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

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Abstract

Aims 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 a revised hydrological 'bucket model' to improve predictions on how plant species will respond to changes in the mean and variance of groundwater resources.

Methods We leveraged spatiotemporal variation in long-term datasets of riparian vegetation cover and groundwater levels to build the first *groundwater sensitivity functions* 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 layered with declining groundwater stores.

Important Findings Riparian plant species differed in sensitivity to both the mean and variance in groundwater levels. Rio Grande cottonwood (*Populus deltoides* ssp. *wislizenii*) cover was predicted to decline with greater inter-annual groundwater variance, while coyote willow (*Salix exigua*) and other native wetland species were predicted to benefit from greater year-to-year variance. No non-native species were sensitive to groundwater variance, but patterns for Russian olive (*Elaeagnus angustifolia*) predict declines under deeper *mean* groundwater tables. Warm air temperatures modulated groundwater sensitivity for cottonwood, which was more sensitive to variability in groundwater in years/sites with warmer maximum temperatures than in cool sites/periods. Cottonwood cover declined most with greater intra-annual coefficients of variation (CV) in groundwater, but was not significantly correlated with inter-annual CV, perhaps due to the short time series (16 years) relative to cottonwood lifespan. In contrast, non-native tamarisk (*Tamarix chinensis*) cover *increased* with both intra- and inter-annual CV in groundwater. Altogether, our results predict that changes in groundwater variability and mean will affect riparian plant communities through the differential sensitivities of individual plant species to mean versus variance in groundwater stores.

Keywords: climate change, climate variability, riparian, Rio Grande, New Mexico, cottonwood, willow, tamarisk

摘要：确定气候的长期缓慢变化与放大的气候变异性之间相互作用的生态后果是植物生态学的一个重要前沿研究。我们将最近的气候敏感性函数方法与修订的水文“水桶模型”相结合，以改进对植物物种如何响应地下水资源平均值和方差变化的预测。利用河岸植被覆盖和地下水位长期数据集的时空变化，构建了旱地河岸廊道常见植物种类的首个地下水敏感性函数。我们的研究结果展示了这种方法的重要性，它可以识别在日益变化的气候层，随着地下水储量的下降，哪些植物物种能够繁茂的生长(或衰落)。研究结果表明，河岸带植物物种对地下水位平均值和方差的敏感性各不相同。杨树(*Populus deltoides* ssp. *wislizenii*)随着地下水年际方差的增大，植被覆盖度预计将下降，而狼柳树(*Salix exigua*)和其他原生湿地物种预计将受益于更大的年际方差。非本地物种对地下水变化不敏感，但俄罗斯橄榄(*Elaeagnus angustifolia*)在更深的平均地下水位条件下敏感性将降低。暖空气温度调节了杨树对地下水的敏感性，在最高温度更高的年份/地点，杨树对地下水的变化比在低温地点/时期更敏感。地下水年内变异系数越大，杨树覆盖度下降幅度越大，但与年际变异系数相关性不显著，这可能因为相对于杨

树的寿命，这个时间(16 a)太短。与此相反，非本地柳树(*Tamarix chinensis*)覆盖度随地下水年内和年际变异系数的增加而增加。总之，我们的研究结果预测，地下水变异性和平均值的变化将通过单个植物物种对地下水储量中的平均值和方差的不同敏感性影响河岸带植物群落。

关键词：气候变化，气候变异，河岸，格兰德河，新墨西哥，杨树，柳树

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 Vázquez *et al.* 2017). Many climate models predict increases in year-to-year variability in climate (Fischer *et al.* 2013; Gutzler and Robbins 2011), and increasing seasonal variability has been documented even where the mean climate has not changed (Petrie *et al.* 2014). Determining the ecological consequences of interactions between slow changes in long-term climate means and amplified intra- or inter-annual variance in climate is thus an important research frontier (Lawson *et al.* 2015b; Vázquez *et al.* 2017). For example, the interaction between increasingly variable precipitation and warmer temperatures may increase evapotranspiration rates and dry soils (Seager *et al.* 2013). The effects of climate variability, and inter-annual variability in particular, are difficult to predict in part because experimentation would require long-term manipulations. However, observational data over spatiotemporally variable climates can be leveraged to predict the potential for interactions between the mean and variability in abiotic drivers of vegetation, such as precipitation.

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 availability; Fig. 1). The function captures nonlinear ecological responses to climate variables (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 the variance of the climate driver alone 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 (Lawson *et al.* 2015b)—the mathematical principle of Jensen's Inequality. A concave function (Fig. 1c) yields net negative effects of increasing variance, because low values of the climate variable (e.g. low precipitation) cause large decreases in the ecological response (e.g. plant cover), while high values of the climate variable (e.g. high precipitation) cause only small increases. In contrast, a convex function results in a net positive influence of increasing variance (Fig. 1d), because increases in the ecological response during wet conditions are greater than the losses during dry conditions. If the function changes concavity over the full range of the climatic driver (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 shape of the nonlinearity in the sensitivity function (Rudgers *et al.* 2018).

Identifying nonlinear climate sensitivities requires long time series over naturally or experimentally variable climates (Vázquez *et al.* 2017), which are difficult to achieve in field experiments. Careful laboratory experiments that expose species to a wide range of environmental conditions can be valuable for characterizing sensitivity (Lawson *et al.* 2015b), but are impractical for large, long-lived species. Direct field manipulations of climate variance are possible (Gherardi and Sala 2015) but require long-term investment, are very expensive for large plants like trees (Pangle *et al.* 2015) 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 (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 ecohydrological bucket model also predicts sensitivities of plant species to increasing variability in water resources (Fig. 2). The bucket model hypothesizes that a species' response to climate variance depends not only upon mean climate (as also occurs with climate sensitivity functions) but also on species' individual stress tolerance thresholds (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 a plant species 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 a species' stress threshold (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 conditions more often.

