

# 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 strategies. The sensitivity of riparian vegetation to climate and other abiotic factors depends on interactions between properties of the ecosystem, like flood regime, and plant characteristics. To explore these interactions, we addressed three questions: (a) does the composition and diversity of riparian vegetation vary with the flood regime; (b) do abiotic correlates of vegetation, including climate and groundwater, differ between sites that flood compared to locations that did not experience floods; and (c) which plant functional groups account for differential plant community sensitivity to abiotic factors between flood regimes?

**Location:** Middle Rio Grande Valley, New Mexico.

**Methods:** We used long-term observations of plant community composition, groundwater depth, precipitation and interpolated temperature from 24 sites spanning 210 km of the Rio Grande riparian cottonwood–willow forest to explore the relative importance of climate and hydrologic correlates of riparian vegetation diversity and composition.

**Results:** Riparian plant diversity was higher at sites flooding compared to non-flooding sites. Plant diversity positively tracked shallower groundwater depth at flooding sites, but was best predicted by intra-annual groundwater variability at non-flooding sites. Plant community composition correlated with groundwater depth and air temperature at all sites, but at non-flooding sites, also with intra-annual groundwater variability and precipitation. Relationships between native plant cover and potential environmental drivers diverged strongly between the two flood regimes; non-native plant cover had only weak relationships with most environmental predictors.

**Conclusions:** The current flood regime of a site determined the climate and hydrologic factors that best predicted riparian plant community composition and diversity. Relationships between plant diversity or total cover and groundwater, temperature, precipitation, or groundwater variability can change in strength or direction depending on a site's flood history, highlighting the importance of flood regime to predicting the sensitivity of riparian woodlands to future environmental change.

## KEYWORDS

climate change, climate variability, cottonwood, flood, groundwater, New Mexico, plant diversity, plant invasion, Rio Grande, riparian, *Tamarix*, warming

## 1 | INTRODUCTION

Riparian ecosystems are some of the mostly highly disturbed ecosystems globally (Perry et al., 2012; Klove et al., 2014), yet they provide essential ecosystem services, particularly in dryland regions (Capon & Pettit, 2018). Riparian corridors can promote biodiversity (Selwood et al., 2017; Rolls et al., 2018), store carbon (Matzek et al., 2018), and provide flood protection for adjacent lands and human settlements (Brauman et al., 2007). However, a century of flood control, water diversion, and non-native species invasions has altered 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 vegetation is important for effective 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. While flooding was once a regular occurrence, it is now rare to non-existent in many locations 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). Flood events, which promote recruitment for many riparian plants (Kehr et al., 2014), can increase plant species richness and diversity relative to adjacent woodlands and forests that do not flood (Stromberg et al., 2012; Muldavin et al., 2017). However, additional factors that include both climate and groundwater dynamics also influence riparian plant species composition (Stromberg et al., 1996; Hingee et al., 2017; Butterfield et al., 2018).

Specifically, during the last several decades, potential 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; Butterfield et al., 2018; Palmquist et al., 2018). River regulation and groundwater usage has caused declines in the groundwater table in many regions (Margat & Van Der Gun, 2013). Several studies have linked groundwater supply to riparian vegetation (Stromberg et al., 1996; Sommer & Froend, 2014; Yin et al., 2015). However, the degree to which the maintenance of a historical flood regime influences the relative importance of groundwater or other environmental correlates of vegetation has been little studied. Here, we investigated whether the current flood regime altered which environmental factors best correlated with riparian plant community composition and diversity, and determined how the importance of environmental correlates varied among plant groups that differed in life history and provenance.

A few studies suggest that in addition to average groundwater supply, seasonal fluctuations 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. For example, 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). Similar to variation in groundwater levels, seasonal variability in river flow has been shown to influence riparian vegetation. 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). 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 resources were the most variable due either to flooding or stream intermittency. Therefore, studies that evaluate hydrologic correlates of riparian vegetation, such as groundwater levels, should consider not only the influence of mean conditions but also the potential roles of seasonal or intra-annual *variability*.

Finally, climate change adds additional stressors to riparian ecosystems (Wang et al., 2012; Capon & Pettit, 2018), but the relative importance of climate change to the ecosystem may vary with the riparian flood regime (Death et al., 2015). For example, in drylands of the southwestern US, both warming temperatures and changing precipitation regimes (Gutzler & Robbins, 2011; Cook et al., 2015; Maurer et al., 2020) may affect riparian plant species composition and diversity, although how these changes interact with flood regime are unresolved. For instance, the importance of rainfall, or climate warming-driven aridity, may be stronger for sites that are disconnected from flooding than for sites that receive new inputs to groundwater from local flood 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 interacts with the flood regime to shape plant communities. Riparian ecosystems that consist of a mosaic of isolated, non-flooding and flooding sites may give insight into how the composition and diversity of riparian vegetation changes under modern environmental drivers.

