Regional coordination between riparian dependence and atmospheric demand in willows (Salix L.) of western North America

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Abstract

Aim: Plants vary in their hydrological and climatic niches. How these niche dimensions covary among closely related species can help identify co-adaptations to hydrological and climatic factors, as well as predict biodiversity responses to environmental change.

Location: Western United States.

Methods: Relationships between riparian dependence and climate niches of willows (Salix L.) were assessed, incorporating phylogenetics and functional traits to understand the adaptive nature of those relationships. The riparian dependence niche was estimated as the mean distance between georeferenced occurrence records and the nearest stream based on the National Hydrography Database. Results were compared to oaks (Quercus L.), a less riparian-dependent clade, with the expectation of different niche relationships.

Results: Willows generally occurred closer to streams than expected by chance, but riparian dependence varied substantially among species. Riparian dependence was positively correlated with mean annual temperature and diurnal temperature range niche, both indicators of atmospheric demand on evapotranspiration. Phylogenetic independent contrast correlations for these relationships were significant as well, and the high degree of niche convergence among species indicated evolutionarily labile co-adaptations to riparian dependence and atmospheric demand. Plant height increased with mean annual temperature niche, and specific leaf area increased with residual variation in height, indicating underlying morphological correlates of niche variation. Oaks, on the other hand, exhibited no relationship between atmospheric demand and riparian dependence, and weaker niche relationships with riparian dependence overall.

Main conclusions: These results support the assertion that hydric-adapted, woody riparian plants compensate for increased atmospheric demand on transpiration with a reliable supply of water provided by riparian habitats and that this trade-off may be unique from mesic-xeric woody plants. Conservation of warm-adapted riparian trees...
and shrubs under increasing temperatures and atmospheric demand may necessitate reversal of groundwater depletion. Cool-adapted species may be best conserved through maintenance or expansion of riparian buffers as they become more riparian obligate with warming.

KEYWORDS
facultative riparian, groundwater depletion, hydrological gradient, niche evolution, obligate riparian, plant hydraulics

1 | INTRODUCTION

Riparian vegetation is an important component of freshwater ecosystem structure and function (Naiman & Décamps, 1997; Tab acchi et al., 2000). Variation in vegetation structure and function can be tightly linked to local hydrological gradients (Corenblit et al., 2015; Diehl et al., 2017), along which species differ in their groundwater dependence (Wei et al., 2017), disturbance tolerance (Lawson et al., 2015a) and water economies (McCoy-Sulentic et al., 2017; Silvertown et al., 2015). These hydrological gradients are nested within broader variation in climate, creating the potential for shifting adaptations to hydrological conditions depending upon other selective forces such as frost or aridity. Understanding how riparian species hydrological and climatic niches may be linked has important implications for understanding indirect effects of climate change on freshwater ecosystem structure and function (Kominoski et al., 2013; Moor et al., 2015), as well as understanding how flow alteration influences the climate sensitivity of vegetation (Butterfield et al., 2018).

Hydrology and climate both impact the water and carbon economies of plants, creating potential for strong interactive effects on plant performance and habitat occupancy (Silvertown et al., 2015). Functional strategies of woody plants vary in similar ways across local hydrological gradients (Merritt et al., 2010), shifting from water demanding to water conservative with increasing elevation above the water table (Cornwell & Ackerly, 2009; Lawson et al., 2015b; McCoy-Sulentic et al., 2017; Savage & Cavender-Bares, 2012). What remains unclear is how climate influences species reliance on the persistent soil moisture afforded by riparian areas. On the one hand, increasing aridity (either due to declining precipitation or increasing atmospheric demand) can select for greater water-use conservatism through functional strategies that reduce the risk of drought-induced cavitation or excessive water loss (Pfautsch et al., 2016; Reich et al., 1999), which could consequently reduce reliance on persistent soil moisture derived from streams ("Aridity Tolerance" hypothesis in Figure 1). Alternatively, some tree taxa appear to compensate for increasing atmospheric demand with greater hydraulic conductance efficiency (Hultine et al., 2020), or compensate for decreasing precipitation with allocation to deeper root growth in order to maintain contact with the water table (Rood et al., 2011), which should result in increased riparian dependence in more arid environments. This "Riparian Compensation" hypothesis (Figure 1) may be more relevant to hydric-adapted clades that can only tolerate high atmospheric demand when soil moisture is very high, or conversely lower soil moisture when atmospheric demand is very low. Determining whether hydric woody plants experience unique ecological and evolutionary trade-offs from those of more mesic–xeric clades (Grady et al., 2013) could be critical for predicting and mitigating their unique responses to climate change.