Within an ecosystem, plant species may differ in their stress tolerance thresholds, dependent on their life history, root structure or provenance (Silvertown *et al.* 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 *et al.* 2017). Similarly, non-native plant species that differ in provenance because they evolved in different locations can diverge in their traits and stress tolerance thresholds from the native community (Drenovsky *et al.* 2012; Glenn and Nagler 2005; van Kleunen *et al.* 2010). Understanding how differences among plant species interact with mean climate has improved predictions on the impacts of species invasions on ecosystem processes (Martin *et al.* 2017). Although differences among plant species in resource acquisition traits are common knowledge, the influence of these species differences on sensitivity to *variance* in water resources has received much less attention (Xi *et al.* 2018). 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 time scales have been predicted to increase in variability under recent climate models (Fischer *et al.* 2013; Gutzler and 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 and

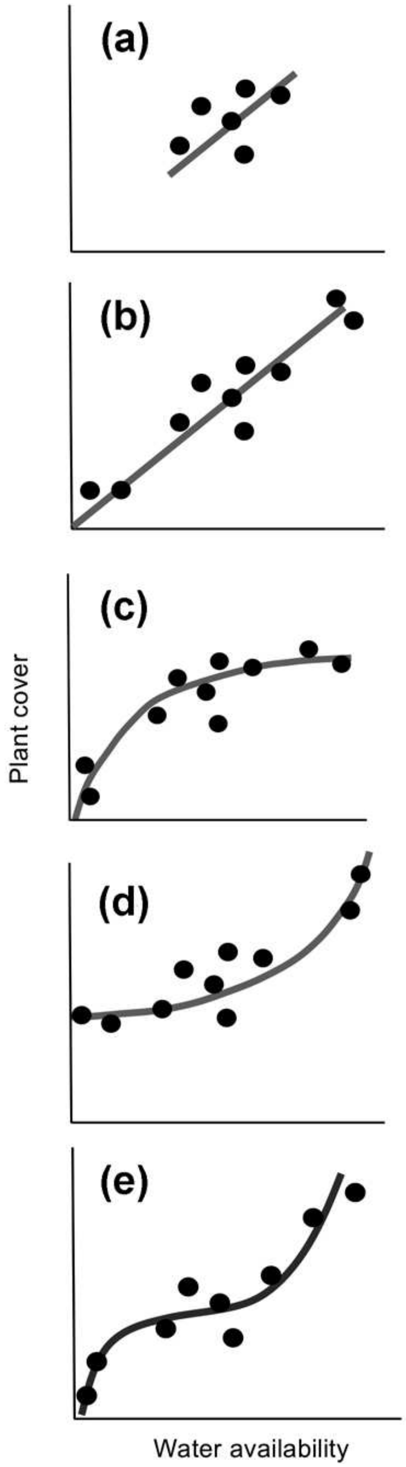

Figure 1: Hypothesized types of GSFs. The relationship between an environmental driver (e.g. groundwater availability) and an ecological response (e.g. plant cover) may appear linear under 'normal' conditions that have low variability in groundwater (**a**). If the function remains linear over a wide 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 groundwater levels (**e**), the effect of variability in groundwater interacts with the mean (mean × variance interaction).

found that increased intra-annual variance reduced aboveground net primary production. Gherardi and Sala (2015) 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 2015). 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 thus far focused on a single time scale, observational data provide opportunities to explore both inter- and intra-annual variation.

Here, we leveraged 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 both inter- and intra-annual variability. In dryland riparian forests, water resources are primarily driven by the shallow water table, which varies with changes in stream flow at both seasonal and annual scales. Riparian plant communities have been shown to be sensitive to seasonal variance in water availability in a few studies (Katz *et al.* 2012; Lawson *et al.* 2015a). By building the first *groundwater sensitivity functions* (GSFs) for common plant species of dryland riparian corridors, our goals were to investigate how much plant species differ in sensitivities and predict which plant species will be winner or losers under future increases in environmental variability. Our case study was the Middle Rio Grande riparian corridor in central New Mexico. Arid rivers experience large variability in both local climate and the climate of their upper watersheds, and these ecosystems are expected to become increasingly more variable in the future (Gurnell *et al.* 2012; Osterkamp and 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 spatiotemporal approach to address the following questions. (i) Do riparian plant species differ in sensitivity to the mean or variance in groundwater levels? (ii) At what temporal scale (intra- vs. inter-annual) is variance in groundwater most important to riparian plant species?

MATERIALS AND 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 (Supplementary Table S1 and Fig. S1). Sites had to have at least 2 years of plant cover and groundwater data to be included in analysis.

Study design

Each BEMP site (Supplementary Fig. S2) is 100 m × 200 m, with the 200 m side running north–south in parallel to the Rio Grande. Each site is divided into ten equal 20 m × 100 m sections and a 30 m vegetation transect is randomly placed within each section, running east to west. Each BEMP site has two rain gauges and five groundwater wells (Supplementary Fig. S2, described below).