To explore potential interactions between key aspects of environmental change and the flood regime, we determined environmental variability over time and space to investigate climate and hydrologic correlates of riparian vegetation. We chose a representative corridor ecosystem of the southwestern US, along the Rio Grande, which stretches 2,900 km from southern Colorado to the Gulf of Mexico. Specifically, we used a 16-year observational data set from 24 sites along a 210 km stretch of the Middle Rio Grande Valley in central New Mexico, dominated by a cottonwood–willow forest, to evaluate the relative importance of flooding, groundwater depth and its intra-annual variability, and climate (temperature, precipitation) as explanatory variables of riparian plant species composition and diversity. We addressed three questions: (a) how much does the composition and diversity of riparian vegetation vary with the flood regime and environmental conditions? We hypothesized that sites that continue to flood have greater plant diversity than sites that no longer flood. Because plant communities differed between flooding and non-flooding sites, we then asked (b): 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 environmental drivers. Specifically, we expected larger influences of variability in groundwater and precipitation on plant communities in site that no longer flood than in those that do flood. Lastly, we asked (c): which plant functional groups account for differences between flood regimes in a plant community's sensitivity to abiotic factors? We specifically compared native vs non-native plant species and canopy vs understorey species. We hypothesized that the dominant, native canopy trees would explain the differences in plant community sensitivity to abiotic factors between flood regimes because of their historical dominance under regimes of riparian flooding.

## 2 | METHODS

### 2.1 | Study sites

We collected vegetation data, 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 (Figure 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 with long-term observational data. Sites were dominated by native cottonwood canopy trees, native willow species, and non-native trees and shrubs that included Russian olive, Siberian elm, and tamarisk (Eichhorst, 2020; Steinberg et al., 2020).

### 2.2 | Study design

Each BEMP site (Figure 2) is 100 m × 200 m, the 200-m side runs north-south in parallel with the Rio Grande. Sites are divided into 10 equal sections of 20 m × 100 m and one 30-m vegetation transect is randomly placed within each section running perpendicular to the river. Elevation changes little within sites; transects are at a similar elevation above the river. Each BEMP site also has two rain gauges and five groundwater wells (described below).

### 2.3 | 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 3,000 cm per transect. For plants < 1 m tall, 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, 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, and these samples were nested within each site, which enabled our analyses to estimate both year-to-year variability and between-site variability in vegetation.

### 2.4 | Groundwater

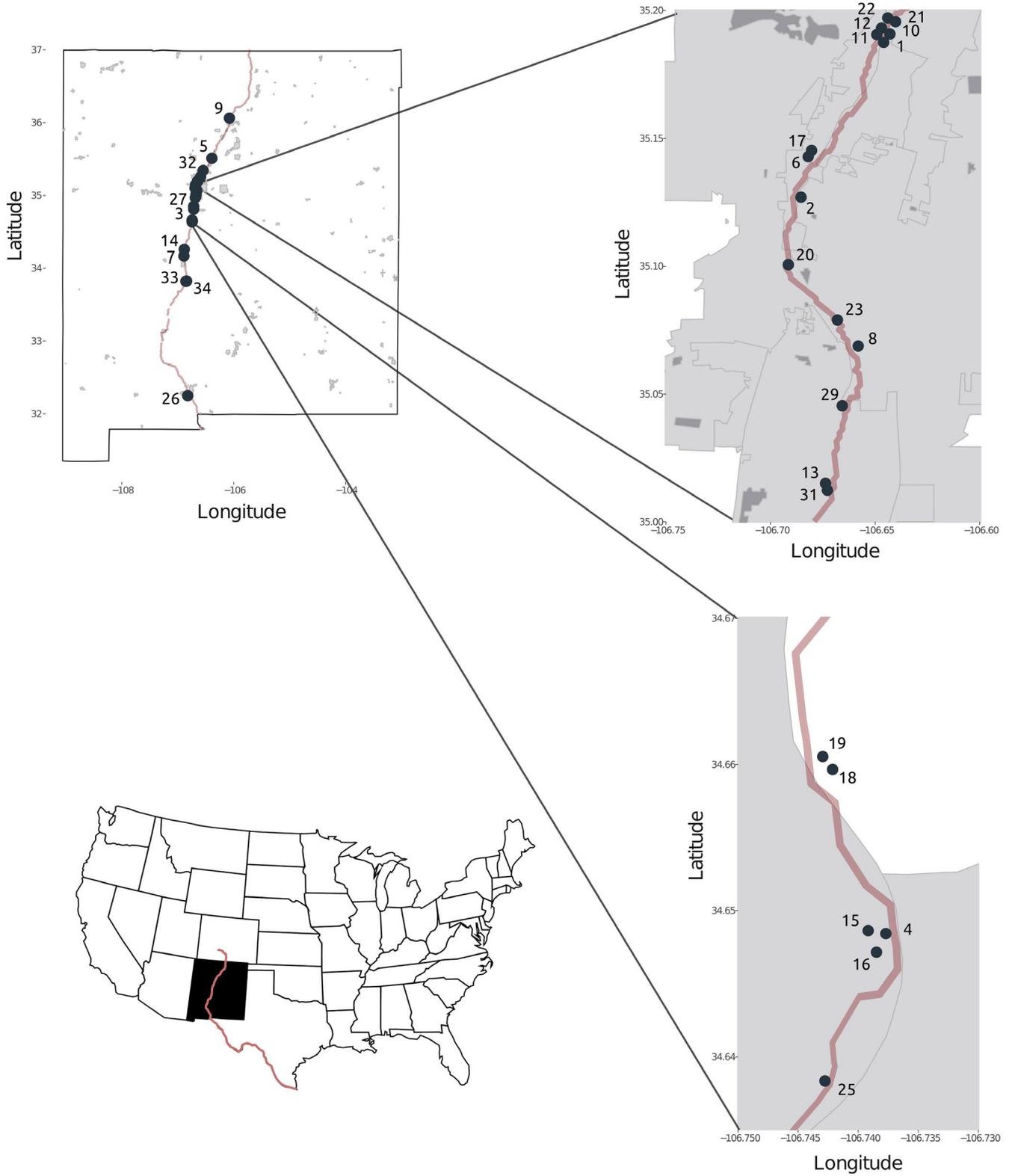
At each BEMP site, there are five groundwater wells, one located in the center of the site, the other four wells installed 40 m from the center in each of the four cardinal directions. We measured depth to groundwater (cm) at each well monthly using a Solinst water level meter (Georgetown, ON, Canada), 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.

