurring, plant communities take divergent trajectories due to variation among local sites in the other abiotic drivers of plant community composition, factors that emerge as important only when sites no longer flood.

Differences between flood regimes and the abiotic factors that correlate with community composition might be explained using the bucket model proposed by Knapp et al. (2008). The bucket model suggests that the influence of variability in soil moisture on an ecosystem depends on the average water availability at a site. Variability can be beneficial to plants in environments where average water levels are generally at stressful levels (either too wet or too dry), because the variability in water levels is more likely to push the environment into better conditions. In contrast, where average water levels are within an optimal range for the plant community, increasing variability around the mean may push water levels outside of that range into more stressful conditions, a net negative effect of variability. Although the bucket model was initially developed for precipitation-driven soil moisture in grasslands (Knapp et al. 2008; Thomey et al. 2011), it provides a useful conceptual model for groundwater dynamics in riparian ecosystems. For example, we found that at flooding sites, which have a shallower, but more variable water table than non-flooding sites, intra-annual variability in groundwater depth was not correlated with plant diversity, or cover for any of the four plant groups, perhaps because water table stayed within optimal levels. However, at non-flooding sites where the average water table depth was 27% (44cm) deeper than at flooding sites, intra-annual variability correlated positively with plant diversity, results that are consistent with the bucket model if we assume that deeper water levels are more stressful for most riparian plants. Under the stressful conditions caused by a deep water table, variability in water levels may benefit many plant species, increasing coexistence and species diversity. This also explains why at non-flooding sites, herbaceous and exotic cover both increased with increasing groundwater variability. Although native cover decreased, that may have been driven by deep rooted trees, which prefer deeper water tables.

Past work has shown that riparian vegetation in drylands relies heavily on the shallow water table for a consistent water source, and for seedling establishment of foundational plant species (Kehr et al. 2014; Cleverly et al. 2015; Thibault et al. 2017). We expected plant cover to increase with shallower groundwater at all of our sites, but surprisingly, at non-flooding sites, only herbaceous species cover increased as the water table rose. Cover of native and woody species instead declined with a shallower water table at non-flooding sites, which could indicate stress from short-term anoxia of roots (Naumburg et al. 2005) or other unmeasured differences among sites. Unexpectedly, at flooding sites, no plant group was significantly correlated to average depth to groundwater, and total non-native plant cover was unaffected by average groundwater depth in both flooding regimes. These results highlight the importance of evaluating multiple abiotic correlates of vegetation composition and diversity within the same system.

Our study detected surprisingly strong correlations between air temperature and plant cover, relationships that depended strongly on the flood regime. Although temperature is implicitly a component of studies on drought (Vicente-Serrano et al. 2010), temperature alone has been studied less often than water dynamics as a driver of dryland riparian vegetation. Observational studies have correlated temperature with lower cottonwood growth and increases in non-native plants, *Tamarix chinensis* and *Elaeagnus angustifolia* (McShane et al. 2015; Philipsen et al. 2018), but temperature changes coincided with changes in stream flow. In our analysis, at flooding sites, plant cover for all groups except for herbaceous plants increased at sites and in years with warmer temperatures. However, at non-flooding sites, both native and woody cover declined with warmer temperatures. Where water is available as shallow groundwater, warmer temperatures may be beneficial for trees and shrubs, but where groundwater is more limited, warming may be stressful, perhaps exacerbating water limitation. Consistent with other studies, non-native species cover increased in warmer sites and years at all sites. Herbaceous species increased with warmer temperatures at non-flooding sites and declined with warming at flooding sites. These opposite relationships could result from competition for light between the canopy and understory, with drivers that increase canopy cover causing understory cover to decline due to competition. In future studies, it would be useful to explore how competitive dynamics differ between flooded and non-flooded sites (Garcia-Arias & Frances 2016).

In addition, our dataset leveraged variation in temperature that occurred over both space and time, either of which could contribute to the relationships between vegetation and temperature. In analysis of temporal patterns within each site, temperature relationships with cover were more strongly driven by differences among sites than by changes in warming over time. While temporal trends at some sites matched the overall pattern in cover versus temperature, other sites showed no clear trend over the study period. These results are not surprising because warming trends over the monitoring period are not as large as differences among sites over the north-south gradient of 210 km. Space-for-time substitution has been used to predict future community trajectories (e.g., (Stromberg et al. 1996)); however, we suggest observational studies, such as ours, should be applied cautiously because they cannot decouple temperature differences from other, unmeasured differences among sites. There are likely many other factors important in riparian plant communities that we have not examined, including the amount of snowpack and timing of spring runoff (Perry et al. 2012b), edaphic factors such as soil nutrients (Andersen et al. 2014), fire (Pettit & Naiman 2007), and both river and land management strategies (Samson et al. 2018).

Because riparian vegetation has been related to depth to groundwater in numerous prior studies (Scott et al. 1999; Naumburg et al. 2005; Mata-Gonzalez, McLendon, et al. 2012; Gurnell et al. 2012; Sommer & Froend 2014), we were surprised to find that precipitation explained variation in plant cover for most plant groups we examined, particularly at flooded sites. We did observe greater herbaceous cover with greater precipitation at both flooding and non-flooding sites, which was expected because this group includes annuals and shallow rooting plants that acquire water primarily from precipitation (Darrouzet-Nardi et al. 2006). Unexpectedly, at all sites, the relationship between precipitation and woody and native was negative. A negative influence of precipitation could be driven by short term anoxia of roots when water tables rise quickly following large rain events (Naumburg et al. 2005), which contribute the majority of precipitation in our region. This would explain why the relationships between precipitation and cover mirror the relationships between groundwater and cover at non-flooding sites. Alternatively, shallow-rooted understory, herbaceous plants may use limited rain water before it reaches deep-rooted canopy plants, reducing canopy cover. Understory cover was 66% higher at flooding sites than non-flooding sites, which could explain why the relationship between precipitation and both native and woody cover was weaker at non-flooding sites.

It is possible that some of the relationships we observed between abiotic variables and vegetation are causal in the reverse direction – for example, plants driving changes in groundwater depth or intra-annual variability in groundwater. Potential for such biophysical feedbacks have been investigated in some detail for riparian ecosystems, mostly through modeling efforts (Rodriguez-Iturbe et al. 2007; Wang et al. 2012). At least one prior study proposed that vegetation was the cause, rather than the response, to intra-annual variability in groundwater (Butler et al. 2007). While observational data cannot easily separate correlation from causation, the application of new statistical approaches, such as spatial convergent cross-mapping (Clark et al. 2015) may yield new insight when applied to time series data in riparian ecosystems.

In riparian forests where dams, river channelization, and incised banks make flooding unlikely in a majority of the historic floodplain, we determined that plant communities correlate with different climate factors in remnant non-flooding forests than in forests that retain the capacity to flood. We leveraged variation across both time and space to demonstrate that relationships between vegetation and abiotic variables changed in both their magnitude and direction between flooding and non-flooding sites. The flood regime appears to play a strong role in how riparian plant communities may change with future changes in temperature, groundwater depth and seasonal groundwater variability.

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Supplementary Material

Figure S1. Relationships between plant cover and abiotic factors at flooding and non-flooding sites for total native plant cover (A, C, E, G) or non-native plant cover (B, D, F, H). Lines show best fit model with 95% confidence bands, plotted using visreg (Breheny & Burchett 2017). Points represent the average cover at one site in one year.

