

DISSERTATION

THE RELATIONSHIP OF RIPARIAN VEGETATION GUILDS TO ALLUVIAL  
GROUNDWATER, FLOOD DISTURBANCE, AND THE PROVISIONING OF BIRD  
HABITAT ALONG RIVERS IN THE COLORADO RIVER BASIN

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## ABSTRACT

### THE RELATIONSHIP OF RIPARIAN VEGETATION GUILDS TO ALLUVIAL GROUNDWATER, FLOOD DISTURBANCE, AND THE PROVISIONING OF BIRD HABITAT ALONG RIVERS IN THE COLORADO RIVER BASIN

Riparian ecosystems provide essential services including flood mitigation, organic matter and energy, nutrient cycling, and wildlife habitat with their structure and function strongly influenced by fluvial processes and shallow groundwater. Riparian areas across the world have been degraded by land development and the alteration of streamflow by dams, diversions, dikes, and groundwater pumping. Climate change will further stress riparian ecosystems and the Colorado River is predicted to experience the largest decrease in streamflow of the major basins in the western US. Changes in the patterns of stream flow can result in the alteration of plant communities, physical structure, and overall ecosystem functioning. Efforts to understand how plant species are distributed along hydrologic gradients in riparian zones have focused on individual species. The use of vegetation guilds, groups of plants with similar functional traits, may be useful in generalizing plant responses to streamflow alterations across rivers. The identification of trait-based guilds with member species that respond similarly to stressors common along rivers directly links plant performance to environmental processes. The range of traits within a vegetation guild can also help explain how functionally similar species contribute to vegetation structure and heterogeneity that supports habitat for wildlife, including birds that rely on riparian ecosystems for breeding, foraging, nesting, and migration.

In Chapter 1, I investigate the relationship between riparian vegetation guilds, vegetation structure, and bird habitat along the Verde River in Arizona. Five woody and seven herbaceous

guilds were classified using a suite of functional traits including specific leaf area, potential rooting depth, and seed mass. Bird abundance, diversity, and richness were best predicted by the cover of the tall tree guild dominated by *Salix gooddingii* and the drought tolerant shrub guild dominated by *Prosopis velutina*. These results highlight the need to conserve not only riparian forests, but shrubs that provide food and nesting sites for bird species that prefer low-statured vegetation. In Chapter 2, I assess the connection between Verde River streamflow, alluvial groundwater, and the occurrence of woody and herbaceous riparian vegetation guilds. Groundwater depth was strongly controlled by streamflow changes and tall tree guild members were more likely to occur where groundwater was less than 2.5 m from the floodplain surface. The distribution of woody vegetation guilds was explained by groundwater depth and flood exceedance probability, but hydrologic attributes only explained variation in occurrence of two herbaceous guilds. Simulations of lowered groundwater indicate that presences of tall trees, short trees, and flood tolerant shrubs will decrease while drought tolerant shrubs and generalist shrubs will increase along the Verde River.

In the final chapter I determine if riparian vegetation guilds occupy similar habitat controlled by groundwater depth and flooding in river basins with different climate and streamflow regimes. I compared trait composition of guilds in two study regions, Arizona and Colorado, and assessed how guild occurrence could change under conditions of lowered inundation exceedance probability and deeper groundwater levels using simulation modeling. I compared vegetation guilds along the Verde River with those along the Dolores and San Miguel Rivers in Colorado and found that the structural dominant guilds were different in each study region. Flood tolerant shrubs dominated at high elevation reaches in Colorado while lower elevation reaches were characterized by a mix of flood tolerant shrubs, tall trees, and generalist shrubs. Tall trees were the dominant guild along the Verde River. Two vegetation guilds had similar trait composition between study regions, but my results imply that hydrologic processes supporting them are different. Hillslope groundwater contributions

and higher average annual precipitation at higher elevation reaches in Colorado maintained high floodplain groundwater levels that varied less compared to lower elevation reaches in Colorado and the Verde River. Riparian vegetation zonation was less distinct at Colorado study reaches than Arizona.