### 2.5 | Precipitation

At each site, two rain gauges were used to monitor precipitation. One gauge is located in an open area and the other under forest canopy, which allows canopy cover to intercept precipitation before it hits the ground. Each Tru-Chek rain gauge (Edwards Manufacturing Company, St. Albert Lea, MN) was accurate to < 1mm and mounted to a metal bracket on a wooden post at ~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 Climate Group, 2019; see next section).

### 2.6 | Climate

We obtained annual and monthly temperature and precipitation data at the 4-km spatial resolution from the PRISM database (PRISM Climate Group, 2019). Annual values were used for minimum, maximum, and average daily temperatures and cumulative precipitation at each site. We averaged monthly average, minimum, and maximum



**FIGURE 1** Bosque Ecosystem Monitoring Program 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. Site #7 was not included in the analysis because it sits outside the floodplain (no historical flood regime)

**TABLE 1** Location of Bosque Ecosystem Monitoring Program monitoring sites. geographic coordinates, years of data used in the analysis, county location, and designated flood regime of the 24 sites included in this analysis. Site 7 was not included in the study, as it was located outside the floodplain. Rio Arriba coordinates are not available for reasons of cultural sensitivity

Site number	Years of data available	Latitude	Longitude	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	35.342	-106.545	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	35.509	-106.389	Sandoval	Non- flooding
25	8	34.640	-106.742	Valencia	Flooding

daily temperatures over the months of June, July and August to calculate summer temperatures for each site.

## 2.7 | Data analysis

### 2.7.1 | How much does the composition and diversity of riparian vegetation vary with the flood regime and environmental conditions?

#### *Plant community composition*

Analyses on community composition were performed in PRIMER (Clarke & Gorley, 2015), which included PERMANOVA, permDISP, distance-based linear models (Dist-LM), and non-metric multidimensional scaling (NMDS) visualization plots. Community composition included 253 plant species, recorded in 299 site-year combinations (24 individual sites sampled over 16 years). The ten transects from each site were averaged, then using PRIMER we calculated Bray-Curtis distances between each pair of sites and years across the entire data set. 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. We created

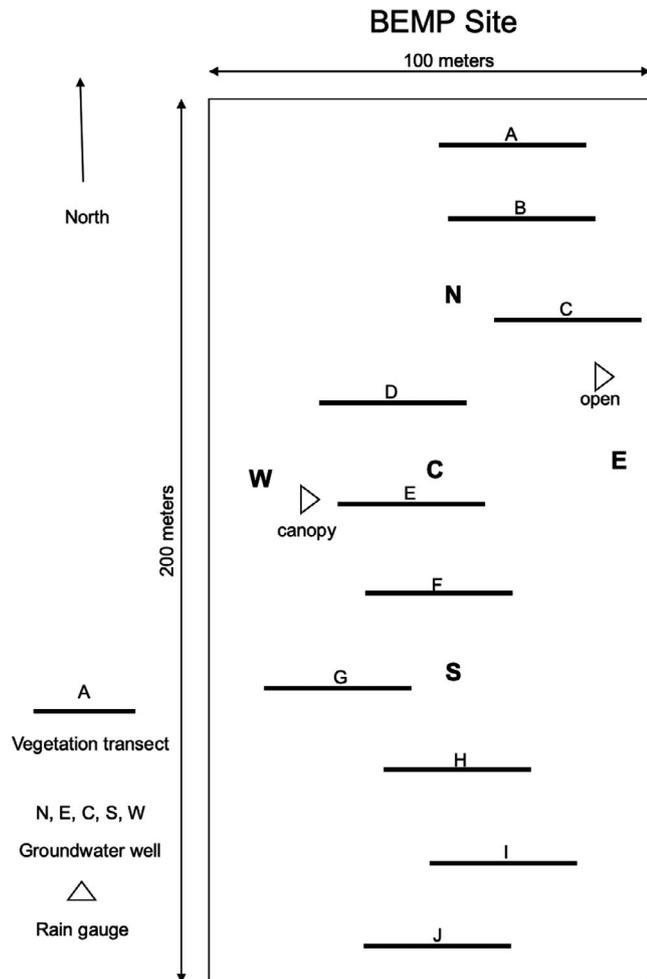
NMDS plots to visualize differences among flood regimes in plant community composition. We also compared dispersion in community composition between flooding and non-flooding sites using permDISP; this analysis tested for the magnitude of divergence of plant community composition across the sites representing each flood regime.