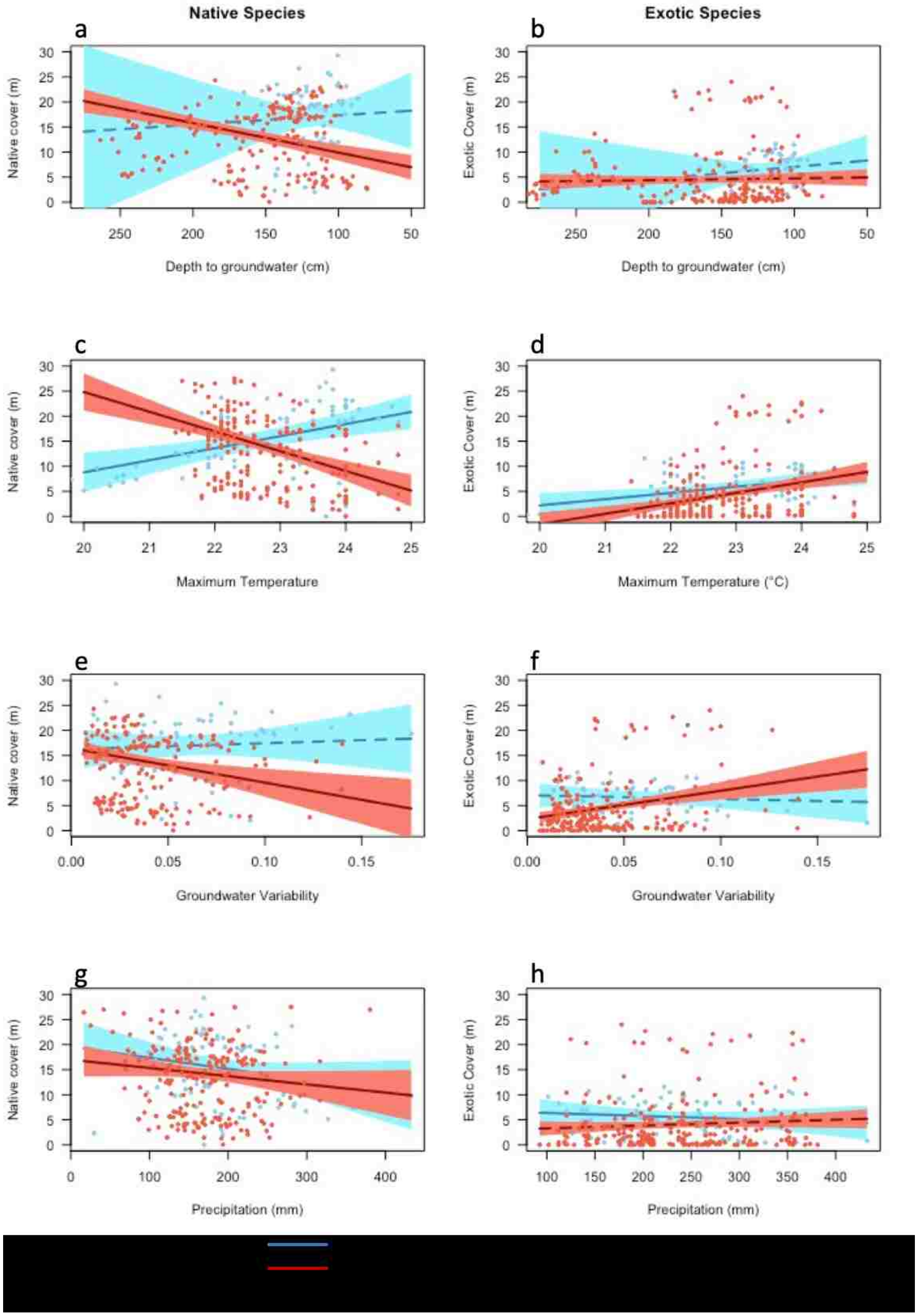
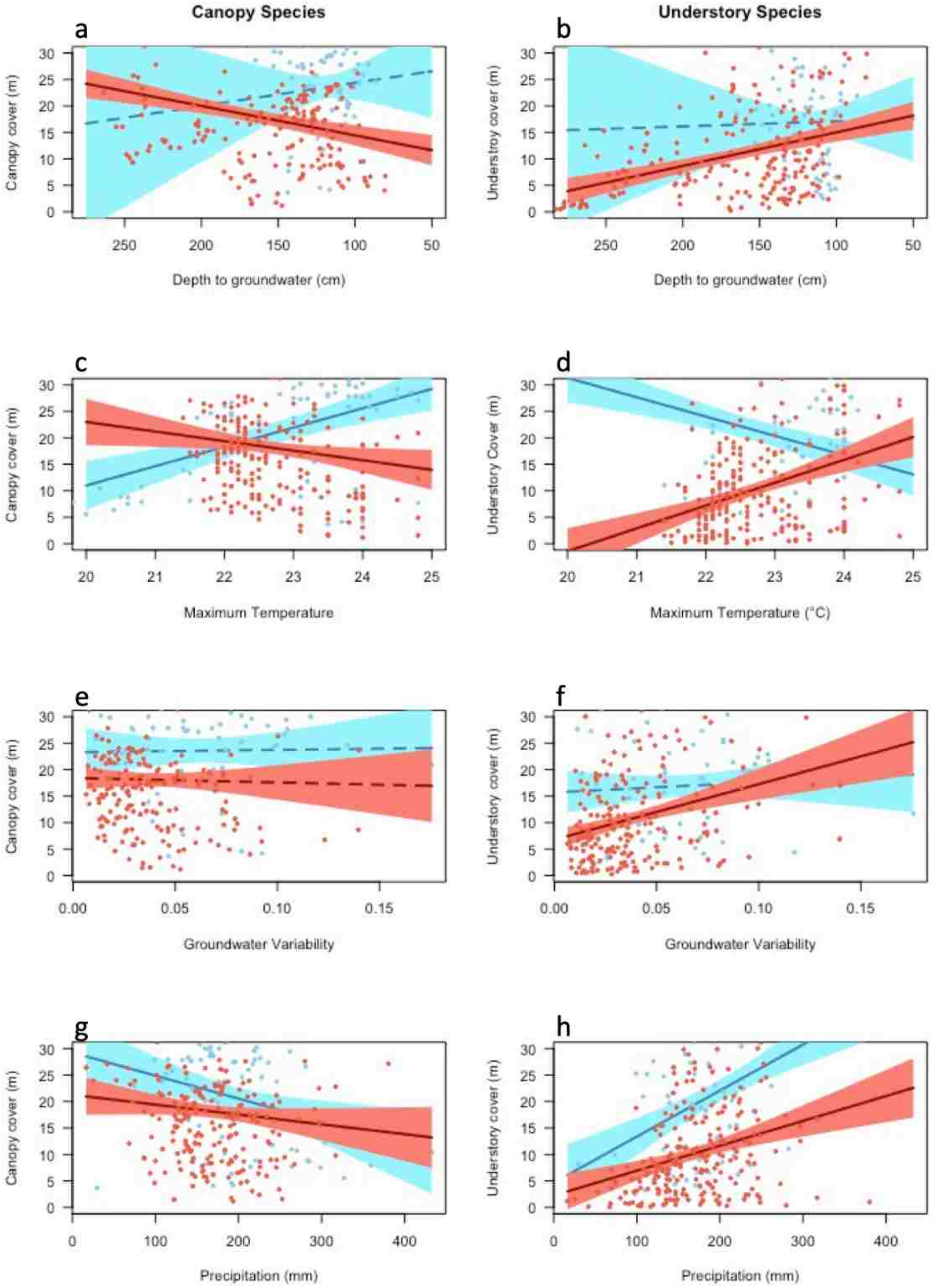


Figure S2. Relationships between plant cover and abiotic factors at flooding (blue) and non-flooding (red) sites for woody plant cover (A, C, E, G) or herbaceous understory plant cover (B, D, F, H). Lines show best fit model with 95% confidence bands, plotted using visreg (Breheny & Burchett 2017). Points represent the average cover at one site in one year.



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Chapter 2: Riparian plant species differ in sensitivity to both the mean and variance in groundwater stores

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Abstract

Determining the ecological consequences of interactions between slow changes in long-term climate means and amplified variability in climate is an important research frontier in plant ecology. We combined the recent approach of climate sensitivity functions with the revised ‘bucket model’ to improve predictions on how plant species will respond to future changes in both the mean and variance of groundwater resources. We leveraged spatiotemporal variation in a long-term dataset of riparian vegetation cover to build the first *groundwater sensitivity function*s (GSFs) for common plant species of dryland riparian corridors. Our results demonstrate the value of this approach to identifying which plant species will thrive (or fail) in an increasingly variable climate. Riparian plant species differed in sensitivity to both the mean and variance in groundwater levels. Rio Grande cottonwood (*Populus deltoides* ssp. *wislizeni*) cover was predicted to decline with greater interannual variance in groundwater, while coyote willow (*Salix exigua*) and other native wetland species were predicted to benefit from greater variance. No non-native species were sensitive to groundwater variance, but patterns for Russian olive (*Elaeagnus angustifolia*) suggested declines would occur with deeper *mean* groundwater tables. Warm air temperature modulated groundwater sensitivity for cottonwood, which was more sensitive to groundwater variance in years/sites with warmer maximum temperatures than in cool sites/periods. The temporal scale of variance mattered. Intra-annual and inter-annual coefficients of variation (*CV*) in groundwater differentially affected plant species. Cottonwood cover was negatively associated with intra-annual *CV*, but was not significantly correlated with inter-annual *CV*, perhaps due to the relatively short time series (16 years) relative to cottonwood lifespan (70-100 y). Tamarix (*Tamarix chinensis*) cover increased with both intra- and inter-annual *CV* in groundwater. Altogether, our results indicate that changes in groundwater variability as well as mean may alter riparian plant communities.

Introduction

Understanding the environmental factors that constrain plant growth is a major goal in plant ecology and has become especially important for predicting how species will respond to climate change. While many studies have investigated how changes in mean climate variables, such as temperature or precipitation, affect ecological responses, the impacts of environmental variance around the mean are poorly understood [reviewed by (Vazquez, Gianoli, Morris, & Bozinovic, 2017)Many climate models predict increases in year-to-year variability in climate(Fischer, Beyerle, & Knutti, 2013; Gutzler & Robbins, 2011), and increasing seasonal variability has been documented even where the mean climate has not changed (Petrie, Collins, Gutzler, & Moore, 2014). Determining the ecological consequences of interactions between slow changes in long-term climate means and amplified intra- or interannual variance in climate is thus an important research frontier (C. R. Lawson, Vindenes, Bailey, & van de Pol, 2015; Vazquez et al., 2017). For example, the interaction between increasingly variable precipitation and warmer temperatures may lead to higher evapotranspiration rates and drier soils (Seager et al., 2013).

Climate sensitivity functions have been proposed as a tool for understanding the relationship between environmental variance and ecological responses (Rudgers et al., 2018). A sensitivity function depicts the complex relationship between an ecological response (e.g., plant species cover) and its climatic driver (e.g., precipitation or groundwater; Fig. 1). The function has the potential to capture nonlinear ecological responses to climate variables (Hsu & Adler, 2014; Huxman et al., 2004) because sensitivity is characterized by the shape of the curve, rather than by the conventionally used slope of a linear relationship [e.g., (Munson, 2013), Fig. 1A]. When a sensitivity function is linear, increases in only the variance of the climate driver should not change the ecological outcome (Fig. 1B). However, when a sensitivity function is nonlinear, increased variance of the driver can alter the long-term ecological outcome, even if mean climate does not change (C. R. Lawson et al., 2015) - the mathematical principle of Jensen's Inequality. A concave function (Fig. 1C) yields net negative effects of increasing variance, because low values of the climatic variable (e.g., low precipitation, Fig. 1) cause large decreases in the ecological response (e.g., plant cover), while high values of the climatic variable (e.g., high precipitation) cause only small increases. In contrast, a convex function results in net positive effects of increasing variance (Fig. 1D), because increases in the ecological response during wet conditions are greater than the losses in dry conditions. If the function changes concavity over the full range of the climatic driver