Differences in trait–environment relationships between hydric and mesic–xeric taxa can be expected for a number of niche dimensions. Three traits frequently used in the study of plant functional strategies are specific leaf area (SLA), maximum height and seed size, commonly referred to as the LHS scheme (Westoby, 1998). These traits represent biophysically independent axes of trait variation and are well represented in global databases (Kattge et al., 2020). Specific leaf area is integral to the leaf economics spectrum, and is positively related to tissue turnover rates and negatively related...
to resource use efficiency (Wright et al., 2004). SLA tends to decrease with aridity or water limitation at broad spatial scales (Poorter et al., 2009), and with increasing elevation above the riparian zone along local hydrological gradients (Cornwell & Ackerly, 2009). However, transpirational cooling from high SLA leaves is a strategy employed by many hydric woody plants that are adapted to extreme thermal stress in arid environments (Hultine et al., 2020), which runs counter to the general trend of SLA declining with aridity. Height is positively associated with precipitation and potential net primary productivity (Moles et al., 2009). Greater height results in longer hydraulic path length resulting in increasingly negative water potentials with canopy height, resulting in rapid declines in canopy conductance under water limited conditions (Koch et al., 2004).

However, access to persistent groundwater allows riparian taxa to achieve tall canopies relative to woody taxa in xeric upland habitats. Lastly, seed size is representative of variation in regeneration niche and is positively associated with shade tolerance (Hewitt, 1998) and root allocation in dryland systems (Butterfield & Briggs, 2011), but negatively related to seed longevity (Bekker et al., 1998) and disturbance tolerance (Grime, 1977). Seed size is fairly invariant across global climatic gradients (Westoby et al., 1992), with the exception of a stepped increase in the tropics (Moles et al., 2007). However, along local hydrological gradients in drylands, seed size increases with distance from stream channels (Stromberg & Boudell, 2013). In summary, the functional strategies of hydric woody plants may sort them along both local hydrological gradients and broad climatic gradients in ways that differ from mesic-xeric taxa.

Understanding how functional strategies vary across environmental gradients can benefit from comparative analysis of closely related species (Cavender-Bares, 2019). Differences among closely related species are more likely to reflect homologous evolutionary adaptations from similar initial conditions (i.e. a recent common ancestor). Functional traits directly measured on organisms, as well as their niche positions along different environmental gradients, can be used as point estimates of species ecology in comparative phylogenetic analysis (Ackerly et al., 2006). Changes in trait (or niche) values between descendant nodes in a phylogeny can be used to assess how evolutionarily labile different traits or niche dimensions are, and which trait (niche) combinations represent coordinated evolutionary responses (Ackerly, 2003). The latter suggest similar solutions to selective pressures over the course of clade diversification, implicating a common underlying trade-off in trait expression. The degree to which traits (niche dimensions) exhibit coordinated evolution within species-rich model clades can help to provide context for interpreting and predicting responses of other taxa to selective forces (Cavender-Bares, 2019).

In this study, we use willows of western North America to assess relationships between riparian dependence and climate, based on mediating functional traits. There are many obligate and facultative phreatophytic riparian willow species in this region, though many species occur in moist upland habitats as well. Willows are foundation species in many wetland ecosystems, and are widely used in riparian restoration, bioremediation and biofuels production (Frédette et al., 2019).

While a great deal is known about the trade-offs that shape willow hydraulic strategies (e.g. Savage & Cavender-Bares, 2011, 2012, 2013), how these trade-offs play out at with respect to species broader hydro-climatic niches, particularly in the more arid regions of North America, are less well understood. As such, willows may be a model clade (sensu Cavender-Bares, 2019) for understanding variation in habitat requirements of hydric woody plants along broad climatic gradients, providing insight into viable conservation strategies for riparian vegetation in different biomes and in a changing climate. We began by testing the alternative hypotheses that willow species occurring in hotter and drier environments should either be more restricted to riparian habitats (Riparian Compensation Hypothesis) or less restricted (Aridity Tolerance Hypothesis), based on climate conditions and proximity to streams of georeferenced occurrence records across the western USA. We also tested the hypothesis that LHS trait values would be correlated with hydrological and climatic niches of species in order to better understand functional strategies that underpin climatic and hydrological trade-offs. Lastly, we analysed all niche and trait relationships using phylogenetic independent contrasts (PICs) to test the hypothesis that niche and trait covariation represents coordinated evolutionary change, rather than conserved combinations of traits. For a biologically informed comparison, we also analysed patterns of niche and trait covariation in oaks (Quercus L.). Oaks are a species-rich genus of trees and large shrubs that are rarely riparian obligate in the western US. Our expectation was that oaks would not show strong links between riparian dependence and climate, while willows would. As the objective of this work was to understand controls on the niche relationships of willows as a representative of hydric woody plants, and given the extensive ecological and evolutionary work that has already been done on oaks (Cavender-Bares, 2019), we primarily use oaks as a backdrop against which to interpret the patterns found for willows.