Vegetation monitoring

Vegetation monitoring began in 2000 at seven sites and continued to the present; new sites were included in annual monitoring as they were established (Supplementary Table S1). This analysis used data from 2000 through 2015. We monitored ten vegetation transects per site (Supplementary Fig. S2) once annually during peak biomass production (August–September). Plants were monitored using

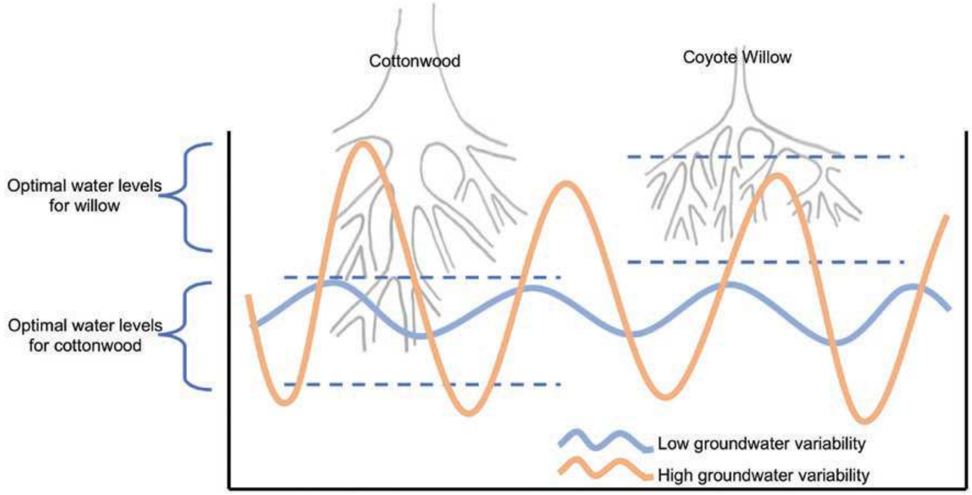

Figure 2: A revised bucket model for predicting plant responses to groundwater variability from species-specific stress tolerance thresholds. Here, we illustrate how two codominant species (cottonwood vs. willow) can diverge in responses to environmental variability. At low groundwater variability (blue 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 fall more frequently within the optimal threshold for willow, thereby increasing plant growth.

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 (Supplementary Fig. S2). We measured depth to groundwater (cm) at each well monthly using a Solinst water level meter (Georgetown, Ontario, Canada), subtracting the aboveground 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 2019). We obtained annual and monthly temperature and precipitation data at the 4 km 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 groundwater records that spanned the full time series 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. We also investigated the relationship between groundwater and stream flow using a linear model (Supplementary Fig. S3). BEMP reports stream flow data from United 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 or variance in groundwater levels?

We examined the nine most common plant species within our study sites to avoid zero-inflated data (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 GSF for each species based on the relationship between groundwater depth and plant cover (Burnham and Anderson 2002). We compared linear, non-linear models and models including only random intercepts against models including both random slopes and random intercepts for the individual sites. Mixed effects models were fit via maximum likelihood using the *lme4* package in R (Bates *et al.* 2015). 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 R^2 values with piecewiseSEM (Lefcheck 2016). We also considered an alternative approach to nonlinearity suggested by Pearse *et al.* (2018) that uses log-linear models, but found equal or better model fits via AICc for the quadratic model approach suggested by Rudgers *et al.* (2018). 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. Plant and groundwater datasets are available at bemp.org. R code and processed data are accessible through the Environmental Data Initiative. Data can be found at the Environmental Data Initiative (Eichhorst 2020).

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). Models

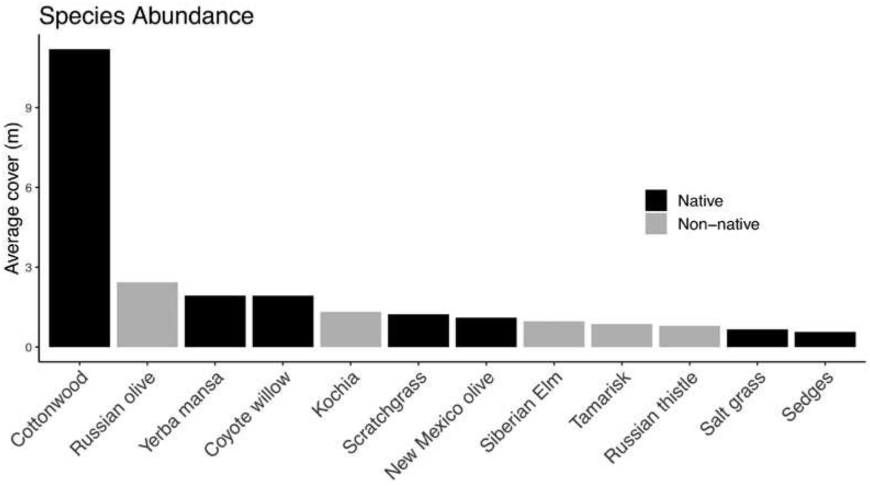

Figure 3: Mean plant cover across all sites and years for the 12 most abundant species across BEMP sites in the Middle Rio Grande Valley of New Mexico. Native species are cottonwood (*Populus deltoides* ssp. *wislizenii*), yerba mansa (*Anemopsis californica*), coyote willow (*Salix exigua*), scratchgrass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