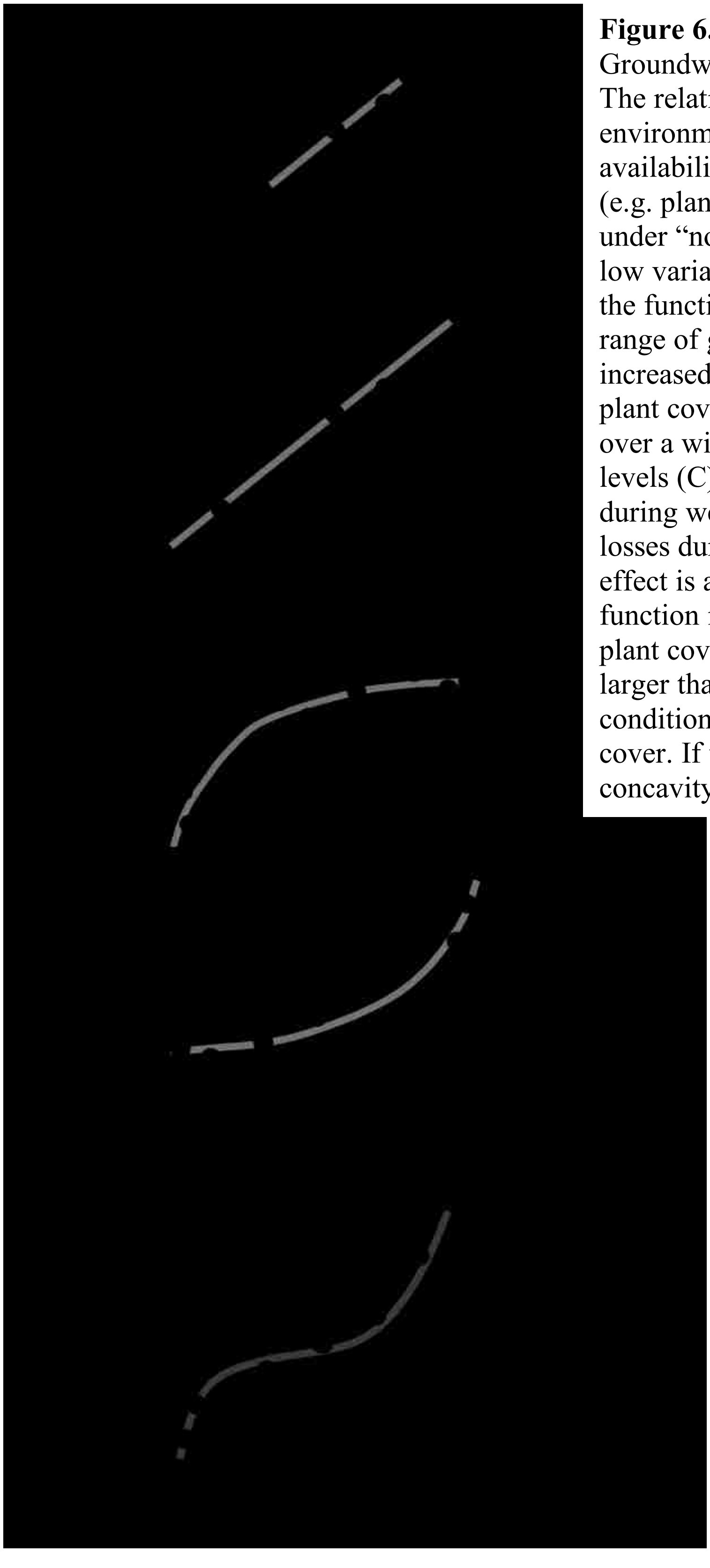

Figure 6. Hypothesized types of Groundwater Sensitivity Functions. The relationship between an environmental driver (e.g. groundwater availability) and an ecological response (e.g. plant cover) may appear linear under “normal” conditions that have low variability in groundwater, (A). If the function remains linear over a wide range of groundwater levels (B), then increased variability will not affect plant cover. If the function is concave over a wide range of groundwater levels (C), then gains in plant cover during wet conditions are smaller than losses during dry conditions; the net effect is a decline in plant cover. If the function is convex (D), then gains in plant cover during wet conditions are larger than losses during dry conditions; there is a net gain in plant cover. If the function changes concavity across the range of

(Fig. 1E), then variance in the driver could have positive or negative effects depending on the mean, *because the mean and variance interact*. The magnitude of a species' sensitivity to variance in climate is thus predicted by the degree of nonlinearity in the sensitivity function.

Identifying nonlinear climate sensitivity functions requires long time series over naturally or experimentally variable climates (Vazquez et al., 2017), which is often difficult to achieve with field experiments. Careful laboratory experiments that expose species to a wide range of environmental conditions can be valuable for characterizing sensitivity (C. R. Lawson et al., 2015), but are impractical for large, long-lived species. Direct field manipulations of climate variance are possible [e.g., (Gherardi & Sala, 2015b, 2015a)], but require long-term investment and are exceedingly rare. Using observational data to construct climate sensitivity functions can generate initial predictions on future ecological responses to changes in both the mean and variance in the environment (Hsu & Adler, 2014; Rudgers et al., 2018). Insight from climate sensitivity functions could be useful in conservation and management to identify species that will thrive (or fail) in an increasingly variable climate.

In addition to the mathematics of climate sensitivity functions, the bucket model has been proposed as a graphical, conceptual framework for predicting the sensitivity of plants to increasing variability in water resources (Alan K. Knapp et al., 2008). The bucket model

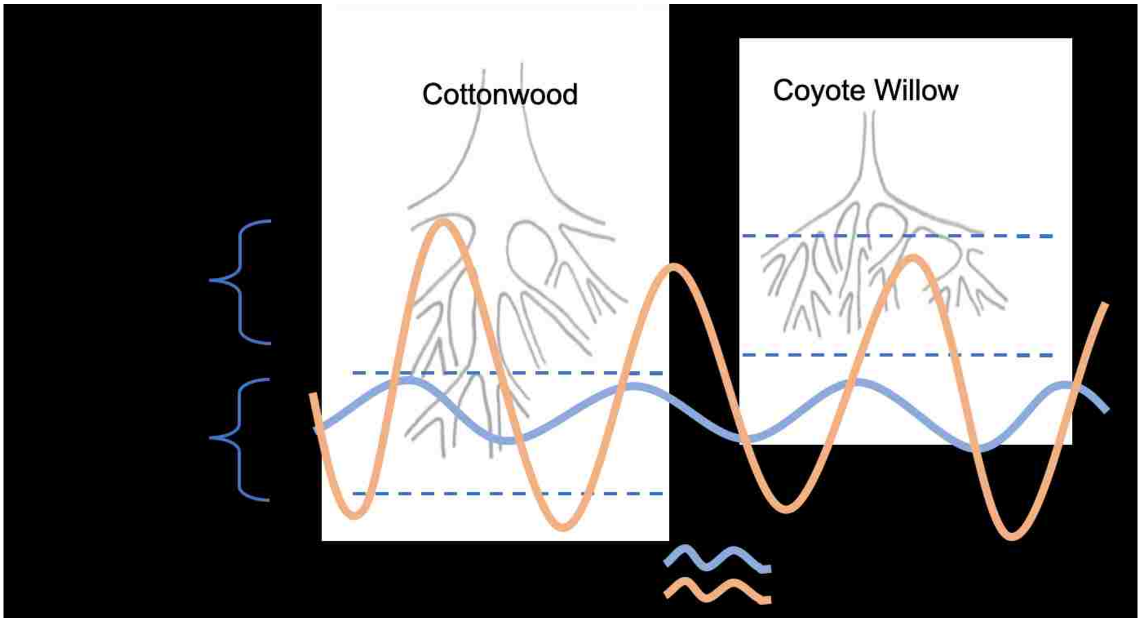

Figure 2. A revised bucket model for predicting plant responses to groundwater variability from species-specific stress tolerance thresholds. Here, we illustrate how two co-dominant species (cottonwood vs. willow) can diverge in responses to environmental variability. At low groundwater variability (blue line), the water table remains within optimal levels for both cottonwood and willow, and variability in water availability should have little impact on plant growth. At high groundwater variability (orange line), groundwater levels frequently fall outside the tolerance threshold for cottonwood, reducing plant growth; however, groundwater levels more frequently fall within the optimal threshold for willow, thereby increasing plant growth.

hypothesizes that a species' response to climate variance is contingent not only on mean climate (as also occurs with climate sensitivity functions) but also on the species' individual stress tolerance thresholds (Alan K. Knapp et al., 2008; Thomey et al., 2011). Where mean water levels are within the optimal thresholds for a plant species, increasing the variability in water resources can push the plant outside of its optimal range. Thus, increasing variability around the mean is predicted to be costly. In contrast, where mean water levels fall outside of the species' stress threshold (either too dry or too wet), increasing variability can push water availability into the optimal range. Therefore, an increase in the variability of water stores benefits the plant by creating favorable resources more often.

Within an ecosystem, plant species may differ in their stress tolerance thresholds, dependent on their life history, root structure, or provenance (Silvertown, Araya, & Gowing, 2015; Stromberg, 2013). Therefore, each species may respond differently to increasing variance in water resources. For example, tree species diverge in rooting depth, thereby experiencing different stress thresholds for groundwater availability(Fan, Miguez-Macho, Jobbagy, Jackson, & Otero-Casal, 2017; Jackson, Moore, Hoffmann, Pockman, & Linder, 1999). Similarly, plant species that differ in provenance because they evolved in different locations can diverge in their traits and stress tolerance thresholds when brought together in a common environment following species invasions (Drenovsky et al., 2012; Glenn & Nagler, 2005; van Kleunen, Weber, & Fischer, 2010). Understanding how differences in plant traits interact with mean climate has improved predictions on the impacts of species invasions on ecosystem processes (Martin, Newton, & Bullock, 2017). Although differences among plant species in resource acquisition traits are common knowledge, the influence of these trait differences on sensitivity to *variance* in water resources has received much less attention (Xi, Di, Liu, Zhang, & Cao, 2018a). We propose that combining the approach of climate sensitivity functions (Fig. 1) with the bucket model (Fig. 2) can improve predictions on how plant species will respond to future changes in both the mean and variance of water resources.

Variability can occur at different time scales, including intra-annual variability caused by seasonal changes, and inter-annual variability caused by climate phenomena such as the El Niño Southern Oscillation or Pacific Decadal Oscillation, as well as by anthropogenic climate change. Both scales have been predicted to increase in variability under recent climate models (Fischer et al., 2013; Gutzler & Robbins, 2011; IPCC, 2014). Some experiments have manipulated variability at one scale and detected plant responses. For example, Knapp et al. (2002) altered intra-annual precipitation in a tallgrass prairie; increased intra-annual variance reduced aboveground net primary production. Gherardi and Sala (2015a,b) altered inter-annual variance in rainfall, which also decreased total primary production. However, dominant plant species responded divergently: the dominant shrub benefitted from increased inter-annual variance, whereas the dominant grass declined (Gherardi and Sala 2015a,b). Investigating both temporal scales of variability is valuable because the sensitivity of plants could depend on the scale at which variability occurs. While experiments have generally examined one scale or the other, observational data provide opportunities to explore both inter- and intra-annual variation.