#### *Plant diversity*

We completed analyses on plant diversity metrics in R (R Core Team, 2018). We calculated the Simpson diversity index, richness and evenness for each transect using the *vegan* package (Oksanen et al., 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).

#### *Environmental correlates of vegetation composition*

Our resolution on climate and hydrologic correlates came through variation in both space (e.g., sites that differed in climate variables) and time (years that differed in climate). We examined the relative importance of abiotic drivers (continuous variables) on the distance matrix of plant community composition using Dist-LM. We then used the Akaike Information Criterion (AIC) in model selection procedures (Burnham & Anderson, 2002) to identify the variables that



**FIGURE 2** Layout of a Bosque Ecosystem Monitoring Program 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

explained the most variation in community composition across the full data set. Sites 5, 9, and 24 were omitted from this analysis because groundwater depth data were not available. Environmental variables 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). Flood regime was not included as a continuous variable because the number of flooding sites was relatively low. Instead flood regime was included as a binary factor (flooding and non-flooding sites) to avoid zero-inflated data. All predictor 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 the analysis of individual environmental correlates, we constructed a multivariate model using forward model selection; we did not include minimum, average or summer temperature, or monsoon precipitation, due to multi-collinearity with maximum summer

temperature and annual precipitation, which were determined as the best predictors in AIC-based model selection procedures. In addition, we plotted vectors for climate and hydrologic variables onto the NMDS plots to visualize their relative importance.

### 2.7.2 | 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 per MANOVA and Dist-LM do not allow the inclusion of categorical and continuous variables within the same model; therefore, it was not possible to statistically evaluate interactions between abiotic variables and flood regime type in these analyses of plant community composition. We followed the same steps as in question (1) to conduct Dist-LM analysis with AIC-based model selection—imposed 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 the set of flooding versus 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 [a]) 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  $\times$  abiotic factor interaction term statistically indicated that *drivers of diversity significantly differed between the two flood regimes*. AIC-based model selection (Burnham & Anderson, 2002) was also used to rank the relative importance of the candidate abiotic variables for explaining variation in plant diversity metrics.

### 2.7.3 | Which plant functional groups account for differences between flood regimes in plant community sensitivity to abiotic factors?

We classified each plant species into categories for *life form*: canopy vs understorey and *provenance*: native vs non-native. Canopy plants were defined as trees and shrubs, understorey 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 and one of the four abiotic variables described above to determine the slope of the

relationship between total plant cover and each abiotic variable (e.g., Figure 5; Bates et al., 2015).

### 3 | RESULTS

#### 3.1 | How much do the composition and diversity of riparian vegetation vary with the flood regime and environmental conditions?

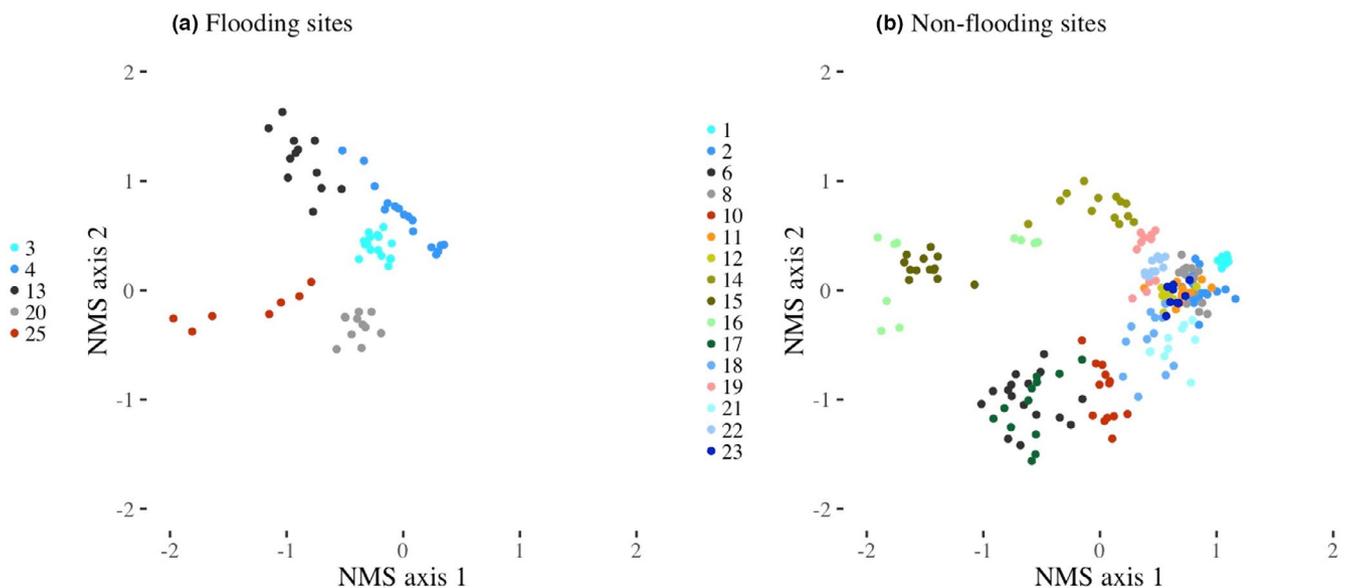
Riparian plant community composition and diversity significantly differed between flooding and non-flooding sites (PERMANOVA, flood regime, pseudo- $F = 2.42$ ,  $p = 0.025$ ). Across all sites combined, plant community composition was most strongly correlated with groundwater depth ( $R^2 = 0.08$ ,  $p = 0.0001$ ), average maximum temperature ( $R^2 = 0.08$ ,  $p = 0.0001$ ) and intra-annual groundwater variability ( $R^2 = 0.06$ ,  $p = 0.0001$ ), although no single correlate explained substantial variation in plant community composition when all sites were binned together.