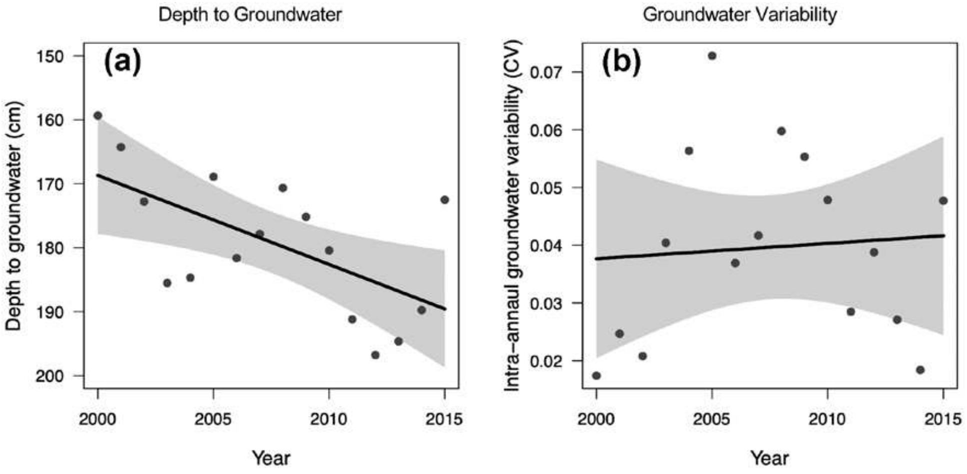

Figure 4: Trends in groundwater mean and variability in the Middle Rio Grande Valley. Depth to groundwater and groundwater variability over time averaged from the four BEMP sites with complete groundwater data from 2000 to 2015 (sites 1–4, see Table 1). (**a**) Average annual groundwater depth increased from 2000 to 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).

predicted plant cover as a function of either the intra- or inter-annual coefficient of variation (CV) in groundwater depth for each BEMP site. Because inter-annual variability could be calculated for every site except site 30, which had only 2 years of groundwater data (Supplementary Table S1), we used the same subset of 21 sites for all analyses. Inter-annual variation at each site was calculated for sites with >5 years 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 with maximum likelihood, and again, models included the random effects of site and year to account for the non-independence of observations. Then, we compared model fits for each temporal scale using model selection based on the second-order AICc.

RESULTS

The changing groundwater context

Groundwater depth varied both seasonally and annually, and the annual changes in groundwater depth correlated positively with changes in stream flow (Supplementary Fig. S3). Between 2000 and 2015, mean average depth to groundwater across the four longest running sites significantly decreased (Fig. 4a; R^2 = 0.37, P = 0.01). In contrast, intra-annual variability in groundwater depth did not change significantly during this time period (Fig. 4b; R^2 = 0.006, P = 0.70).

Do riparian plant species differ in sensitivity to the mean or variance in groundwater levels?

The bucket model predicts that plant species have divergent responses to increases in environmental variability, and our observations supported this prediction. The predicted ecological impact of changes in the mean and variance of a climatic driver is derived from the linear slope (predicts response to mean) and the nonlinear shape (predicts response to variance) of the GSF (Fig. 1). Of the nine riparian plant species we investigated, four had significantly nonlinear relationships between cover and groundwater, one had a linear relationship and four were insensitive (*n.s.*) to the observed range of groundwater levels (Fig. 5). The three native, woody species [Rio Grande cottonwood (*Populus deltoides* ssp. *wislizenii*), coyote willow (*Salix exigua*) and New Mexico olive (*Forestiera pubescens*)] diverged the most in their GSF (Fig. 5).