Here, we leveraged both spatial and temporal variation in a long-term dataset of riparian vegetation cover and groundwater levels to explore the relationships between mean and variance of groundwater and inter- and intra-annual variability. In dryland riparian forests water resources are primarily driven by the shallow water table, which varies both seasonally and annually with changes in streamflow (Naumburg, Mata-Gonzalez, Hunter, Mclendon, & Martin, 2005; Steinberg, Eichhorst, & Rudgers, in review; Tron, Laio, & Ridolfi, 2014; Xi, Di, Liu, Zhang, & Cao, 2018b). Riparian plant communities have been shown to be sensitive to seasonal water variance (Katz, Denslow, & Stromberg, 2012; J. R. Lawson, Fryirs, Lenz, & Leishman, 2015). By building the first *groundwater sensitivity function*s (GSFs) for common plant species of dryland riparian corridors, our goal was to improve predictions about how riparian dominants will differ in their sensitivity to future increases in environmental variability under a warming climate. Our dataset comes from the Middle Rio Grande riparian corridor in central New Mexico. Arid rivers already experience large variability, as they are driven by both local climate and the climate of their upper watersheds, and these ecosystems are expected to become increasingly more variable in the future (Crawford et al., 1993; Gurnell, Bertoldi, & Corenblit, 2012; Osterkamp & Hupp, 2010). We combined information on variability across time with spatial variability along a 110 km stretch of the Rio Grande to generate predictions on plant species sensitivity to groundwater across a wide range of possible groundwater conditions. We used this space-for-time approach to specifically address the following questions. (1) Do riparian plant species differ in sensitivity to the mean and variance in groundwater levels? (2) At what temporal scale (intra- vs. inter-annual) is variance in groundwater most important to riparian plant species?

Methods

Study Sites. Groundwater, precipitation, and vegetation cover data were collected as part of the Bosque Ecosystem Monitoring Program (BEMP) in the Middle Rio Grande Valley of New Mexico (bemp.org). BEMP monitors county, state, federal, and tribal land along 420 km of the Rio Grande; we used data from 22 sites spanning 110 km (Table S1, Fig. S1).

Study Design. Each BEMP site (Fig. 2 is 100 m X 200 m, with the 200 m side running north-south parallel to the Rio Grande. Each site is divided into ten equal 20 X 100m sections and a 30m vegetation transect is randomly placed within each section running east to west. Each BEMP site has two rain gauges and five groundwater wells (described below).

Vegetation Monitoring. Vegetation monitoring began in 2000 at seven sites and has continued to the present; new sites were included in annual monitoring as they were established (Table S1). This analysis used data from 22 sites from 2000 through 2015. We monitored ten vegetation transects per site (Fig. S2) once annually during peak biomass production (August-September). Plants were monitored using line-intercept sampling: for each plant species that crossed a transect, we recorded species identity and the length of the transect covered in cm. When individual plants of the same species overlapped, cover was recorded as continuous; therefore, total cover for a single species never exceeded 3000 cm per transect. For plants < 1 m tall (predominantly grasses and forbs), we excluded gaps < 1 cm between individuals of the same species, and recorded plant cover as continuous. For plants 1-3 m tall, we excluded gaps of < 10 cm between individuals of the same species. For plants taller than 3 m (predominantly canopy trees), we excluded gaps of < 1 m. We then summed the transect length covered by each individual plant species over the 30 m transect and divided by 30 to obtain plant cover per meter for each plant species. Transect identity was our smallest unit of observation; thus, we had 10 samples per site per year.

Groundwater. Each BEMP site included five groundwater wells: one located in the center of the site and the other four installed 40 m from the center in each of the four cardinal directions (Fig S2). We measured depth to groundwater (cm) at each well monthly using a Solinst water level meter (Georgetown, Ontario, Canada), subtracting the above-ground height of the well from the total measurement. Wells were constructed and installed using published methods (Martinet et al., 2009). We averaged the five wells within each BEMP site to obtain the arithmetic mean depth to groundwater for each month of observation. Monthly groundwater levels were then averaged to estimate mean annual groundwater level for each site.

Climate. Temperature data came from the PRISM database (PRISM Climate Group, 2018). We obtained annual and monthly temperature and precipitation data at the 4km spatial resolution. Annual values were used for minimum, maximum, and average daily temperatures and cumulative precipitation at each BEMP site.

Data Analysis

The changing groundwater context. We investigated temporal trends in groundwater depth and intra-annual variability across the monitoring period at the four sites with complete groundwater records from 2000 to 2015. We averaged groundwater depth and intra-annual variability across the four sites and used a linear model to determine the temporal trends for each variable. The relationship between groundwater and stream flow was also investigated using a linear model. BEMP reports stream flow data from United

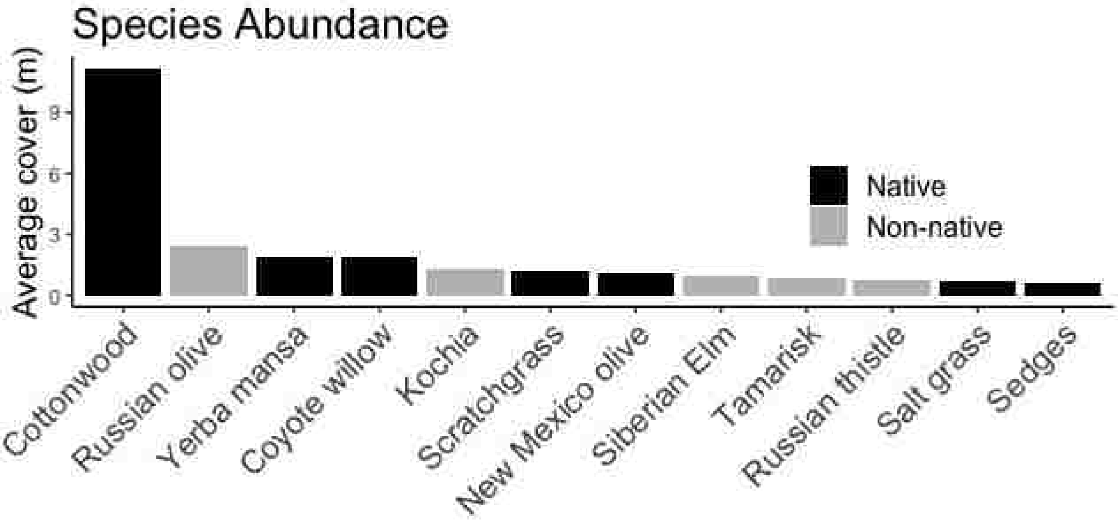

Figure 3. Mean plant cover across all sites and years for the 12 most abundant species across BEMP sites in the Middle Rio Grande Valley of New Mexico. Native species are cottonwood (*Populus deltoides* ssp. *wizlizeni*), yerba mansa (*Anemopsis californica*), coyote willow (*Salix exigua*), scratchgrass (*Muhlenbergia asperifolia*), New Mexico olive (*Forestiera pubescens*), saltgrass (*Distichlis spicata*), and sedges (*carex* spp.). Non-native species are Siberian elm (*Ulmus pumila*), Russia olive (*Elaeagnus angustifolia*), Tamarisk (*Tamarix chinensis*), kochia (*Bassia scoparia*) and Russian thistle (*Salsola tragus*).

States Geological Survey stream flow gauges nearest the site for the day of each groundwater data collection.

Do riparian plant species differ in sensitivity to the mean and variance in groundwater levels? We evaluated the nine most common plant species within our study sites (Fig. 3). This set included both native and non-native species as well as non-wetland, obligate wetland, and facultative wetland species. We used model selection procedures to determine the best groundwater sensitivity function (GSF) for each species based on the relationship between groundwater depth and plant cover, we compared linear and non-linear models, and models that used the current year groundwater depths and the previous year's groundwater depths. Mixed effects models were fit via maximum likelihood using the *lme4* package in R (Bates et al 2015, R Core Team 2016). We included the random effects of site and year to account for non-independence of observations. We selected the best model using the second order Akaike Information Criterion (*AICc*) and determined marginal and conditional R^2 values using the piecewiseSEM package (Lefcheck, 2016). Where variability in temperature interacted with groundwater levels, we split the dataset by median maximum temperature, binning data into hot versus cold years/sites. Then, we examined the relationship between mean groundwater depth and plant cover for each temperature bin.

At what temporal scale (intra- vs. inter-annual) is variance in groundwater most important to riparian plant species? We compared the importance of inter-annual versus intra-annual variance in groundwater within long-term BEMP sites using mixed effects models in the *lme4* package in R (Bates et al 2015, R Core Team 2016). Models predicted plant cover as a function of either the intra- or inter-annual coefficient of variation in groundwater depth for each BEMP site. Inter-annual variation at each site was calculated for sites with >5 y of data using mean annual groundwater levels. Intra-annual variation was calculated at each site for every year of data using mean monthly groundwater levels. We fit linear models of plant cover separately at each temporal scale, then compared model fits for each temporal scale using the second order Akaike Information Criterion (*AICc*). Again, models included the random effects of site and year to account for the non-independence of observations.