2 | METHODS

2.1 | Data

Line shapefiles of stream channels were acquired from the United States National Hydrography Dataset Plus V2 (NHDPlus V2; USEPA & USGS, 2019) for Vector Processing Units (VPUs) 10 (U/L) to 18, covering the United States and small portions of Mexico and Canada west of the Mississippi River drainage (Figure 2). These VPUs represent hydrologically linked drainage basins of the Upper and Lower Missouri River, Arkansas-Red-White Rivers, Texas, Rio Grande River, Upper Colorado River, Lower Colorado River, Great Basin, Pacific Northwest and California regions. Occurrence records of individual plants for the genera Salix and Quercus were downloaded from the Southwest Environmental Information Network (SEINet, 2020) and masked to the focal NHDPlus V2 VPUs. Habitat and locality information were used, when available, to exclude planted specimens, and duplicate records with the same coordinates were removed. Coordinates were in decimal degrees, and only points with 4-5
the hottest months of the year, as well as during the period of peak metabolic activity. MAT was selected to represent a single gradient from frost to heat limitation, as minimum and maximum temperatures are highly correlated with MAT across the study region (Butterfield & Munson, 2016). TDiurn was selected as a proxy for atmospheric demand on the water column within plants, where higher TDiurn indicates higher saturated vapour pressure of water (i.e. more water vapour is required to saturate the air; Allen et al., 2005). Mean values of each environmental variable across all occurrence records for each species were used to estimate mean niche values for each species.

LHS trait data were extracted from the TRY database (Kattge et al., 2020). Species mean trait values were estimated when multiple values were available, with equal weights applied to each data source. Data were not available for all species (Appendix S2), so analyses reflect different combinations of species and should be interpreted with caution. While this approach does not account for intraspecific variability, it does provide estimates that are comparable in scope to species mean climate niche and distance from water body values.

### 2.2 Environmental niche and trait analysis

Occurrence records provide imperfect location data, and their use in estimating riparian dependence is not well established. As an initial assessment of the utility of this approach in generating a relative estimate of riparian dependence, the mean distance from stream was compared between occurrence points and background points. The expectation was that willow occurrence points would be closer to streams than the background points, whereas oak occurrence relative to streams would not diverge from the distribution of background points. This analysis was conducted in two ways. First, log-transformed data were used to estimate 95% confidence intervals for distance from stream with all willow (or oak) species combined within each VPU to account for differences in stream density among regions. Second, the same procedure was performed for each willow (oak) species individually and compared only to background points from the VPUs in which that species was present. Occurrences were considered closer to streams than expected if the 95% confidence intervals did not overlap with that of the background distances.

Relationships between species mean climate niche and mean log10 distance from stream were tested with bivariate and multiple regression. A quadratic term was included for MAT niche of willows (not oaks) based on visual inspection of bivariate plots, and MAP was log10-transformed to achieve normality. Backward stepwise model selection using AIC was performed with the stepAIC function in the MASS package (Venables & Ripley, 2002). Variables were removed in order based on the maximal decrease in AIC until removing additional variables did not further reduce AIC. Bivariate relationships between species mean log10 distance from stream and mean climate niche were further explored for variables included in the most parsimonious multiple regression model for each genus. Two additional steps were undertaken to assess possible spatial correlation among variables. First, the correlation between mean log10 distance from

#### FIGURE 2 Map of study area. Vector processing units (VPUs) from the National Hydrography Database used in this study are superimposed on variation in mean annual temperature (MAT). VPUs excluded from this study are grey. Legend: 10U—Upper Missouri River, 10L—Lower Missouri River, 11—Arkansas-Red-White Rivers, 12—Texas, 13—Rio Grande River, 14—Upper Colorado River, 15—Lower Colorado River, 16—Great Basin, 17—Pacific Northwest and 18—California