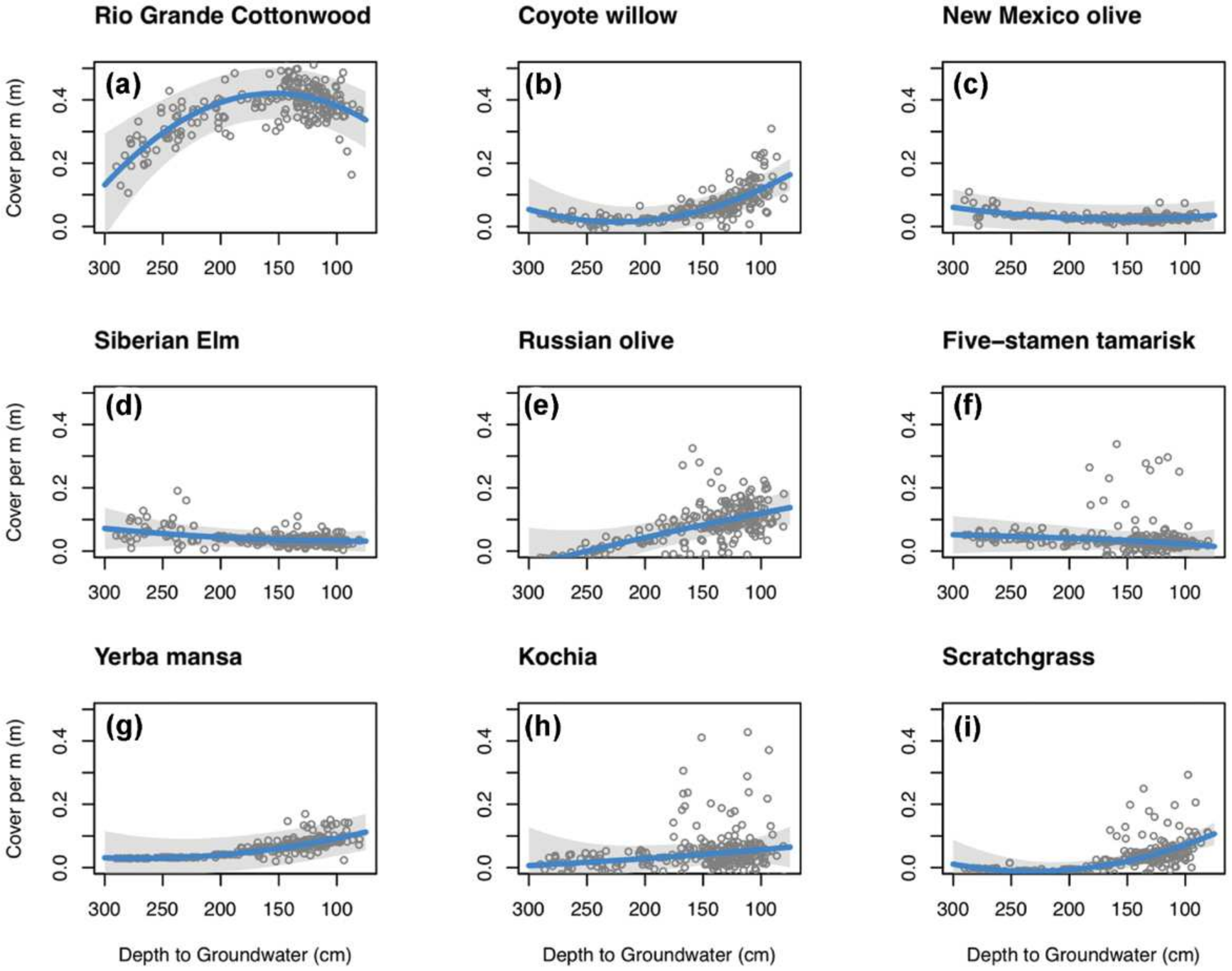

Figure 5: GSFs for the nine most abundant plant species across the Middle Rio Grande Valley of New Mexico. Concave functions predict a negative response to groundwater variability, whereas convex functions predict a positive response to variability (see Fig. 1). Linear functions indicate sensitivity to mean groundwater levels, but not to groundwater variability. Native species are cottonwood (*Populus deltoides* ssp. *wislizenii*), 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*), Russian olive (*Elaeagnus angustifolia*), tamarisk (*Tamarix chinensis*) and kochia (*Bassia scoparia*).

Cottonwood had a concave GSF that indicated increasingly variable groundwater levels could be costly (marginal R^2 = 0.07, conditional R^2 = 0.92, $P < 0.0001$; Fig. 5a, Table 1). The previous year's groundwater level was a better predictor of cottonwood cover than the current year (ΔAICc= 25, Table 1), and cottonwood was the only species for which the best GSF used groundwater lagged 1 year behind plant cover. In addition, including average maximum temperature improved the model fit for cottonwood (ΔAICc= 11, marginal R^2 = 0.11, conditional R^2 = 0.93, X^2=11.88, P = 0.0005) and revealed that the relationship between groundwater and cottonwood cover was non-significant in years/sites with cooler temperatures (Fig. 6a, P = 0.14), but strong in years/sites with warmer temperatures (Fig. 6b, 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 (marginal R^2 = 0.11, conditional R^2 = 0.88, $P < 0.0001$), where cottonwood had the greatest cover. Maximum temperature did not improve the predictive power of the model for willow (ΔAICc = −8, Table 1), and the interaction between groundwater depth and temperature was not statistically significant (Fig. 6c and d, P = 0.15).

New Mexico olive was insensitive to the observed range of groundwater depths (Fig. 5c, marginal R^2 = 0.003, conditional R^2 = 0.98, Table 1). This plant species, while common in our sites, is not a riparian specialist and may simply be less dependent on groundwater than other taxa. The inclusion of maximum temperature did not improve the model (ΔAICc = −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, non-native, woody species: Siberian elm (*Ulmus pumila*), Russian olive (*Elaeagnus angustifolia*) and tamarisk (*Tamarix chinensis*). Neither elm (marginal R^2 = 0.016, conditional R^2 = 0.87, P = 0.76) nor tamarisk (marginal R^2 = 0.008, conditional R^2 = 0.55, P = 0.60) was sensitive to groundwater depth (Fig. 5d–f, Table 1). Russian olive did not significantly increase with average groundwater stores (Fig. 5e, Table 1; slope = 0.0006, R^2 = 0.13, conditional R^2 = 081, P = 0.4), and a nonlinear model was not a substantially better fit than a linear model (ΔAICc = 2). Temperature was not a significant predictor for any of the non-native species as indicated by declines in model fit when temperature was included (Siberian elm ΔAICc = −1.2, Russian olive ΔAICc = −5, tamarisk ΔAICc = −5).

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), ~intra-annual groundwater variability (CV) Marginal R^2 values are shown for both nonlinear models

	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 × 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 × 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 × 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 × 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

P values <0.05 are shown in bold.