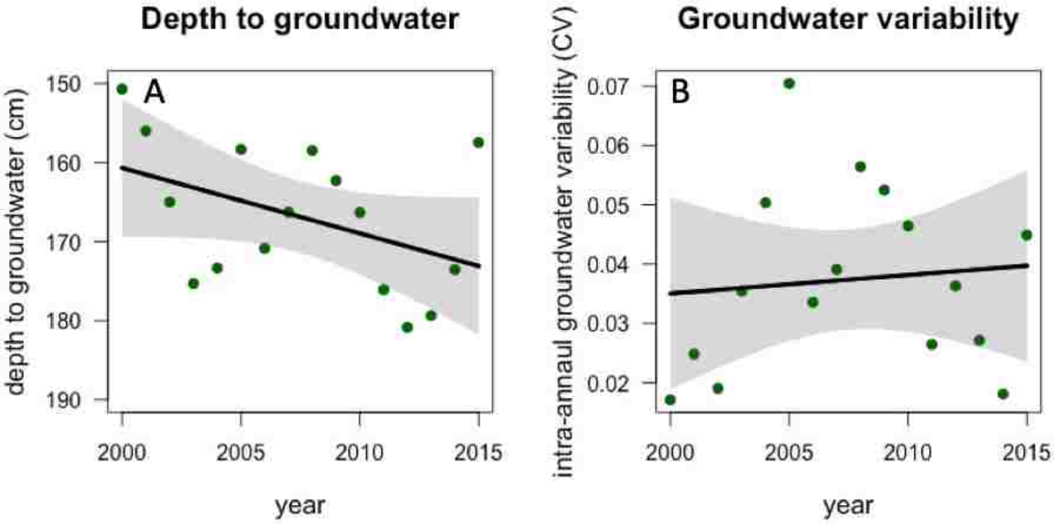

Figure 4. Trends in groundwater and variability in the Middle Rio Grande Valley. Depth to groundwater and groundwater variability over time averaged from the four BEMP sites with complete groundwater data from 2000-2015, (sites 1-4, see Table S1). (A) Average annual groundwater depth increased from 2000-2015 (slope=1.39, r^2=0.37, P=0.01). (B) Intra-annual variability in groundwater depth did not change significantly in that time (slope=0.0002, r^2=0.006, P=0.7).

Results

The changing groundwater context. Groundwater depth varies seasonally and annually, changes in groundwater depth correlates with changes in stream flow (Fig. S3). Between 2000 and 2016 mean average depth to groundwater across the four longest running sites significantly decreased (Fig. 4A) (r^2=0.37, P=0.01). Intra-annual variability in groundwater depth has not changed significantly in that time (Fig. 4B) (r^2=0.006, P=0.7).

Do riparian plant species differ in sensitivity to the mean and variance in groundwater levels? Observational results predict that plant species will diverge in response to environmental variability. The predicted ecological impact of changes in the mean and variance of a climatic driver is derived from the linear slope (mean) and the nonlinear shape (variance) of the GSF. Of the nine riparian plant species we investigated, four had significantly nonlinear relationships between groundwater and cover, 1 had only linear relationships, and 4 were not sensitive to the observed range of groundwater levels (n.s.). The three native, woody species [Rio Grande cottonwood (*Populus deltoids ssp. wislizenii*), coyote willow (*Salix exigua*), and New Mexico olive (*Forestiera pubescens*)] diverged the most in their GSF.

Cottonwood had a concave GSF that indicated variability in groundwater levels could be costly (R^2=0.07, P<0.0001; Fig. 5A, Table 1). The previous year's groundwater level was a better predictor of cottonwood cover than the current year ($\Delta AICc$=25, Table 1); cottonwood was the only species for which the best GSF used groundwater lagged one year behind plant cover. Including average maximum temperature improved the model fit ($\Delta AICc$=11, R^2= 0.11, X^2=11.88, P=0.0005) and revealed that the relationship between groundwater and cottonwood was non-significant in years/sites with cooler temperatures (Fig. 6A, R^2=0.05, P=0.14), but strong in years/sites with warmer temperatures (Fig. 6B, R^2=0.05 P=0.0006).

In contrast to cottonwood, coyote willow had a convex GSF (Fig. 5B), with more cover at either the highest or lowest water table depths and reduced cover in the middle depths, where cottonwood had the highest cover (r^2=0.11, P<0.0001). Maximum temperature did not improve the predictive power of the model ($\Delta AICc$=-8, Table 1), and the interaction between groundwater depth and temperature was not statistically significant (Fig. 6C&D, r^2=0.10, P=0.15). The contrasting spatial distributions of co-dominant cottonwood and willow species across groundwater depths could result from competition.

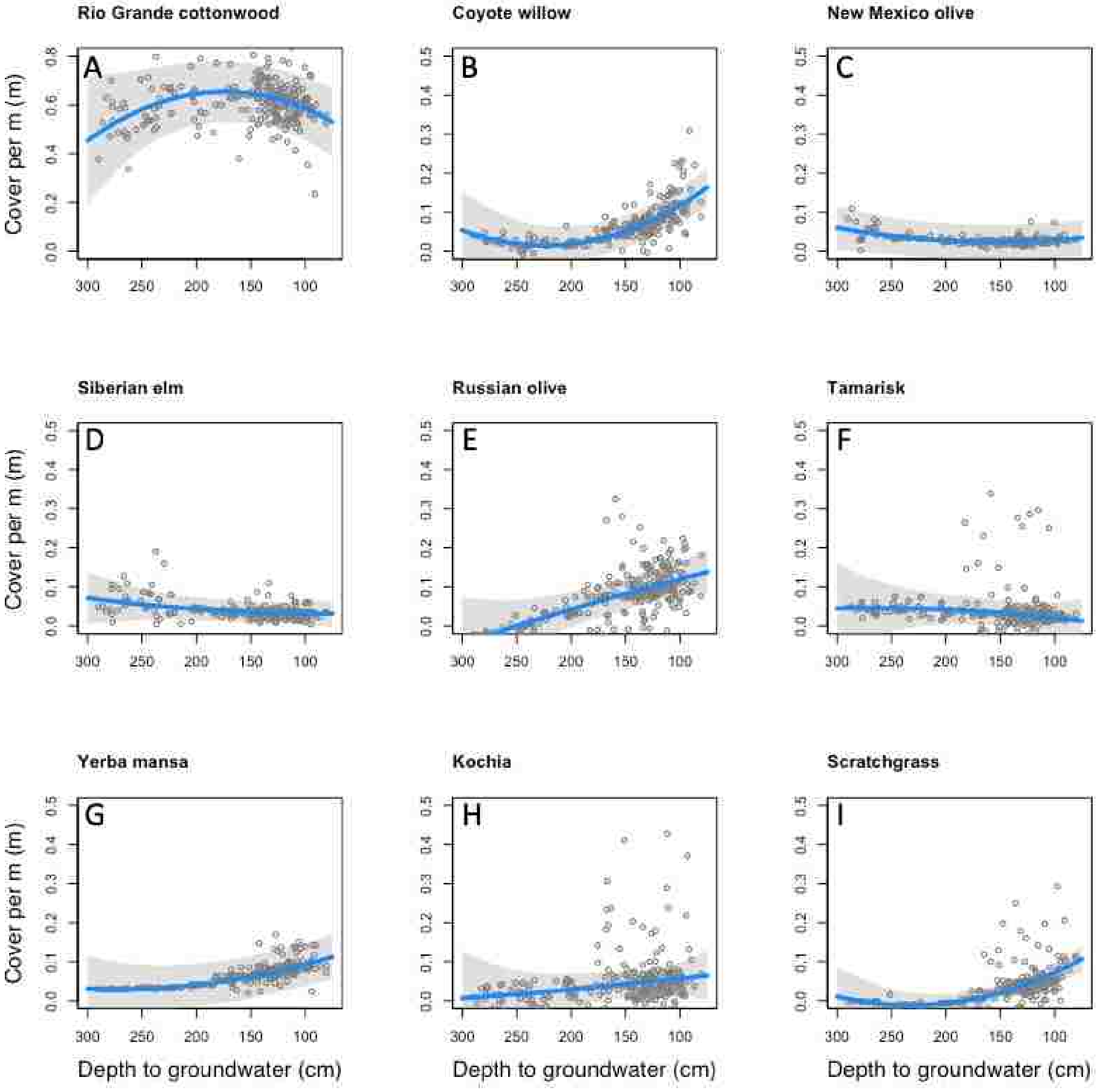

Figure 5. Groundwater sensitivity functions (GSFs) for the nine most abundant plant species across the Middle Rio Grande Valley of New Mexico. Concave functions predict a negative response to groundwater variability, whereas convex functions predict a positive response to variability (see Figure 1). Linear functions indicate sensitivity to mean groundwater levels, but not to groundwater variability. Native species are cottonwood (*Populus deltoides* ssp. *wizlizeni*), coyote willow (*Salix exigua*), New Mexico olive (*Forestiera pubescens*), yerba mansa (*Anemopsis californica*), and scratchgrass (*Muhlenbergia asperifolia*). Non-native species are Siberian elm (*Ulmus pumila*), Russia olive (*Elaeagnus angustifolia*), Tamarisk (*Tamarix chinensis*), and kochia (*Bassia scoparia*).