Simulations of lowered groundwater levels indicate declines in dominant riparian vegetation guilds within both study regions, but not all study reaches. A water table decline of greater than 0.50 m is predicted to decrease tall trees, short trees, and flood tolerant shrubs in Arizona while in Colorado, Uravan and Bedrock were the only reaches modeled to experience a decrease in flood tolerant shrubs. Overall, riparian guilds with narrower groundwater ranges were predicted to decrease the most and the magnitude of change was higher in response to lowered groundwater levels compared to altered flood regimes. All study reaches along the Verde River and the Uravan study reach on the San Miguel were predicted to experience expansions of the generalist shrub guild in response to altered hydrologic condition. The following dissertation contributes to our understanding of plant distributions in riparian areas, hydrologic thresholds, and hydrologic variability within and between rivers. We found that riparian vegetations may be more transferable within regions while plant-hydrologic relationships between regions may be dissimilar due to climate, valley morphology, groundwater sources, and flow regimes.

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## 1 Introduction

Riparian zones are identified as areas adjacent to flowing freshwater where flood processes and shallow groundwater levels create distinct plant communities. Environmental heterogeneity within these ecosystems leads to high plant diversity and complex physical structure that contribute vital services and functions such as nutrient and carbon cycling, water filtration, and habitat for wildlife (Naiman and Décamps 2005). Streamflow regimes vary greatly across river systems and are driven by climatic factors of precipitation and temperature, basin size, and topography. For example, 60-80% of precipitation becomes streamflow in the US Pacific Northwest while in the arid Southwest, only 10% of precipitation becomes streamflow due to high vapor pressure deficit, solar radiation, and evapotranspiration (Naiman et al. 2005a). Differences in streamflow across basins influence water availability and disturbance regimes that structure plant communities (Poff et al. 1997).

Patterns of streamflow and water availability are the most commonly studied environmental drivers of riparian plant assembly on large alluvial rivers (Merritt and Cooper 2000, Stella et al. 2013) since they play a major role in species dispersal, establishment, and abundance (Biggs et al. 2005, Gurnell et al. 2012). Hydrologic gradients of groundwater depth and flood frequency can create distinct zones between upland and riparian plant communities based on species abilities to reproduce and persist in response to these environmental stressors (Araya et al. 2011). Understanding current distributions of riparian plants along environmental gradients is essential for predicting future plant responses to changes in climate, flow, and other perturbations (Lozanovska et al. 2018). Alterations to riparian vegetation and its structure may have profound effects on ecosystem functions and services.

The damming of rivers for hydropower, water diversions for agriculture, groundwater pumping, and climate changes have resulted in lowered riparian plant diversity (Nilsson et al. 2000), loss of dominant species (Sabo et al. 2005), encroachment of upland species (Huxman et al. 2005), and overall degradation of ecosystem processes (Balvanera et al. 2006). Decreases in the magnitude of high flows can lead to changes in erosion and depositional processes resulting in channel narrowing (Grams and Schmidt 2002, Shafroth et al. 2002, Lind et al. 1996, Ligon et al. 1995) and stream incision that lowers alluvial groundwater levels (Schilling et al. 2004). Temporal shifts in flow regimes can decrease substrate heterogeneity and limit the recruitment and establishment of native woody plant riparian species (Rood et al. 2003). On regulated rivers, hydrologic changes can result in the expansions of upland species that are more tolerant of drought conditions and less reliant on alluvial groundwater (Marchetti and Moyle 2001, Cooper et al. 2006).