Several climate variables relevant to water supply and demand were extracted from WorldClim for each plant occurrence record. The climate variables were mean annual temperature (MAT), mean monthly diurnal temperature range (TDiurn), mean annual precipitation (MAP) and precipitation of the warmest quarter (PWrmQtr). MAT was fairly independent of the other variables ($r = 0.56, -0.11, 0.21$ with TDiurn, MAP and PWrmQtr, respectively), TDiurn was moderately correlated with MAP and PWrmQtr ($r = -0.54, -0.42$), and MAP and PWrmQtr were substantially correlated ($r = 0.79$). Both precipitation variables were included in order to account for differences in their biological relevance: MAP was selected as a proxy for total soil moisture derived from precipitation, and PWrmQtr as a proxy of soil moisture that might compensate for groundwater declines during

decimal places (~<10m resolution) were retained. Species with a minimum of 30 occurrence records were retained, resulting in a total of 15,470 occurrence records distributed across 48 species of willows, and 17,209 records across 54 species of oaks. A random sample of 3x the number of occurrence records was selected as background points within each VPU for modelling purposes. Background sampling was conducted separately within each VPU to account for differences in stream density across regions. Distance to the nearest stream was calculated using the gDistance function in the R package rgeos (Bivand & Rundel, 2019) for each occurrence record and background point using NHDPPlus V2. Distance to other water bodies (ponds, lakes, wetlands) was similarly calculated to assess their influence on the distribution of willows. Willows were on average more than an order of magnitude further from other water bodies (ponds, lakes, wetlands) than from streams (Appendix S1); thus, only distance from stream was used in subsequent analyses. All analyses were conducted in R version 3.6.2 (R Core Team, 2014).

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stream and all four climate variables was assessed across all occurrence points, ignoring species identity. Second, species identity was permuted while maintaining observed abundance distributions, and then, the correlations between pseudo-species mean log10 distance from stream and mean climate niche for all four variables were calculated. This was done 999 times, and the mean ± 2SE of the correlations were calculated. This provides a more conservative null hypothesis for correlations among species mean niche values, as it accounts for correlations that can arise from averaging values after binning by species (Butterfield, 2015).

The same multiple regression approach applied to distance from stream was also conducted for each LHS trait separately, using climate niche and distance from stream as predictor variables. Additional analyses of residual trait variation not explained by climate niche were conducted to identify potential interactions between traits.

2.3 | Phylogenetic analysis

A published phylogeny of American willows based on a Bayesian consensus tree of matK and rbcl plastid genes was used for phylogenetic analysis of willows (Lauron-Moreau et al., 2015). A published phylogeny of oaks based on a RAD-seq crown tree was used for phylogenetic analysis of oaks (Hipp et al., 2020). Phylogenetic signal in niche or trait values was analysed in a two-step process. First, Blomberg’s K was calculated as an index of phylogenetic signal with the phylosignal function in the picante package (Kembel et al., 2010). A value of K \( > 1 \) supports a Brownian motion model of niche (or trait) evolution, whereas K \( < 1 \) indicates niche (trait) conservatism (i.e. closely related species are ecologically more similar than expected based on Brownian motion), and \( 0 < K < 1 \) indicates niche (trait) convergence (i.e. distantly related species are more similar than expected). Second, in order to determine whether the values of K represented consistent patterns of niche (trait) divergence throughout a phylogeny, the variance in observed phylogenetic independent contrasts (PICs) was compared to a null distribution based on the independent swap algorithm (Münkemüller et al., 2012). PICs are niche (trait) differences between species scaled by the phylogenetic distances between those species. As such, PICs are also useful for examining niche (trait) relationships among species to determine whether those relationships can be interpreted as adaptive, or simply a consequence of suites of conserved traits among different clades. Thus, PICs were used to test for bivariate correlations among niche and trait dimensions as a final analysis.

3 | RESULTS

3.1 | Riparian dependence

Willows occurred significantly closer to streams than expected based on a random sampling of points within each VPU (Appendix S3). At the species level, 38/48 had a mean distance from stream that was significantly smaller than expected from the background data, with the distance of the other 10 species not significantly different than expected. On average, the back-transformed mean distance from stream was 224 m for willow species and 631 m for background points. The most riparian-dependent species was S. lutea (76 m from stream), and the least was S. cascadensis (865 m from stream), with the remaining species evenly distributed between these extremes, and an average confidence interval of 182 m (Appendix S3). These results are in concordance with willows generally being a hydric genus, but also indicate that species vary substantially in their degree of riparian dependence.