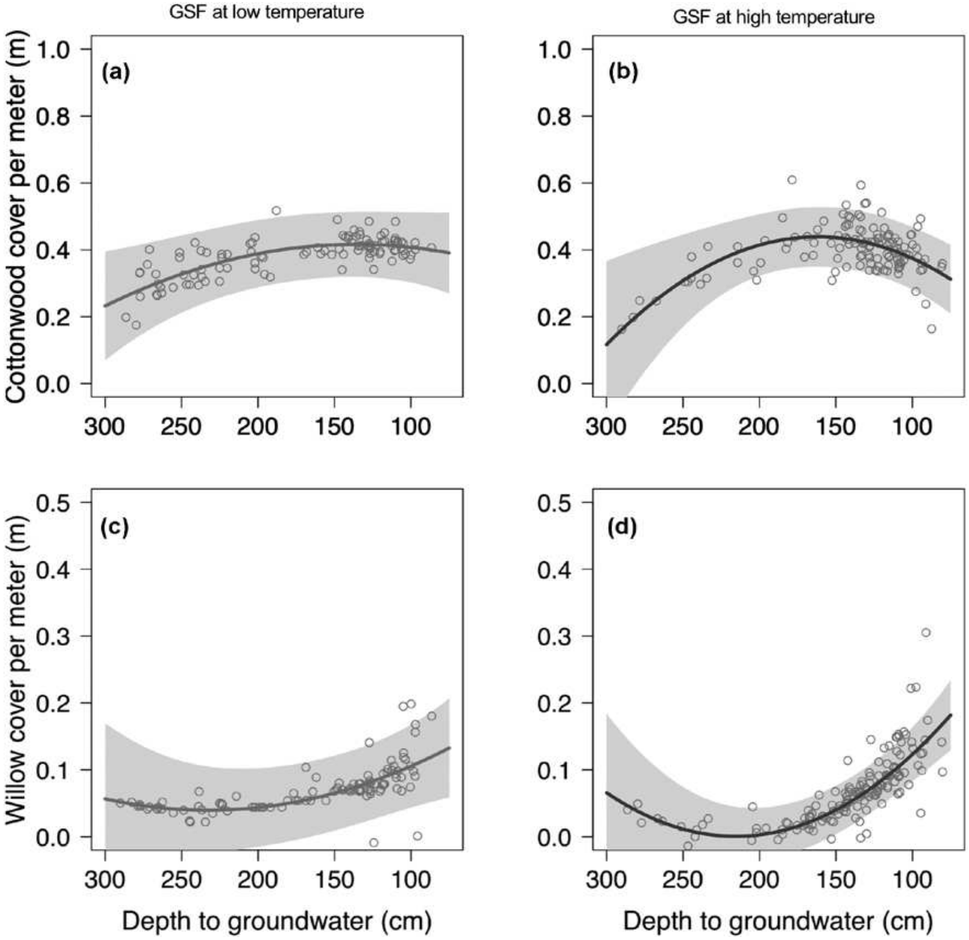

Figure 6: Interaction between air temperature and the GSF for Rio Grande cottonwood (*Populus deltoides* ssp. *wislizenii*) and coyote willow (*Salix exigua*). In years/sites with low average maximum air temperature (<22.5°C), (**a**) the cottonwood GSF was flat, indicating little sensitivity to inter-annual 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 differ significantly between low average maximum air temperature (**c**) and high average maximum air temperature (**d**); both GSF were convex, signaling positive consequences of increasing variability.

We evaluated the three most abundant herbaceous plants: yerba mansa (*Anemopsis californica*), an herbaceous perennial and obligate wetland species; kochia (*Bassia scoparia*), a non-native annual; and scratchgrass (*Muhlenbergia asperifolia*), a perennial, 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 low cover at deep water tables, as expected for wetland species. The GSF for scratchgrass (marginal $R^2 = 0.17$, conditional $R^2 = 0.64$, $P = 0.001$) explained more variation in plant cover than the GSF for yerba mansa (marginal $R^2 = 0.02$, conditional $R^2 = 0.96$, $P = 0.008$). Kochia had a flat GSF (Fig. 5h, Table 1) and was not sensitive to the observed range of groundwater depths (marginal $R^2 = 0.017$, conditional $R^2 = 0.41$, $P = 0.76$). Temperature was not a significant predictor for any of these herbaceous species (yerba mansa ΔAICc = −1.6, kochia ΔAICc = −7, scratchgrass ΔAICc = 0.3, Table 1).

The shape of the GSFs derived more from spatial variation rather than temporal variation. Spatial variation in groundwater between sites was greater than temporal variation within a site, and no individual sites spanned the entire observed range of groundwater depths. When random slopes were included in the model, results were qualitatively similar for seven out of the nine species, although marginal R^2 values were smaller than in the random intercepts models. For both New Mexico olive and yerba mansa, relationships with groundwater were not significant in models with random slopes (New Mexico olive marginal $P = 0.2$, yerba mansa $P = 0.78$). Because we set out to leverage both spatial and temporal variation to find a general pattern between plant cover and groundwater depth, rather than characterizing unique slopes at each site, we focused presentation on the results from random intercepts models. To provide a case study to illustrate the relative importance of spatial versus temporal variability, we explored the sensitivity of cottonwood cover to groundwater depth over time at each individual site. This analysis demonstrated that the relationship between groundwater and cottonwood cover depended largely on spatial, rather than temporal, variation in groundwater depth (Supplementary Fig. S4).

At what temporal scale (intra- vs. inter-annual) is variance in groundwater most important to riparian plant species?

Plant species differed in their sensitivity to the time scale of groundwater variance, specifically whether variance matter more at inter- or intra-annual time scales (Table 1). As predicted by climate sensitivity function theory, species identified as sensitive to groundwater depths using GSFs (Fig. 5) had the strongest relationships with measured groundwater variability on at least one time scale. In addition, plant species' relationships to groundwater variance supported predictions that a concave GSF signaled a cost of increased variability, while a convex GSF signaled a benefit from variability. Specifically, cottonwood cover was negatively related to intra-annual variability (slope = −1.36,

P = 0.004) and negatively, but not significantly, correlated to inter-annual variability (slope = −0.48, P = 0.106). Coyote willow correlated positively 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; intra vs. inter ΔAICc= 0.2). Positive relationships between plant cover and groundwater variability at both time scales also occurred for yerba mansa (inter-annual slope = 1.44, P < 0.0001; intra-annual slope = 0.96, P = 0.0008; ΔAICc = 13) and scratchgrass (inter-annual slope = 0.54, P < 0.0001; intra-annual slope = 0.68, P < 0.0001; ΔAICc = 1). Inter-annual variability was a better fit than intra-annual for yerba mansa, but the two time scales did not significantly differ in their ability to predict the cover of scratchgrass.