Flooding and non-flooding sites significantly differed in some of the abiotic variables that we considered as correlates of vegetation composition. Flooding sites had shallower depth to groundwater (mean  $\pm$  standard error [SE] = 118 cm  $\pm$  0.69) than non-flooding sites (161 cm  $\pm$  1.2;  $p < 0.001$ ). Groundwater levels at flooding sites were also significantly more variable throughout the year (mean groundwater CV = 0.23  $\pm$  0.039) than levels at non-flooding sites (mean groundwater CV = 0.03  $\pm$  0.006,  $p < 0.001$ ). However, other abiotic variables did not significantly differ between flooding and non-flooding sites.

Sites that flood had nearly 40% greater plant diversity (Simpson index,  $0.73 \pm 0.005$ ) than non-flooding sites ( $0.53 \pm 0.005$ ; log-likelihood  $\chi^2 = 51.4$ ,  $p < 0.0001$ ). Differences between the flood regimes in plant species diversity were due primarily to differences in species richness, which was 63% greater at flooding sites ( $10.9 \pm 0.19$  species) than at non-flooding sites ( $6.7 \pm 0.08$  species,  $\chi^2 = 56.9$ ,  $p < 0.0001$ ). Species evenness was 17% greater at flooding sites ( $0.69 \pm 0.004$ ) than non-flooding sites ( $0.59 \pm 0.004$ ;  $\chi^2 = 23.7$ ,  $p < 0.0001$ ). However at non-flooding sites spanned a larger range in plant diversity than flooding sites, 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. The greater range of diversity among non-flooding sites may simply be due to the larger sample size (180 transect  $\times$  year combinations) than flooding sites (60 transect  $\times$  year combinations). Finally, plant community composition was more similar among sites that flooded than among non-flooding sites (permDISP,  $p = 0.009$ ); this result should be interpreted cautiously because the sample sizes for each flood regime were uneven, and a larger number of sites increases the ability to detect dispersion among sites.

#### 3.2 | 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 vegetation composition than did flooding sites. At flooding sites (Figure 3A), two



**FIGURE 3** Community composition at (a) flooding sites and (b) non-flooding sites. Each dot represents one site/year combination and its color represents one of 21 Bosque Ecosystem Monitoring Program sites (sites 5, 9 and 24 were excluded due to lack of groundwater data). Plots are results of non-metric multidimensional scaling analysis (NMDS, Primer v. 6, Plymouth, UK). NMDS stress was 0.12 for flooding sites and 0.16 for non-flooding sites, indicating an adequate two-dimensional solution. Variation in plant communities was correlated with depth to groundwater and average maximum daily temperature at flooding sites ( $R^2 = 0.24$ ). At non-flooding sites annual precipitation and groundwater variation were additional correlates of variation in community composition ( $R^2 = 0.18$ )