Oaks had on average a further distance from stream than willows, as well as a warmer mean MAT niche (Figure 3). No other climatic niche dimensions differed significantly between genera. Most oaks (39/54) occurred closer to streams than expected (minimum mean distance: Q. lobata at 147 m), and one (Q. pungens at an average of 1,045 m) further than expected (Appendix S3). The mean species distance from stream was on average 115 m (34%) closer for willows than oaks \( t_{59} = -3.9, p < .001 \). This difference increased to 165 m (51%) when only species that overlapped in MAT niche space were compared \( t_{37} = -6.1, p < .001; \) right side of Figure 2). MAT niches of oaks were on average 7.7 °C warmer than those of the willow species \( t_{51} = 8.9, p < .001 \).

3.2 | Climatic correlates of riparian dependence

The best model of willow species mean distance from stream (adjusted \( R^2 = 0.80 \); Appendix S4) included a negative relationship

![FIGURE 3](image)

**FIGURE 3** Species median distance from stream as a function of species median mean annual temperature (MAT) niche for willows and oaks. OLS regression models and 95% confidence intervals, as well as marginal distributions for each niche axis, are presented for willows and oaks separately.
with species TDiurn niche, a negative linear and positive quadratic relationship with species MAT niche, and a positive relationship with species PWrmQtr niche (Figure 4a-c). The direction of the relationships was retained after accounting for partial correlations among climate variables (Appendix S4). Both permutation methods for assessing spatial correlation among distance from stream and climate variables produced similar results \( r_{\text{MAT}} = -0.20, r_{\text{TDiurn}} = -0.23, r_{\text{MAP}} = 0.14, r_{\text{PWrmQtr}} = 0.17 \), which were significantly lower than for the observed species relationships with MAT, TDiurn and PWrmQtr (Figure 4). In other words, underlying spatial correlations between distance from stream and climate variables accounted for only a small part of the observed relationships across willow species.

The best model for oak species distance from stream (adjusted \( R^2 = 0.21 \); Appendix S4) included positive relationships with MAT and PWrmQtr. The bivariate correlations between these variables and distance from stream were greater than for the randomized data (permuted \( r_{\text{MAT}} = -0.01, r_{\text{TDiurn}} = -0.05, r_{\text{MAP}} = 0.07, r_{\text{PWrmQtr}} = 0.15 \)). However, the bivariate relationship of distance from stream with MAT was weak for oaks \( r = 0.25, p = .06 \), and notably of opposite sign from that of willows (positive versus mostly negative).

### 3.3 Trait–environmental niche relationships

Height \((n = 38)\) of willows varied significantly with species environmental niches, whereas seed size \((n = 23)\) and specific leaf area \((n = 21)\) did not. The best model for height (adjusted \( R^2 = 0.52 \); Appendix S5) included positive relationships with MAT and distance from stream (the bivariate relationship with distance from stream was negative), and a negative relationship with mean annual precipitation (MAP), though only MAT was significant on its own. The explanatory power of distance from stream and MAP did not increase after accounting for partial correlations with MAT (Appendix S5). The height–MAT relationship exhibited two distinct groups of species (Figure 5), and upon further investigation, the residuals from the height–MAT relationship exhibited a significant positive correlation with specific leaf area \( (r = 0.61, p = .002; \text{Figure 5 inset}) \). Further exploration revealed that while the two primary subgenera of willows (Salix, upper clade, left panel in Figure 6; and Vetrix, lower clade) differed in height \( (\mu_{\text{Salix}} = 10.6\,\text{m}, \mu_{\text{Vetrix}} = 5.2\,\text{m}; t_{23} = 2.7, p = .01) \) and MAT niche \( (\mu_{\text{Salix}} = 10.8^\circ C, \mu_{\text{Vetrix}} = 4.4^\circ C; t_{30} = 4.6, p < .001) \), this phylogenetic subdivision did not account for the divergent height–MAT relationship \( (\mu_{\text{Salix OLS}} = 0.82 \pm 0.86, \mu_{\text{Vetrix OLS}} = 0.82 \pm 0.15) \).

All three traits varied significantly with oak species environmental niches, though height had the least variance explained, unlike for willows. Height \((n = 42; \text{adjusted } R^2 = 0.18; \text{Appendix S5})\) had a negative relationship with TDiurn. Seed size \((n = 31; \text{adjusted } R^2 = 0.45; \text{Appendix S5})\) had a negative relationship with TDiurn, PWrmQtr and distance from stream. Specific leaf area \((n = 25; \text{adjusted } R^2 = 0.58; \text{Appendix S5})\) had a positive relationship with PWrmQtr and a negative relationship with MAT.