For some species, cover was not strongly correlated with groundwater depth in the GSFs, but did correlate with the CV in groundwater on at least one time scale. For instance, Siberian elm had no significant nonlinear relationship with groundwater depth in our GSF analysis (Fig. 5), but declined with greater inter- or intra-annual variability in groundwater, with a similar degree of sensitivity to each time scale (ΔAICc = 0.02). New Mexico olive also declined with increases at both time scales of variability in groundwater; however, inter-annual variability was a better fit (ΔAICc = 13). Both exotic shrub species (Russian olive and tamarisk) correlated positively with groundwater variability on both scales. Inter-annual variability was a somewhat better fit in explaining cover for both exotic shrub species than was the intra-annual CV (Russian olive ΔAICc = 6, tamarisk ΔAICc = 4). The only species not significantly related to groundwater variability on either time scale was the non-native herb, kochia (inter-annual slope = −0.18, P < 0.15; intra-annual slope = 0.25, P < 0.22).

DISCUSSION

Using 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 on dominant riparian plant species. 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 (Rudgers *et al.* 2018) and plant species (Angert *et al.* 2009) differ strongly in their responsiveness to environmental variance. Our results raise the question, *what factors explain differences among plant species in their sensitivity to the mean and variance in groundwater?*

Differences among plant species in their sensitivity to variance in groundwater may depend on 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 *et al.* 2019). Genetic differences as well as phenotypic plasticity in water-use efficiency under stress influence how plants respond to groundwater variability (Silvertown *et al.* 2015). For example, when groundwater tables are >3 m, cottonwood can invest up to 50% more root biomass in the top 1 m of soil (Lines 1999), indicating large capacity for phenotypic plasticity. In riparian systems specifically, changes in plant traits across water gradients aligned with wetland status, where wetland indicator plants were more likely to be sensitive to average groundwater than upland species (McCoy-Sulentic *et al.* 2017). Our results align with this prior finding, since the four species we identified as sensitive to groundwater variability were either 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 had cover that significantly correlated to groundwater depth, although Russian olive had a trend of increasing with shallower water tables, and groundwater depth explained 13% of its variation in cover. These non-native dominants are often targeted for removal by land managers, and most of our sites experienced at least one clearing event since monitoring began. Thus, management interventions may explain why we found no significant trends, although management could alternatively amplify sensitivity to groundwater due to stress during recovery from clearing. Alternatively, the lack of sensitivity could arise if invasive species have traits that increase performance over native plants across a range of environments, including higher tolerance of water stress (i.e. wider thresholds in the bucket model) than native wetland and riparian species (van Kleunen *et al.* 2010).

The bucket model (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 range of depth to groundwater, which is constrained in part by rooting depth (Lite and 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 (e.g. Fig. 2). The two native, foundational species of the Rio Grande riparian ecosystem differed substantially in their GSFs, suggestive of differences in their optimal groundwater range (or of interspecific competition, see next). Rio Grande cottonwood had a concave GSF, while coyote willow had a convex GSF, predicting differing responses to variability in groundwater levels, despite their growth in close proximity. Cottonwood and willow differ in rooting depth. Whereas Rio Grande cottonwood's maximum root depth is ~300 cm (Lite and Stromberg 2005; Stromberg 2013), the wetland shrub, coyote willow, has a maximum rooting depth of ~150 cm (Caplan *et al.* 2013). If cottonwoods, with their deeper roots, were growing where the water table was already near optimal conditions (average depths to groundwater at our sites ranged from 80 to 290 cm), then the bucket model predicts that a highly variable water table will be costly for cottonwood. In contrast, if willow growing in the same locations as cottonwood experienced average groundwater depths that were outside of their optimal threshold, then the bucket model predicts a highly variable water table would cause a greater frequency of occurrences of shallow water that benefit willow. Thus, the bucket model (Fig. 2) predicts increased variability would be net beneficial for willows, but net costly for cottonwood, based on these species' differences in average rooting depth. 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 shallow-rooted neighbors (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). The symmetry in the GSF of wetland species may indicate these species have a physiological optimum for water depth, decline both with drought on the dry end and anoxic water logging at the wet end. However in a global synthesis, Araújo *et al.* (2013) found that thermal tolerance of plants and animals was strongly asymmetrical around the thermal optimum, with much steeper declines in fitness with high heat than cold. More data will be required to understand the question of symmetry in divergence from optimum groundwater or soil moisture levels.

Cottonwood-willow riparian forests are common along rivers of western North America, and an alternative hypothesis for why the codominant species strongly diverged in sensitivity to groundwater variability is interspecific competition. As Rorison (1969) showed in a classic study on soil pH, strong interspecific competition may force a plant to grow outside of its fundamental niche. This could be the case for willow, which had greatest cover outside of the groundwater optimum window for cottonwood. To explore this possibility, we examined time-lagged relationships between cottonwood and willow cover to evaluate their potential as possible competitors. Convergent cross mapping (CCM) statistically tests for a cause-and-effect relationships between two time series variables to identify the most parsimonious direction of causation in correlated relationships (Clark *et al.* 2015). Time series provide statistical power for decoupling cause and effect because the direction of causality can be inferred from observational data when one variable is lagged in time behind the other variable. We used multispatial CCM (R package multispatialCCM, Clark *et al.* 2015) to evaluate cottonwood and willow time series, but found no evidence that a change in cover of one species caused a change in the other species when it was lagged in time ($P = 0.5$). This result indicated that the inverse GSFs for these codominants likely does not result from their interspecific interactions, although experimental tests of the competition hypothesis, such as species removal or addition experiments, would be required to confirm our CCM analysis.