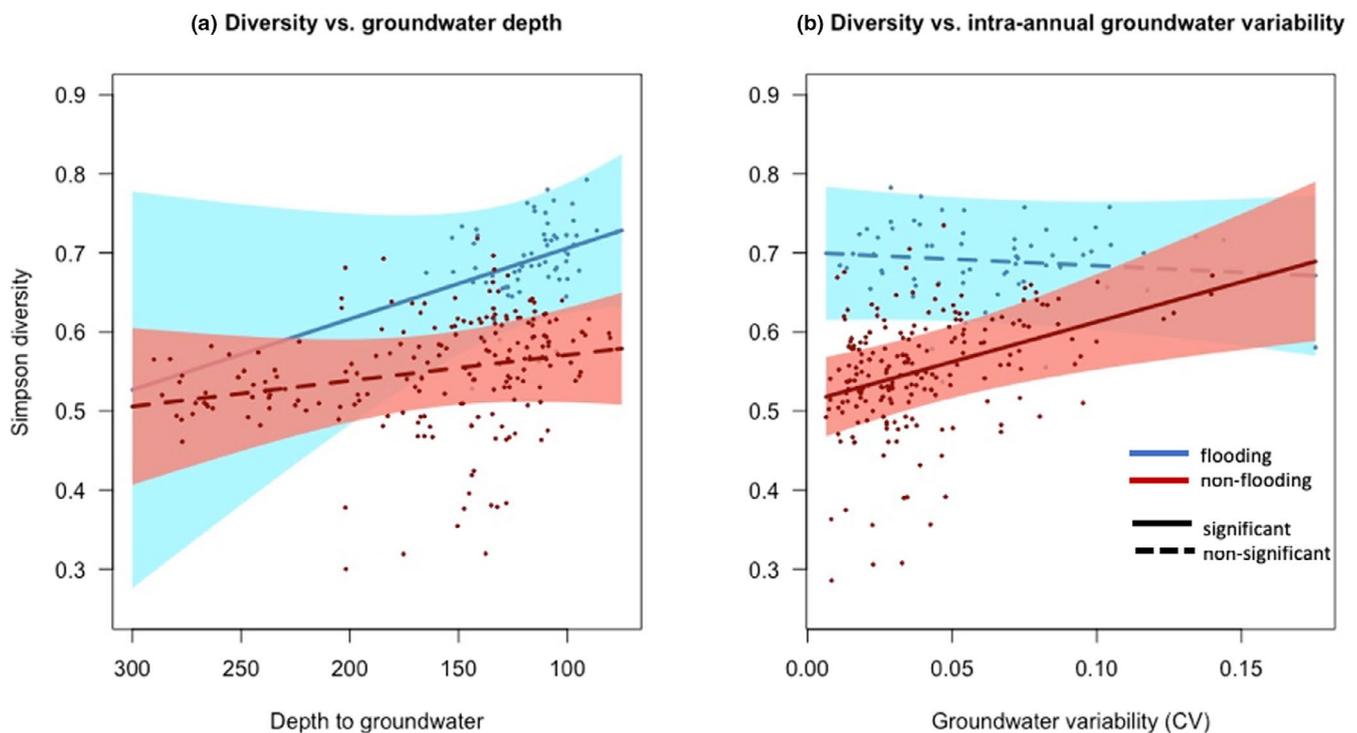
variables, depth to groundwater ( $R^2 = 0.11$ ,  $p = 0.0001$ ) and average annual maximum daily temperature ( $R^2 = 0.17$ ,  $p = 0.0001$ ), explained variation in plant community composition. At non-flooding sites (Figure 3B), four variables explained variation in plant species composition, including groundwater variability ( $R^2 = 0.05$ ,  $p = 0.0001$ ) and mean annual precipitation ( $R^2 = 0.01$ ,  $p = 0.01$ ) as well as depth to groundwater ( $R^2 = 0.09$ ,  $p = 0.0001$ ) and average annual maximum temperature ( $R^2 = 0.11$ ,  $p = 0.0001$ ), both of which explained less variation in plant composition at non-flooding sites than at flooding sites. For non-flooding sites, a multivariate model, including all four abiotic correlates, explained 18% of the variation in plant community composition ( $R^2 = 0.18$ ,  $p = 0.0001$ ). For flooding sites, two abiotic variables (depth to groundwater, average annual maximum temperature) explained 24% of the variation in plant composition, despite the smaller total number of sites ( $R^2 = 0.24$ ,  $p = 0.0001$ ).

Abiotic correlates of plant diversity strongly differed with the flood regime (Figure 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 ( $p = 0.9$ ; Figure 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 ( $\Delta\text{AIC} = 23$ ). At non-flooding sites, plant diversity increased with greater intra-annual variability in groundwater (slope = 0.02,  $p < 0.0001$ ) but there was

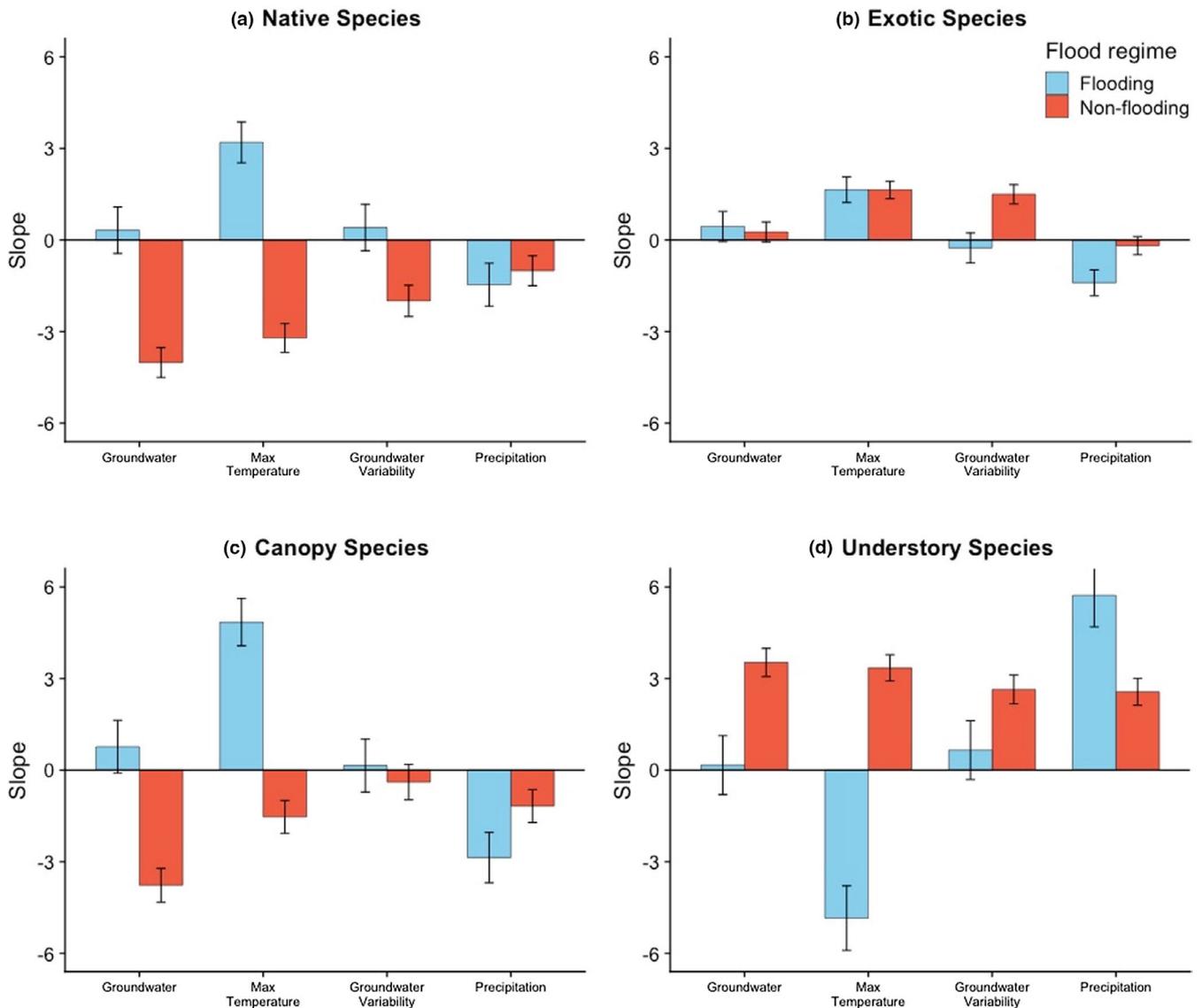
no significant relationship at flooding sites (slope = 0.003,  $p = 0.5$ ; Figure 4B). Again, inclusion of the interaction between groundwater variability and flood regime greatly improved model fit relative to a model lacking the interaction ( $\Delta\text{AIC} = 54$ ), indicating that the best abiotic correlates of plant diversity strongly differed with flood regime. Analyses that included only native plant diversity revealed a similar pattern: 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 ( $p > 0.05$ ).