### 3.4 Phylogenetic signal

MAT niche was the only niche dimension or trait that exhibited significant phylogenetic signal among willow species \((p = .007; \text{Appendix S6})\). The value of Blomberg’s \( K \) for MAT niche was 0.14, indicating a pattern of phylogenetic convergence; that is, sister taxa tended to be dissimilar in their MAT niche (Figure 6). In contrast, all niche dimensions and traits except for height exhibited significant phylogenetic signal among oak species (Appendix S6). Specific leaf area had a \( K \) value of 1.1 \((p = .001)\), indicating a slightly conserved model of evolution. All other significant \( K \) values for oaks ranged from 0.32 to 0.54, indicating a more convergent pattern of niche evolution, though substantially higher than the \( K \) value for MAT niche of willows (Appendix S6).

Both height and distance from stream exhibited significant phylogenetic correlations with climate niche of willows. Distance from

![Figure 4](image-url) **Figure 4** Willow species mean distance from stream as a function of species mean climate niches. \( R^2 \) is provided for the quadratic relationship with MAT.
stream PICs decreased significantly with MAT and TDiurn PICs, and increased with PWrmQtr PICs \((n = 44, \text{adjusted } R^2 = 0.70; \text{Figure 7})\). The quadratic relationship for the non-phylogenetically informed analysis observed for distance from stream and MAT was instead linear for PICs. Height PICs were negatively related to distance from stream PICs and TDiurn PICs \((n = 37; \text{adjusted } R^2 = 0.10; \text{Appendix S7})\). For oaks, the only significant PIC relationships were between distance from stream and PWrmQtr \((n = 54; \text{adjusted } R^2 = 0.05; \text{Appendix S7})\), and between SLA and PWrmQtr \((n = 23; \text{adjusted } R^2 = 0.34; \text{Appendix S7})\).

4 | DISCUSSION

We found support for the riparian compensation hypothesis (Figure 1), with strong relationships between hydrological and climatic niches of willows that indicate compensatory adaptations to water supply and demand: species that occur in regions with greater atmospheric demand (hotter and drier) are constrained to occur closer to streams and, presumably, a more reliable supply of groundwater. This local hydrological compensation for broader climatic constraints may explain the impressive climatic breadth of willows as a genus. The robust phylogenetic correlations and strong convergence (rather than conservatism) in the temperature niche suggest that vicariance events along altitudinal or latitudinal temperature gradients, facilitated by long-distance
dispersal of small seeds by wind and water, were matched with deterministic selection along local hydrological gradients. The relationships between hydrological (specifically, riparian dependence) and climatic niches were different between willows and oaks, and were generally much weaker among the latter. We argue that the patterns found here for willows represent a fundamental ecological trade-off that may be applicable to hydric woody plants more generally, and that is unique from trade-offs experienced by mesic–xeric clades.

The lack of riparian dependence in cold-adapted willows is likely associated with low atmospheric demand. Willows from colder environments tend to have smaller xylem vessels than those from warmer environments (Savage & Cavender-Bares, 2013), indicating some selection for increased protection of stems from frost damage that may also increase safety of water transport from cavitation under dry conditions. The low stature of cold-adapted willows also reduces the exposure of stems and meristems to extreme cold (Körner, 2003). The shorter hydraulic path length of these species also reduces potential water stress. These adaptations combine to reduce groundwater dependence in cold-adapted willows, despite being very hydric taxa. Not only do willows occupy some of the coldest habitats within the study region, some species have very large frost safety margins (Sakai & Weiser, 1973). Other traits, such as sugar-loading, leaf phenology and the ability to vigorously resprout in response to frost damage (Ögren, 1999), may further explain the ability of willows to tolerate extreme cold temperatures.

The efficient water transport strategy of warm-adapted willows reflects adaptations to high vapour pressure deficit (VPD) and heat. Canopy stomatal conductance and transpiration in willow stands are strongly influenced by soil water availability (Frédette et al., 2019; Hultine et al., 2010), and willow species that occur in dryer habitats within a landscape exhibit more water-use efficient functional strategies (Savage & Cavender-Bares, 2012). Overall, the range of moisture conditions over which willows maintain high stomatal conductance is quite narrow and restricted to high water availability, regardless of species hydrological habitat affinity, resulting in stomatal closure under moderately dry soil conditions (Hultine et al., 2010; Savage & Cavender-Bares, 2011; Savage et al., 2009). The range of viable soil moisture conditions likely becomes increasingly constrained with increasing VPD, which would explain the restriction of species to riparian habitats under high diurnal temperature fluctuations (a good proxy for VPD).