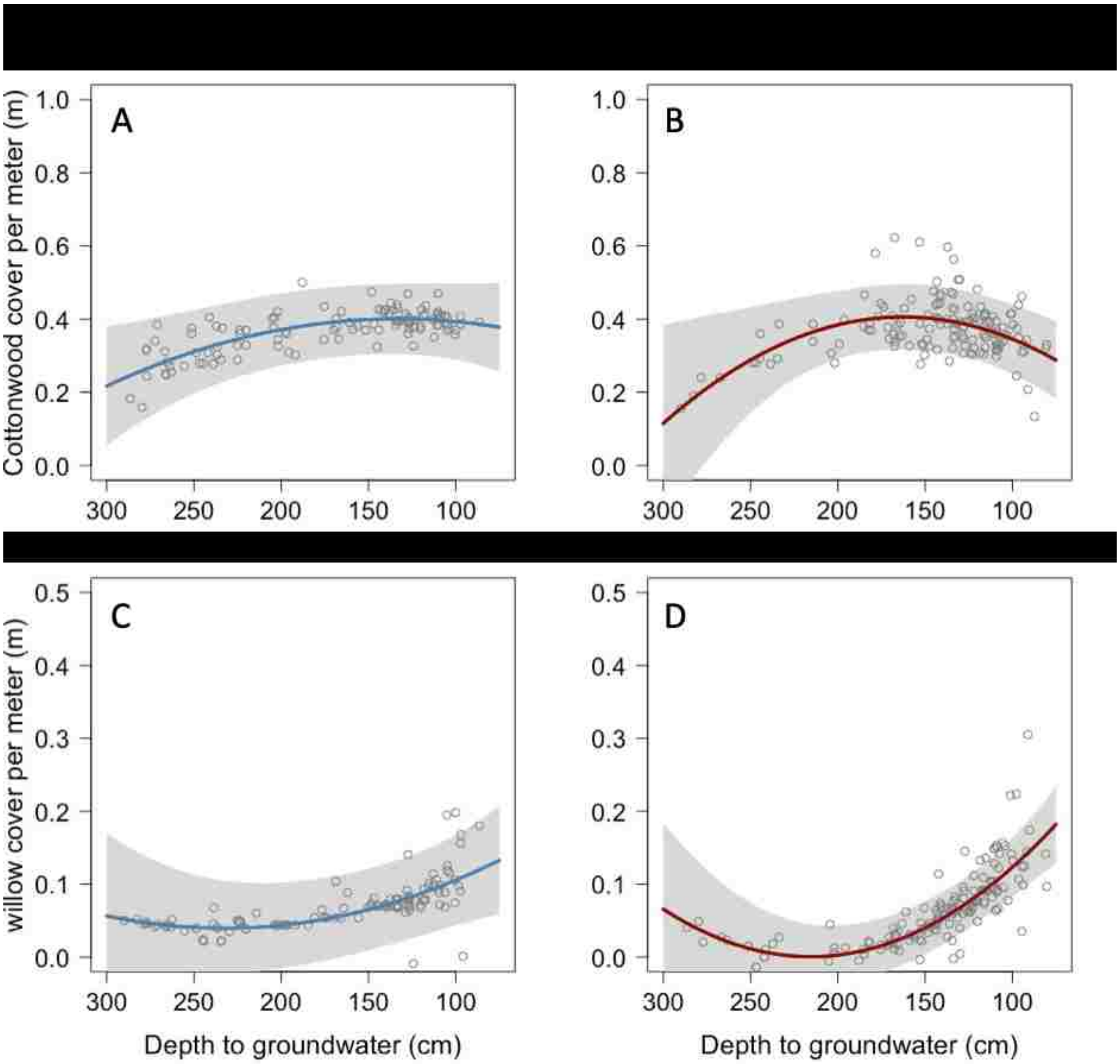

Figure 6. The Groundwater Sensitivity Function (GSF) for Rio Grande cottonwood (*Populus deltoids* ssp. *wizlizeni*) and coyote willow (*Salix* exigua) interacted with air temperature. In years/sites with low average maximum air temperature (< 22.5 °C), (A) the cottonwood GSF was flat, indicating little sensitivity to interannual variability in groundwater. In years/sites with high average maximum air temperature (≥ 22.5 °C), (B) the cottonwood GSF was concave, signaling negative consequences of increasing groundwater variability. The willow GSF did not significantly differ between low average maximum air temperature (C) and high average maximum air temperature (D), both GSF were convex, signaling positive consequences of increasing variability.

Table 1. Model parameters for groundwater sensitivity for nine riparian plant species from linear mixed effect regression models of species cover ~ groundwater depth including parameter estimates for the linear and quadratic (Groundwater depth^2) terms from the best model, ~nonlinear groundwater depth x maximum air temperature, showing log-likelihood X^2 statistics for the interaction terms and finally ~ inter-annual groundwater variability (*CV* = coefficient of variation), ~intra-annual groundwater variability (*CV*) Marginal R^2 values are shown for both nonlinear models. *P* values < 0.05 are shown in bold.

	Populus deltoides				***Salix exigua***				***Forestiera pubescens***				***Anemopsis californica***				***Muhlenbergia asperifolia***			
	Estimate	*s.e.*	*P*	marginal R^2	Estimate	*s.e.*	*P*	marginal R^2	Estimate	*s.e.*	*P*	marginal R^2	Estimate	*s.e.*	*P*	marginal R^2	Estimate	*s.e.*	*P*	marginal R^2
Intercept	0.101	0.084		0.07	0.359	0.058		0.10	0.070	0.029		0.003	0.185	0.044		0.02	0.245	0.054		0.17
Groundwater depth	0.004	0.001	**<0.001**		0.003	0.001	**<0.001**		-0.001	0.000	**0.011**		0.001	<0.001	**0.008**		-0.002	0.001	**0.001**	
Groundwater depth^2	<0.001	<0.001	**<0.001**		<0.001	<0.001	**<0.001**		<0.001	<0.001	**0.010**		<0.001	<0.001	0.120		<0.001	<0.001	**0.011**	
	X^2				X^2				X^2				X^2				X^2			
Groundwater X Temperature	11.880	--	**0.001**	0.11	1.980	--	0.150	0.10	1.360	--	0.241	0.005	1.720	--	0.180	0.02	1.940	--	0.160	0.21
Groundwater^2 X Temperature	8.950	--	**0.003**		1.560	--	0.210		0.871	--	0.351		1.090	--	0.290		1.170	--	0.270	
	Slope			*AIC*	Slope			*AIC*	Slope			*AIC*	Slope			*AIC*	Slope			*AIC*
Inter-annual CV	-0.482	0.297	0.106	-120	0.970	0.168	**< 0.001**	-445	-0.960	0.180	**< 0.001**	**-383**	1.440	0.210	**<0.001**	**-314**	0.540	0.092	**<0.001**	**-759**
Intra-annual CV	-1.366	0.384	**0.000**	**-136**	1.250	0.220	**< 0.001**	-445	-0.874	0.250	**0.001**	-370	0.960	0.290	**0.001**	-301	0.680	0.120	**<0.001**	-758

	Ulmus pumila				***Elaeagnus angustifolia***				***Tamarix chinensis***				***Bassia scopria***			
	Estimate	*s.e.*	*P*	marginal R^2	Estimate	*s.e.*	*P*	marginal R^2	Estimate	*s.e.*	*P*	marginal R^2	Estimate	*s.e.*	*P*	marginal R^2
Intercept	0.036	0.036		0.02	0.186	0.072		0.13	0.017	0.085		0.01	0.091	0.100		0.02
Groundwater depth	<0.001	<0.001	0.760		0.001	0.001	0.460		0.000	0.001	0.630		0.000	0.001	0.760	
Groundwater depth^2	<0.001	<0.001	0.530		<0.001	<0.001	0.830		<0.001	<0.001	0.760		<0.001	<0.001	0.930	
	X^2				X^2				X^2				X^2			
Groundwater X Temperature	0.450	--	0.500	0.01	1.710	--	0.190	0.17	0.002	--	0.959	0.03	0.011	--	0.910	0.02
Groundwater^2 X Temperature	1.250	--	0.260		1.650	--	0.200		0.002	--	0.961		0.016	--	0.890	
	Slope			*AIC*	Slope			*AIC*	Slope			*AIC*	Slope			*AIC*
Inter-annual CV	-0.420	0.100	**<0.001**	-714	1.200	0.150	**<0.001**	**-467**	0.480	0.130	**<0.001**	**-552**	-0.180	0.150	0.220	-469
Intra-annual CV	-0.510	0.130	**0.000**	-714	1.510	0.210	**<0.001**	-461	0.440	0.180	**0.014**	-548	0.250	0.210	0.220	-468

New Mexico olive was insensitive to the observed range of groundwater depths (Fig. 5C, r^2=0.003, P=0.01, Table 1). This plant species, while common in our sites, is not a wetland plant and may simply be less sensitive to groundwater than other taxa. The inclusion of maximum temperature did not improve the model slightly ($\Delta AICc$=-5), and there was no significant interaction between groundwater depth and maximum temperature (X^2=1.3, P=0.24, Table 1).

We analyzed three common, nonnative, woody species: Siberian elm (*Ulmus pumila*), Russian olive (*Elaeangnus angustifolia*) and tamarisk (*Tamarisk chinensis*). Neither elm (r^2=0.016, P=0.76), nor tamarisk (r^2=0.008, P=0.6) was sensitive to groundwater depth (Fig. 5D&F, Table 1). Russian olive, had a positive relationship with groundwater (Fig. 5E, Table 1) (slope=0.0006, r^2=0.13, P=0.4) and nonlinear model was not a better fit ($\Delta AICc$=2). For Russian olive, plant cover increased in years/sites with shallower water tables. Temperature was not a significant predictor for any of these nonnative species (Siberian elm $\Delta AICc$=-1.2, Russian olive $\Delta AICc$=-5, Tamarik $\Delta AICc$=-5).

We evaluated the three most abundant herbaceous plants: yerba mansa (*Anemopsis californica*), a herbaceous perennial and obligate wetland species; kochia (*Bassia scoparia*), a nonnative annual; and scratchgrass (*Muhlengergia asperifolia*), a perennial grass and facultative wetland species. Of these three species, scratchgrass and yerba mansa both had convex GSF (Fig. 5G&I, Table 1), with the most plant cover where the water table was shallow and very little growth at deep water tables, as expected for wetland species. The GSF for scratchgrass (r^2=0.17, P P=0.001) explained more variation in plant cover, than the yerba mansa GSF (r^2=0.02, P=0.008). Kochia had a flat GSF (Fig. 5H, Table 1) and was not sensitive to the observed range of groundwater depths

(r^2=0.017, P=0.76). Temperature was not a significant predictor for any of these herbacious species (yerba mansa $\Delta AICc$=-1.6, kochia $\Delta AICc$=-7, scratchgrass $\Delta AICc$=0.3, Table 1).

Spatial variation in groundwater was greater than temporal variation within a site, and no individual sites spanned the entire observed range of groundwater. Therefore, the shape of the GSFs derived primarily from spatial variation rather than temporal variation. For example, investigation of the sensitivity of cottonwood cover to groundwater depth over time at each individual site demonstrated that the relationship between groundwater and cottonwood cover was largely dependent on spatial variation in groundwater depth (Fig. S4).