### 3.3 | Which plant functional groups account for differences between flood regimes in plant community sensitivity to abiotic factors?

The abiotic correlates of native plant cover differed greatly between flood regimes (Figure 5 and Appendix S1). Across all sites, native plants were 76% of total plant cover. At flooding sites, native cover increased most strongly with warmer temperature (slope = 3.20,  $p < 0.0001$ ), among the abiotic correlates we examined, but native plant cover was not significantly related to average groundwater depth. This pattern indicating that either individual plant species diverged in their associations with groundwater levels such that total



**FIGURE 4** Relationships between plant diversity and water availability differ depending 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



**FIGURE 5** Relationships between plant cover and environmental factors at flooding sites and non-flooding sites by plant group. 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 of the relationships to climate and hydrologic 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 environmental driver and thereby allowed the slopes to differ between flood regimes fit the data better than models that did not include the interaction term

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 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 plant cover was also significantly correlated with precipitation, but only at flooding sites (slope =  $-1.40$ ,  $p < 0.0001$ ).

Responsiveness of tree canopy cover and understory plant cover to abiotic variables also diverged between flooding and non-flooding sites (Figure 5 and Appendix S2). 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, but in opposite directions. At non-flooding sites, understory cover increased with shallower groundwater levels (slope =  $3.52$ ,  $p < 0.0001$ ). Canopy plants decreased with

precipitation at both site types (flooding slope =  $-2.86$ ,  $p < 0.0001$ ; non-flooding slope =  $-1.17$ ,  $p < 0.0001$ ). Understorey plants were the only group that correlated positively with precipitation. Regardless of flood regime, understorey 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 =  $-1.17$ ,  $p < 0.0001$ ).

## 4 | DISCUSSION

The Middle Rio Grande Valley serves as a useful testbed for understanding processes affecting riparian communities in other parts of the world. The legacy of past floods appears in the current dominance of mature Rio Grande cottonwood trees (*Populus deltoides* ssp. *wislizenii*) and the abundance of willow species, both of which require floods to germinate and primarily established in the valley prior to the construction of dams on the Rio Grande. 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 in 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., 2015; Poff, 2018), suggesting that the role of intra-annual variability in groundwater may be a key structuring factor for vegetation composition in dryland riparian corridors (Xi et al., 2018).

Most importantly, our results suggest that the current flood regime alters the strength and the direction of environmental 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 (Butterfield et al., 2018). 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. In addition, both mean annual precipitation and intra-annual groundwater variability were significant correlates of plant community composition only at non-flooding sites, where water is less readily available even at peak stream flows. In contrast, average groundwater depth was the strongest predictor of total and native plant diversity at flooding sites. This result helps to explain the generally low explanatory power of depth to groundwater in prior studies of riparian vegetation from heavily regulated ecosystems, where flooding is infrequent (Mata-Gonzalez, Martin, et al., 2012; Mata-Gonzalez, McLendon, et al., 2012).

Finally, plant diversity and composition were more divergent among non-flooding sites than at flooding sites. This result should be interpreted cautiously because the sample sizes for each flood regime were uneven, due to the nature of long-term, observational data. Thus, although the difference in range could arise due to the larger number of non-flooding than flooding sites in our study, per MANOVA is comparatively robust against such issues, and it may instead indicate that where floods are no longer occurring, plant communities take divergent successional trajectories due to variation among local sites in the other climate drivers of plant community composition or in stochastic processes. These structuring factors may only emerge as important when floods no longer act as a strong filter on plant species composition. Similar results were obtained for drought as a filter on aquatic invertebrate communities – with greater dispersion and stochasticity in community composition in the absence of the strong filter of experimental drought (Chase, 2007).