Adaptations of riparian woody plants to high temperatures, on the other hand, may have as much to do with evaporative cooling as hydraulic failure per se. Whereas stomatal closure protects stems from cavitation, it can expose leaves to high temperatures and irreversible damage to photosystem II (Hultine et al., 2020). The relationship between riparian dependence and temperature niche found in this study may in part reflect the need for evaporative cooling in hot environments, though the weakening of the relationship with riparian dependence among heat-adapted species (right side of Figure 4b) suggests multiple interacting processes. The heat-adapted species that are less riparian-dependent tend to occur in the more humid, eastern portion of the study area. Evaporative cooling via transpiration, and hence dependence upon groundwater and restriction to riparian habitats, may only be necessary in both hot and atmospherically dry conditions.

Alternative functional strategies were also apparent in hotter environments, where willow height diverged along two distinct trajectories with contrasting SLA values (Figure 5). Water use and phenology may both play a role in these divergent strategies. The canopies of taller willow species are supported by one or more large trunks, and sapwood area increases exponentially with trunk

**FIGURE 7** Phylogenetic relationships between distance from stream and climate niche. Points represent species averages (same as in Figure 4), and lines connecting points indicate phylogenetic divergences between sister taxa. Consistent directionality of these phylogenetic “branches” indicates consistent patterns of trait divergences. Phylogenetic independent contrast (PIC) relationships are presented in the insets. The axes are the same as in the primary figure panels and indicate phylogenetically scaled differences between species.
diameter (Bond-Lamberty et al., 2002). If all things are equal, an increase in sapwood area results in greater capacity for water supply to meet demand by the transpiring canopy, resulting in greater potential leaf area (Beyer et al., 2018). When willows have access to persistent water, high sapwood area results in high water use and high photosynthetic rates (Beyer et al., 2018), both of which are consistent with high SLA. In contrast, shorter willows with smaller sapwood areas and potentially shallower rooting distributions may need to exhibit more water-use efficient strategies reflected by lower SLA. Phenology provides a complementary interpretation of the divergent height and SLA strategies, due to the negative relationship between SLA and leaf longevity (Reich et al., 1992). Subcanopy woody species, such as shorter willows, often break bud earlier and senesce later than co-occurring canopy species, which can significantly enhance annual carbon gain during periods when canopy species are dormant and light emission is higher (Miyazawa & Kikuzawa, 2005). Sustaining these leaves throughout a long growing season may necessitate greater structural integrity, resulting in a lower SLA (Poorter et al., 2009). Taller species in hotter environments may also tend to be drought deciduous, much like low-elevation Populus (Salicaceae) trees that regularly shed their leaves mid-summer, producing a second set of leaves at the end of summer as temperatures decline (the authors, personal observation). This dynamic would support a low investment, high rate of return strategy associated with high SLA. Water and carbon economies are inevitably linked in arid environments, so both likely play a role in the divergent strategies of tall and short willows. If these strategies are indeed related to rooting depth and access to groundwater, changes in groundwater depth or stream intermittency should affect these functional groups differentially.

The phylogenetic analyses supported an adaptive interpretation of the niche relationships among willow species and also indicated an important role for temperature in driving diversification within the genus. The phylogenetic signal in MAT niche was one of strong convergence, in which sister taxa were consistently more dissimilar in their MAT niche than expected under a Brownian motion model of niche evolution. Seed size is a highly conserved trait among willow species (coefficient of variation = 0.73), is consistently small and has great potential for long-distance dispersal via wind and water (Karrenberg et al., 2002). This dispersal syndrome creates potential for isolated populations to establish in distant streams or mountains surrounded by unfavourable habitat. Previous studies have also found the temperature niches of willows to be quite evolutionarily labile, such as multiple lineages evolving dwarf shrub growth forms in arctic-alpine habitats of Europe (Wagner et al., 2018), and rapid evolution across latitudes in North America (Karrenberg et al., 2002). The ability of willows to survive in disparate climate niches following vicariance events may be facilitated in part by establishment at points along local-scale hydrological gradients that sufficiently compensate for any mismatches with temperature or VPD conditions. Strong tests of these hypotheses would greatly benefit from improved phylogenetic resolution of this evolutionarily complicated genus (Karrenberg et al., 2002; Lauron-Moreau et al., 2015), as well as more extensive functional trait data in order to account for intra-specific variation and local adaptation.