At what temporal scale (intra- vs. inter-annual) is variance in groundwater most important to riparian plant species? Plant species' relationships to groundwater variance supported predictions that a concave GSF signals a cost of increased variability, while a convex GSF signals a benefit from variability. We investigated temporal variation by exploring the relationship between plant cover versus either inter- or intra- annual groundwater variance within sites (Table 1). We were able to calculate intra-annual variability for all sites and years, and inter-annual variability for every site except site 30, which only had two years of groundwater data. Correlation between plant cover and both scales of groundwater variability of all nine species are reported in Table 1. Species identified as sensitive to groundwater depths using GSF's had strongest relationship with groundwater variability on at least one scale. Cottonwood cover was negatively related to intra-annual variability (slope=-1.36, *P* =0.004) but not significantly correlated to inter-annual variability (slope=-0.48, *P* =0.1). Coyote willow was positively correlated with variability at both the inter-annual time scale (slope=0.97, *P* <0.0001) and the intra-annual time scale (slope=1.25, *P*<0.0001) (Δ*AICc*=0.2). Positive relationships between plant cover and groundwater variability at both time scales were found for yerba mansa (inter-annual slope=1.44, *P*<0.0001; intra-annual slope=0.96, *P*=0.0008, Δ*AICc*=13) and scratchgrass (inter-annual slope=0.54, *P*<0.0001; intra-annual slope=0.68, *P*<0.0001, Δ*AICc*=1), inter-annual variability was a better fit for yerba mansa, but the two were not significantly different for scratchgrass. For some species, cover was not strongly correlated with groundwater depth in the GSFs, but was correlated with groundwater variance on at least one scale. Siberian elm was not significantly related to groundwater depth but was negatively correlated with both inter- and intra-annual groundwater variability (Δ*AICc*=0.02). New Mexico olive was also negatively related to both scales of variability, but inter-annual variability was a better fit (Δ*AICc*=13). Both exotic shrub species (Russian olive and Tamarisk) were positively correlated with groundwater variability on both scales. Inter-annual variability was a better model fit these species (Russian olive Δ*AICc*=6, tamarisk Δ*AICc*=4). The only species not significantly related to groundwater variability on either scale was kochia, (inter-annual slope=-0.18, *P*<0.15; intra-annual slope=0.25, *P*<0.22).

Discussion

With 16 years of observational data spanning 110 km of a dryland riparian corridor, we detected important influences of both inter- and intra-annual variability in groundwater. Groundwater sensitivity functions (GSFs) revealed that riparian plant species differed substantially in their sensitivity to environmental variability. These results from riparian forest ecosystems support recent evidence that both ecosystems (Hsu & Adler, 2014; Rudgers et al., 2018) and plant species(Angert, Huxman, Chesson, & Venable, 2009) can differ strongly in their responsiveness to environmental variance. Our results raise the question, what factors explain plant species differences in sensitivity to groundwater mean and variance?

Differences among plant species in their sensitivity to variance in groundwater may depend many factors including plant traits, provenance and wetland indicator status. Plants can have water-use strategies that avoid dehydration (e.g. deep roots or fast growing roots) or strategies that tolerate dehydration (e.g. low tissue water content or summer dormancy) (Bristiel, Roumet, Violle, & Volaire, 2019). Differences in water-use efficiency and phenotypic plasticity in water-use efficiency under stress will likely influence how plants respond to groundwater variability(Silvertown et al., 2015). For example, when groundwater tables are >3m, cottonwood can invest up to 50% more root biomass in the top 1 m of soil (Lines, 1999), indicating large capacity for phenotypic plasticity. Plant traits that influence water use have been shown to change across water gradients in various ecosystems (Chave et al., 2009). In riparian systems specifically changes in traits across water gradients aligned with wetland status, where wetland indicator plants were more likely to be sensitive to changes in groundwater than upland species (McCoy-Sulentic et al., 2017). Our results align with this finding, since the four species we identified as sensitive to groundwater variability are wetland indicators (coyote willow, yerba mansa and scratchgrass), or phreatophytes (cottonwood). Lastly, provenance was a key factor associated with differences among species in sensitivity to groundwater mean and variance. None of the four non-native species in our study were significantly related to groundwater depth, although Russian olive had a trend of increasing with shallower water tables, and groundwater depth explained 13% of variation in Russian olive cover. These species are often targeted for removal by land managers (Petrakis et al., 2017), and most BEMP sites have experienced at least one clearing event since monitoring began, so it is not be surprising we found no significant trends if the majority of changes in cover were management-driven. However, invasive species also tend to have traits that lead to higher performance over native plants in many environments, and these species may be more tolerant of water stress than the plants that evolved in wetlands and riparian forests (van Kleunen et al., 2010).

The bucket model (Alan K. Knapp et al., 2008) provides an additional explanation for plant species-specific differences in sensitivity to groundwater. Riparian plants are known to differ in their optimal average depth to groundwater, which is driven by rooting depth (Lite & Stromberg, 2005; Stromberg, 2013). Thus, a given average water table depth may be within the optimal range for some plant species, but not for others. The two foundational species of the Rio Grande riparian ecosystem differed strongly in their groundwater sensitivity functions. Rio Grande cottonwood had a concave GSF, while coyote willow had a convex GSF, indicating differing responses to variability in groundwater levels, despite their growth in close proximity. *Populus-Salix* riparian forests are common along rivers of western North America, so is interesting that these two codominant species differed strongly in sensitivity to groundwater variability. Cottonwood and willow differ in rooting depth, and Figure 2 depicts how rooting depth could determine a species' response to variability in groundwater depth by defining its optimal groundwater threshold. Rio Grande cottonwood has a maximum root depth of ~300 cm (Lite & Stromberg, 2005; Stromberg, 2013). In contrast, coyote willow is a wetland shrub with a maximum rooting depth of ~150cm (Caplan, Cothern, Landers, & Hummel, 2013). If cottonwoods, with their deeper roots, are growing where the water table is already near optimal conditions (average depths to groundwater at our sites ranged from 80-290 cm), then a highly variable water table could be costly for cottonwood. In contrast, if willow growing the same locations as cottonwood experience average groundwater depths that are outside of their optimal threshold, then a highly variable water table would result in a greater frequency of occurrences of shallow water that benefits willow. Thus, the bucket model (Fig. 2) predicts increased variability would be net beneficial for willows, but net costly for cottonwood. This application of the bucket model could help explain why prior research has reported that deeply rooted plants were more sensitive to changes in groundwater than their shallower-rooted neighbors [e.g., (Máguas et al., 2011)]. Identifying these stress thresholds may similarly explain differences in sensitivity among other groundwater-dependent plant species (McCoy-Sulentic et al., 2017).

Sensitivity functions can be driven by interactions among multiple environmental factors. We found that temperature played a role in cottonwood sensitivity to groundwater variance. Under warm temperatures, cottonwoods were more sensitive to groundwater than under cooler conditions (Fig. 6B). The nonlinear GSF under warm temperatures may occur if cottonwoods use evapotranspiration as a method of leaf thermoregulation (Blasini, Koepke, Grady, & Hultine, 2019). During hot years, trees at optimal groundwater depths may be better able to regulate temperature, and thus grow better that trees that are water-stressed. During cooler periods, when groundwater is not required to regulate leaf temperature, trees may be less sensitive to groundwater depth. The interaction between water use and temperature is not unique to groundwater-dependent plants. Rudgers et al. (2018) found that increased precipitation variance was only beneficial in a Great Plains grassland under cool temperatures an in a desert grassland ecosystem response to more variable precipitation changed from a net benefit to a cost with an increase in temperature. Interactions between water availability and temperature are predicted to become increasingly important as both aridity and warming increase under climate change (Cook, Ault, & Smerdon, 2015; Seager et al., 2007).

Groundwater variability at both the inter- and intra-annual temporal scales have been shown to influence plant communities in prior research. For example, large seasonal variability was associated with greater species richness in plant communities (Katz et al., 2012), while high inter-annual variability was associated with large changes in the plant community from year-to-year (Dubeau, Assani, Ibrahim, & Rodriguez, 2017). Fremont cottonwood (*P. fremontii*) can tolerate inter-annual groundwater changes of up to 0.8 m, but also show plasticity, whereby trees at variable sites appeared to be more tolerant of changes in depth to groundwater than trees at sites with a relatively stable water table (Lite & Stromberg, 2005). The three species that we expected to respond positively to variability based on their GSF were positively correlated with both inter- and intra-annual variation. A total of six species were positively correlated with variability. Of the six, inter-annual variation was a better fit than intra-annual for all but coyote willow, which had a $\Delta AICc$ if less than 2 between inter- and intra-annual variability. We expected cottonwood to be negatively correlated to variability based on the GSF, we found both trees, cottonwood and elm were negatively related to variability. Across the nine species we examined, all but one were related to groundwater variability on at least one temporal scale.. Kochia (*B. scorpia*) was the only species not significantly correlated with groundwater variability, which is an unsurprising result for a shallow-rooted, annual plant. These results support the use of GSF to understand temporal relationships between plant species and environmental variability, with the caveat that spatial variation may mask the true temporal variation.

Including temporal and spatial variation provided a better picture of groundwater sensitivity across dominant plant species. Our GSFs were primarily driven by spatial variation rather than temporal variability, because the range of groundwater depths across sites was much larger than the range within a single site. However, the slope of the relationship at each site appeared to be driven by the groundwater depths (Fig S4), therefore including spatial variation gives a regional picture of the interaction between plant cover and groundwater over time. If the water table drops, as has happened globally due to river regulation and groundwater use (Margat & Van Der Gun, 2013), a site may shift from one side of the GSF curve to the other, which would cause changes the plant community.

As observational data only allows us to identify correlations, it is possible that some of the relationships we observed between groundwater and plant cover are caused by changes in plants cover rather than water availability. There has been at least one study to suggest phreatophytes caused diurnal and intra-annual groundwater variability (Butler et al., 2007). Potential for feedbacks between groundwater and vegetation in riparian ecosystems has been investigated through modeling efforts (Rodriguez-Iturbe, D'Odorico, Laio, Ridolfi, & Tamea, 2007; Wang et al., 2012). In this dataset, differences in plant cover and groundwater levels and intra- and inter-annual variability between sites are larger than changes with a site over time. Although spatial variation is driving most of the relationships we saw, that spatial variation can be used as a proxy for understanding potential future climate scenarios as well as understanding of changes in plant response across a regional.