Sensitivity functions can be driven by interactions among multiple environmental factors. We found that air temperature played a role in cottonwood sensitivity to groundwater variance. Under warm temperatures, cottonwoods were more sensitive to groundwater than under cooler conditions (Fig. 6). The strong nonlinear GSF under warm temperatures may occur because some trees use evapotranspiration as a method of leaf thermoregulation (Fauset *et al.* 2018). During hot years, trees at optimal groundwater depths may be better able to regulate temperature, and thus grow better than 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. For example, Rudgers *et al.* (2018) found that increased variance in summer precipitation was only beneficial to primary production of a grassland ecosystem under cool temperatures; during hotter periods, more variable precipitation had a concave climate sensitivity function indicative of a cost of variance in precipitation. In dryland ecosystems, which cover >40% of Earth's land area (Pravalie 2016), interactions between water availability and temperature are predicted to become increasingly important as both aridity and warming increase (Seager *et al.* 2007).

Including temporal and spatial variation provided a better picture of groundwater sensitivity across dominant plant species. The shapes of our GSFs were primarily driven by spatial rather than temporal variation, because the possible range of groundwater depths across sites was much larger than the range over time within a single site. Across sites, the slope of the relationship with groundwater tracked mean groundwater depth (Supplementary Fig. S4), but since our data were observational, not experimental, the diversity of GSF shapes among sites may also reflect other factors, such as management or successional history. The results for individual sites (Supplementary Fig. S4) also highlight why statistical models with random slopes fit the data well. Using the spatial variation combined with temporal variation within each site provided a regional picture of the interaction between plant cover and groundwater, using space to infer larger future changes in groundwater depths than have been observed over time at a single site. If the water table for the Middle Rio Grande valley drops further, as has happened globally due to river regulation and groundwater use (Margat and Van Der Gun 2013), our sites may shift from one side of the GSF curves to the other. Our analyses predict this shift would dramatically affect the composition of the plant community, by causing greater dominance by invasive species and willows and declines in cottonwood.

In our analyses, inter-annual variation in groundwater largely trumped intra-annual variation in explaining plant cover. Prior work in other systems supports our findings. Large seasonal variability was associated with greater species richness in plant communities across three rivers of the desert Southwestern USA (Katz *et al.* 2012), and high inter-annual variability was associated with large changes in the plant community from year-to-year on the Matawin River in Quebec, Canada, a mesic ecosystem (Dubeau *et al.* 2017). In North America, Fremont cottonwood trees (*P. fremontii*) can tolerate inter-annual groundwater changes of up to 0.8 m, but they also show plasticity, whereby trees at more variable sites appeared to be more tolerant of changes in depth to groundwater than trees at sites with a relatively stable water table (Lite and Stromberg 2005). The three species that we expected to respond positively to variability based on their GSFs were all positively correlated with both inter- and intra-annual variation in groundwater. Of the six plant species in which cover positively correlated with variability, inter-annual variation was more important to cover than intra-annual variation for all but coyote willow, for which inter- and intra-annual variability were equally important. We expected cottonwood to be negatively correlated to variability based on its GSF, and indeed, both canopy tree species in our study (cottonwood and Siberian elm) were negatively related to variability in groundwater. Kochia (*B. scorpia*) was the only species not significantly correlated with groundwater variability, which is an unsurprising result for a shallow-rooted, annual plant that likely relies on precipitation rather than groundwater (Steinberg *et al.*, unpublished work). Overall, our results support the use of GSF to make predictions on future changes in plant communities in response to environmental variability, with the caveat that spatial variation may not always be substitutable for future changes in temporal variation.

As observational data only allow us to identify correlations, it is possible that some of the relationships we observed between groundwater and plant cover are caused by changes in plant 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), rather than the reverse as we evaluated here. Potential for feedbacks between groundwater and vegetation in riparian ecosystems has also been investigated through modeling efforts (Rodriguez-Iturbe *et al.* 2007). In our dataset, differences in plant cover, groundwater levels and intra- and inter-annual variability in groundwater were much larger between sites than within a site over time. Because spatial variation was driving most of the relationships we documented, we used spatial variation as a proxy for understanding how potential future climate scenarios could influence riparian plant species across our region.

Riparian forests have been a focus for restoration and conservation because of the many ecosystem services they provide, such as promoting biodiversity (Selwood *et al.* 2015), flood and erosion control (Brauman *et al.* 2007) and carbon storage (Matzek *et al.* 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 riparian plant communities (Sommer and Froend 2014; Yin *et al.* 2015), but water tables are dropping world-wide (Margat and Van Der Gun 2013) and increased variation in rainfall will increase the correlated variation in groundwater stores. We demonstrated that GSFs can be useful tools to identify plant species that are most resilient (or most sensitive) to future increases in environmental variability. GSFs confirmed that riparian species were sensitive to average groundwater depth, and newly showed that for eight of nine focal plant species, cover changed in concert with groundwater *variability* on at least one temporal scale. We predict that shallow-rooted, wetland species will benefit from increased variability in groundwater depth, but cover of deep-rooted cottonwood trees will decrease, especially as climate warms. In contrast, non-native plant species were mostly insensitive to changes in both groundwater mean and its variance. Our approach of GSFs indicated that, within an ecosystem, plant species will respond to environmental mean and variance in divergent ways that may reassemble plant communities under a more variable climate.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: Study sites.
Figure S1: Study sites map.
Figure S2: BEMP site layout.
Figure S3: Annual average depth to groundwater correlates positively with annual average stream flow, log-transformed ($R^2 = 0.18$). Groundwater = 532 − 56.3 × stream flow.
Figure S4: Spatial variation in cottonwood groundwater sensitivity across six BEMP sites (A–F) with the longest temporal record.

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Authors' Contribution

All authors contributed to developing research questions, K.E. oversaw data collection, K.S. and J.R. analyzed the data, K.S. led the writing of the manuscript and all authors contributed to drafts and final manuscript.

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