Willows behaved quite differently from oaks, which exhibited weak relationships between hydrological and climatic niches. In contrast with willows, multiple lineages of oaks have evolved similar adaptations to aridity and local hydrological gradients via sympatric parallel evolution (Cavender-Bares, 2019; Cavender-Bares et al., 2004), with many species exhibiting adaptations to xeric upland habitats (Abrams, 1990). The one point of similarity between willows and oaks related to summer precipitation niche, which was positively related to distance from stream in both clades. This corresponds well with the observation that precipitation seasonality, particularly the proportion of precipitation falling during the summer, is a strong driver of woody plant niches across the study region (Butterfield, 2015). In the context of riparian ecosystems, precipitation-derived soil moisture could compensate for a lack of groundwater during summer months. Although there are examples of phreatophytes switching seasonally from groundwater to unsaturated soil water (Sommer & Froend, 2011), the degree to which precipitation may fully compensate for groundwater drawdown in arid regions is unclear.

The coarse scale of the analyses conducted here has limitations, but also provides opportunities for understanding niche evolution. More precise estimates of proximity to streams, or better yet depth to water table, would provide much better proximate estimates of groundwater dependence. The resolution of the occurrence records and hydrological data necessarily resulted in over-estimates of distance from stream for riparian obligate species, so must be treated as estimates of relative riparian dependence among species rather than precise indicators of riparian obligation. Streams also vary substantially in the timing, volume and velocity of base flows and floods. Long-term monthly averages of some of these variables were extracted from the NHDP1us and explored with the present dataset, but did not significantly improve model fit (data not shown). This may be due to the importance of extreme events in shaping riparian plant populations (Naiman & Décamps, 1997), incorporation of non-riparian taxa into the models, or both. Other studies have demonstrated the utility of flow variables in riparian plant niche models (McShane et al., 2015), and the NHDP1us should be further explored in this capacity. Despite these limitations, the large sample size provided by merging occurrence records with coarse-scale climatic, hydrological and trait databases can provide rapid insights and hypotheses that can be tested and refined by experiments informed by biogeographic patterns.

Higher atmospheric demand and heat stress will likely cause hydric woody plants to increase water use to meet demand, which may narrow the hydro-climatic niche of species and populations. Riparian buffer zones are a common conservation measure used to maintain habitat quality for aquatic organisms and migration corridors for terrestrial animals (Naiman & Décamps, 1997). Our results indicate that these zones may become increasingly important for sustaining plant biodiversity as hydric species shift towards increasing riparian obligation. Climate models could be used to predict the breadth
of buffer zones necessary to accommodate species of interest that may lose suitable upland habitat (Perry et al., 2015). In arid regions, increasing reliance on stable groundwater availability means that riparian ecosystems dominated by willows and similar species will narrow or disappear along stream reaches susceptible to increasing intermittency (Reynolds et al., 2015). In these systems, restoration of stream flows and a cessation to groundwater drawdown may be more urgent priorities than buffer zones for conservation of riparian trees and shrubs (González et al., 2018). Restoring already declining populations can be difficult, which in part may be attributable to positive feedbacks on atmospheric demand in areas with reduced gallery forest canopy cover. Lower transpiration and greater albedo created by loss of canopy cover can increase atmospheric demand and consequently reliance on groundwater in a vicious cycle. Interventions such as multi-phase restoration, in which early-successional species are established first to reduce albedo and increase humidity, may be important in these more arid conditions. Solutions to conservation and restoration can hopefully be enhanced through a better understanding of these trade-offs in plant form and function among species are established first to reduce albedo and increase humidity, may be important in these more arid conditions. Solutions to conservation and restoration can hopefully be enhanced through a better understanding of these trade-offs in plant form and function across riparian areas differing in climate. Strategies for maintaining populations of these foundation trees and shrubs are not only important for conserving those species, but also the broader riparian ecosystems that they define and support (Grady et al., 2013).

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data used in this study were downloaded from publically available databases (TRY, SEINET, WorldClim and NHDPlus V2).

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**BIOSKETCH**

Brad Butterfield studies the trade-offs that shape the diversity of plant communities, and the implications of that diversity for ecosystem structure and function. The research team focuses broadly on the ecology, evolution and management of vegetation in dryland biomes.

**SUPPORTING INFORMATION**

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

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