Riparian forests have been a focus for restoration and conservation biology because of the many ecosystem services they provide, such as promoting biodiversity (Selwood, Thomson, Clarke, McGeoch, & Mac Nally, 2015), flood and erosion control (Brauman, Daily, Duarte, & Mooney, 2007), and carbon storage (Matzek, Stella, & Ropion, 2018). Understanding how these ecosystems respond to climate change is important to ensure that they continue to provide these services. Groundwater depth is understood to be the major driver of these plant communities (Sommer & Froend, 2014; Steinberg et al., in review; Stromberg, Tiller, & Richter, 1996; Yin et al., 2015), but water tables are dropping world-wide (Margat & Van Der Gun, 2013) and increased variation in rainfall will lead to increased variation in groundwater levels. We demonstrated that GSFs can be useful as tools to identify those species that are most resilient (or most sensitive) to future increases in environmental variability. Groundwater sensitivity functions showed that some species were sensitive to variance in groundwater depth, and for eight of the nine species, cover was correlated with groundwater variability on at least one scale. Some shallow rooted, wetland species were predicted to benefit from increased variability in groundwater depth, but cover of deep-rooted cottonwood trees was predicted to decrease, especially if temperature increases. Meanwhile non-native species appeared to be mostly insensitive to changes in groundwater and variance. Our approach of groundwater sensitivity functions indicated that, within an ecosystem, plant species respond to environmental mean and variance in a variety of ways.

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Supplementary Material

Table S1. Location of BEMP monitoring sites. Geographic coordinates, years of data used in the analysis, county location, designated flood regime.

Site number	Years of data available	Longitude	Latitude	County
1	16	35.188	-106.647	Bernalillo
2	16	35.127	-106.688	Bernalillo
3	16	34.812	-106.714	Valencia
4	16	34.648	-106.738	Valencia
6	16	35.143	-106.682	Bernalillo
8	14	35.069	-106.658	Bernalillo
10	13	35.192	-106.644	Bernalillo
11	12	35.191	-106.649	Bernalillo
12	10	35.193	-106.647	Bernalillo
13	12	35.015	-106.674	Bernalillo
14	13	34.258	-106.883	Socorro
15	13	34.649	-106.739	Valencia
16	13	34.647	-106.738	Valencia
17	12	35.145	-106.680	Bernalillo
18	12	34.660	-106.742	Valencia
19	11	34.661	-106.743	Valencia
20	11	35.101	-106.692	Bernalillo
21	10	35.196	-106.642	Bernalillo
22	10	35.197	-106.644	Bernalillo
23	9	35.079	-106.668	Bernalillo
25	8	34.640	-106.742	Valencia
30	2	34.967198	-106.68565	Bernalillo

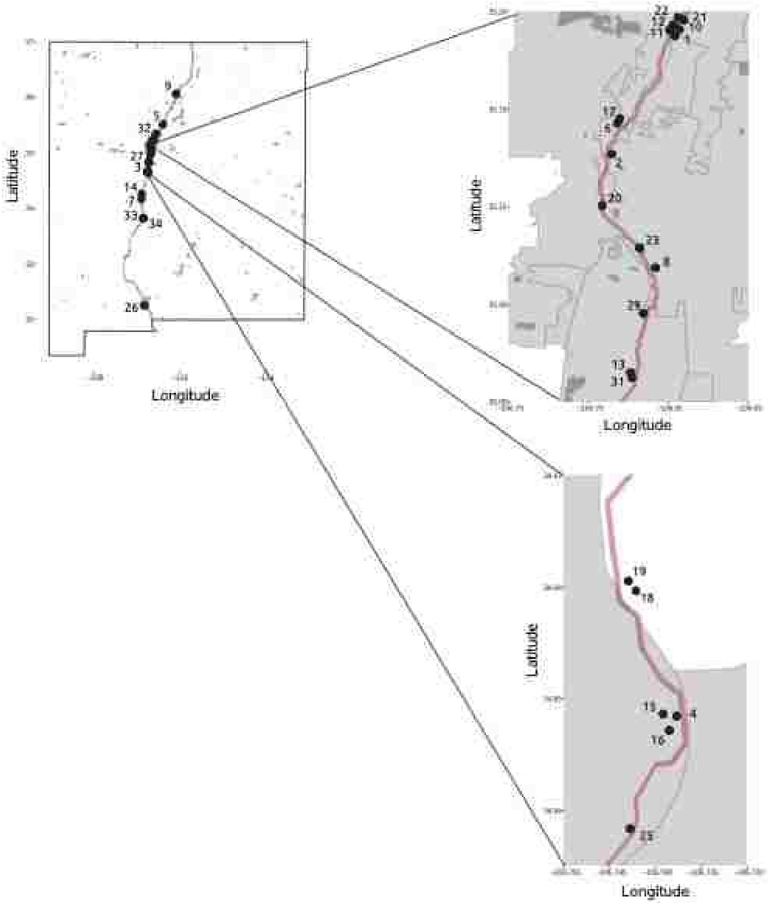

Figure S1. BEMP monitoring sites. Sites used in this analysis cover 110 km of the Rio Grande in central New Mexico. Once established, sites were monitored annually, this analysis used data from 22 sites monitored for 8-16 years between 2000 and 2015.

Figure S2. Layout of a BEMP monitoring site. Sites include five groundwater wells and two precipitation gauges which are measured monthly. Vegetation cover is measured by species annually along 10 vegetation transects that run east to west.

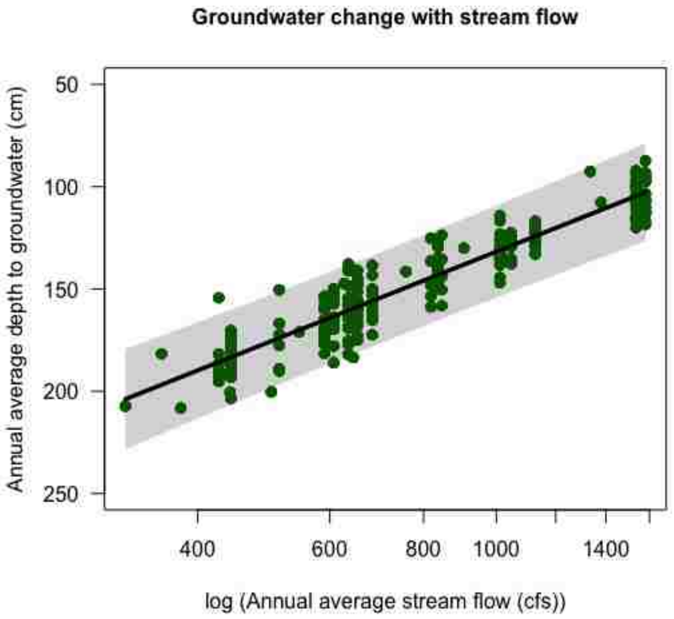

Figure S3. Groundwater changes with stream flow. Annual average depth to groundwater explains changes in annual average groundwater depth (R^2=0.18).

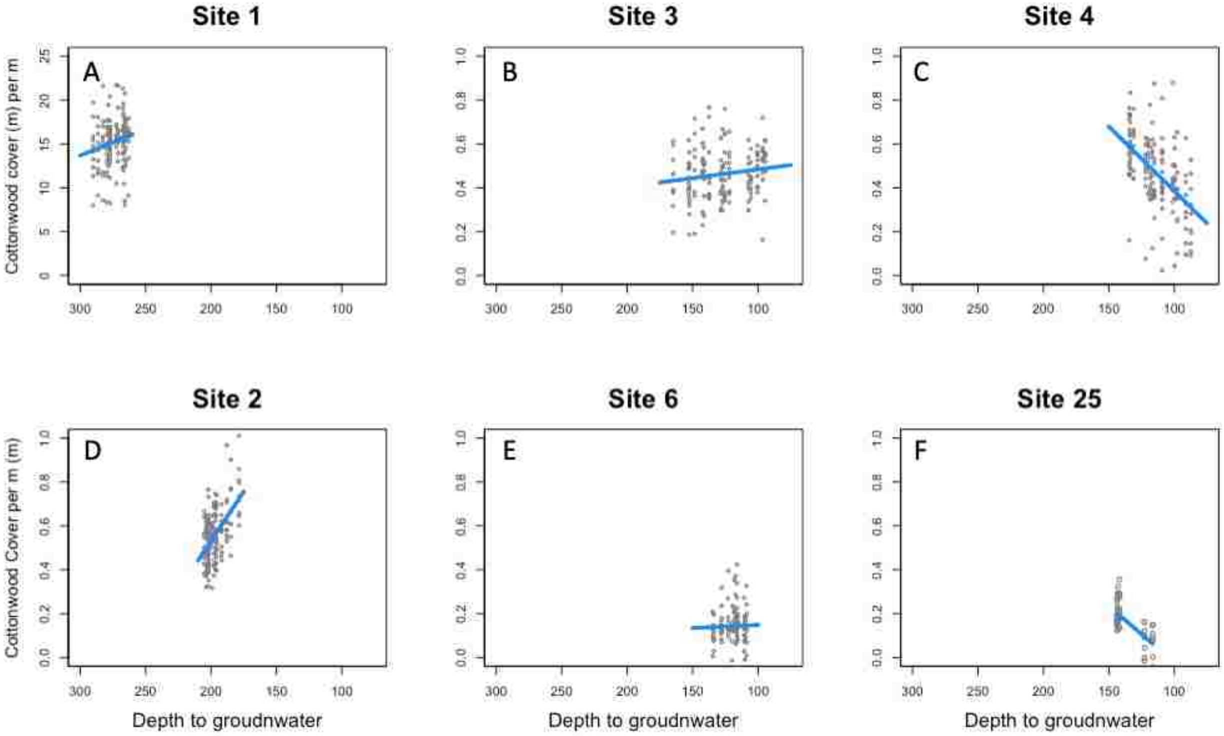

Figure S4. Spatial variation in cottonwood groundwater sensitivity. Cottonwood cover relationship to the prior year's groundwater depth at six sites. The relationship between cottonwood cover and groundwater depth is dependent on site groundwater depth, indicating spatial variation is driving the shape of the groundwater sensitivity function.