Differences between flood regimes and indicators of plant community dependence on environmental variability might be explained using the bucket model proposed by Knapp et al., (2008). The bucket model proposed 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 occur 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. This model, developed to explain precipitation-driven soil moisture in grasslands (Knapp et al., 2008; Thomey et al., 2011), provides a useful conceptual framework 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 the water table stayed within optimal levels. However, at non-flooding sites where the average water table depth was 27% (44 cm) deeper than at flooding sites, intra-annual variability correlated positively with plant diversity. These 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 certain plant species (Steinberg et al., 2020), and increase coexistence and species diversity by creating opportunities for niche differentiation. This mechanism may also explain why, at non-flooding sites, herbaceous and non-native plant 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 and thus, under the bucket model, are predicted to decline with greater variability in the water table.

Past work has shown that riparian vegetation in drylands relies heavily on the shallow water table (Kehr et al., 2014; Cleverly et al., 2015; Thibault et al., 2017). Therefore, we expected plant cover to

increase with shallower groundwater at all of our sites. However, 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 with depth to groundwater, and total non-native plant cover was unaffected by average groundwater depth in both flood regimes. This may be due to species' differences in sensitivity to groundwater, and it may be necessary to look at individual species to understand these relationships. For example, at our sites, cottonwood cover was greatest at middle groundwater depths, and decreased with both extremely high and extremely low groundwater depths, but willow cover had the opposite nonlinear relationship with groundwater (Steinberg et al., 2020).

Our study detected surprisingly strong correlations between air temperature and plant cover, relationships that depended starkly 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. Yet, warming is a key aspect of climate change, and one that is accelerating faster in drylands than in other terrestrial ecosystems (Huang et al., 2017). Observational studies have correlated warmer temperatures with lower cottonwood growth and with increases in the common non-native plants, *Tamarix chinensis* and *Elaeagnus angustifolia* (McShane et al., 2015; Philipson et al., 2018), but temperature changes also 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 benefit trees and shrubs, but where groundwater is more limited, warming may be stressful, perhaps exacerbating water limitation. Consistent with other studies (McShane et al., 2015), but declined with warming at flooding sites. However, it is important to acknowledge that herbaceous species represent diverse strategies, from short-living mud bank specialists to non-native disturbance specialists, and species-level analyses provide deeper insights (Steinberg et al., 2020). These opposite relationships could result from competition for light between the canopy and understorey, with drivers that increase canopy cover causing understorey cover to decline due to competition. In future studies, it would be useful to explore how plant competitive dynamics differ between flooding and non-flooding sites (Garcia-Arias & Frances, 2016).

Because riparian vegetation has been related to depth to groundwater in numerous prior studies (Scott et al., 1999; Naumburg et al., 2005; Gurnell et al., 2012; Mata-Gonzalez, McLendon, 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 flooding 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 plant cover 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, understorey, herbaceous plants may use the limited rainwater before it reaches deep-rooted canopy plants, reducing canopy cover. Understorey cover was 66% higher at flooding sites than at non-flooding sites, which could explain why the relationship between precipitation and both native and woody cover was weaker at non-flooding sites.

Our data set covered variation that occurred over both space and time, either of which could contribute to the relationships we observed. Space-for-time substitution has been used to predict future community trajectories (e.g., Stromberg et al., 1996); however, observational studies such as ours should be applied cautiously because they cannot decouple climate and hydrologic variables from other unmeasured differences among sites. Other factors important in riparian plant communities that we were not able to examine include the amount of snowpack upstream of our sites and subsequent timing of spring run-off (Perry et al., 2012), edaphic factors such as soil nutrients (Andersen et al., 2014), disturbances fire (Pettit & Naiman, 2007), and both river and land management strategies (Samson et al., 2018). It is possible that some of the relationships we observed between hydrologic variables and vegetation are causal in the reverse direction – for example, plants driving changes in groundwater depth or causing intra-annual variability in groundwater. The potential for such biophysical feedbacks has 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).

In riparian forests, where dams, river channelization, and incised banks make flooding unlikely in a large part of the historic floodplain, we determined that plant communities correlate with different climate factors more in remnant non-flooding forests than in forests that retain the capacity to flood. We assessed variation across both time and space to demonstrate that relationships between vegetation and climate and hydrologic variables changed in both their magnitude and direction between flooding and non-flooding sites. The local 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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#### AUTHOR CONTRIBUTIONS

All authors contributed to developing research questions, KE oversaw data collection, KS and JR analyzed the data, KS led the writing of the manuscript and all authors contributed to drafts and final manuscript.

#### DATA AVAILABILITY STATEMENT

Data is available through the Bosque Ecosystem Monitoring Program at [www.bemp.org/data-sets](http://www.bemp.org/data-sets).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**Appendix S1.** Relationships between plant cover and abiotic factors at flooding and non-flooding sites for total native plant cover or non-native plant cover.

**Appendix S2.** Relationships between plant cover and abiotic factors at flooding and non-flooding sites for woody plant cover or herbaceous understory plant cover.

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