Predictions of water scarcity from a warmer and drier climate will exacerbate pressures on freshwater resources (Roo et al. 2016). Climate studies predict decreases in precipitation and substantial increases in air temperatures for southwestern and Rocky Mountain regions (Vicuna and Dracup 2007, Franco et al. 2011). Shifts in some winter precipitation from snow to rain could decrease spring snowmelt runoff and shift peak flows to several weeks earlier than historical averages (Cayan et al. 2008, Young et al. 2009). Increased likelihood of rain on snow events may also increase the occurrence of destructive winter floods (Kattelman 1996) that inundate and disturb riparian plant communities. Riparian ecosystems are highly sensitive to climate changes (Poff et al. 2012), but few studies have modeled how whole plant communities could change along climatic gradients at large, regional scales (Pyne and Poff 2017).

Riparian vegetation structure, diversity, and composition strongly influence bird species distributions (MacArthur and MacArthur 1961, James 1971, Strong and Bock 1990). Rivers in the southwestern US support some of the most productive wildlife habitats (Folliott et al. 2004,

Kirkpatrick 2008) while occupying <2% of the total land area. Vegetation complexity increases microhabitat diversity which, in turn, provides food and cover for a wider range of birds (Whittaker et al. 2001, Hill et al. 2004). Diverse communities of neotropical migrants and resident bird species use river corridors for foraging and breeding (Donovan et al. 2002, Rich 2002). Foliage height diversity, the measure of canopy layering, can strongly influence the abundance of food resources, microclimate, and the risk of nest predation (Jones 2001). Simplification of vegetation structure and composition can reduce diverse habitat and contribute to a reduction in bird species richness (Merritt and Bateman 2012). Tree size, canopy and understory cover, woody debris, and foliage height diversity have been used to create indices to describe patterns in habitat and bird distributions (McElhinny et al. 2005, Merritt and Bateman 2012). Linking riparian vegetation to legally explicit beneficial uses like bird habitat could protect streamflow to aid in conservation efforts.

#### *Riparian Vegetation Guilds*

One of the goals of community ecology is to predict the properties of populations (Keddy 1992) and the assembly of communities from both biotic (competition) and abiotic (environment) attributes. Plants that inhabit river margins have evolved physiological, life history, and morphological traits to withstand flood disturbance, inundated soil conditions, and drought. Traits like seed mass, rooting depth, tissue density, specific leaf area, height, and water use efficiency influence the growth of species along hydrologic gradients in riparian zones. Species that can establish in areas of fluvial disturbance have rapid growth, small seed size, larger leaf area, floating seeds, low wood density, and the ability to resprout after flood damage or burial (Merritt et al. 2010, Stromberg and Merritt 2016). Species of *Salix* have developed traits to tolerate flooding including flexible stems, high density growth patterns, adventitious roots, and the ability to resprout (Lytle and Poff 2004). Combinations of these traits can represent a species habitat preference and tolerances to

hydrologic conditions (Aguiar et al. 2013, Lawson et al. 2015) and a non-random sorting of species based on their traits creates distinct community zonation along these gradients (Merritt et al. 2010).

The distribution of riparian vegetation has mainly been studied through the lens of individual species. Functional trait approaches and the use of vegetation guilds, groups of functionally equivalent species, may establish generalized frameworks to predict composition across commonly measured hydrologic gradients (McGill et al. 2012). Understanding spatial variations in species traits along local hydrologic gradients as well as between rivers with varied streamflow and climate can provide insight into changes in ecosystem processes and functions at both local and regional scales (Pyne and Poff 2017). The quantification of vegetation guild traits provides a link between community structure and aspects of ecosystem functioning, in contrast to studies of individual species that may not demonstrate a mechanistic connection between species and functioning. Degradation of ecosystem function can occur when species playing functional roles in ecosystems are lost due to environmental change (Diaz et al. 2013).

Riparian vegetation guilds have been described along rivers in Sweden, Portugal, Spain, Australia, and the United States (Merritt et al. 2010, Lawson et al. 2015, Hough-Snee et al. 2015, Stromberg and Merritt 2016, Aguilar et al. 2018). Clear relationships between water availability and trait composition have been reported along intermittent, ephemeral, and perennial streams in Arizona (Stromberg and Merritt 2016) where shorter species with low specific leaf area (SLA) are found in areas of water shortage. Riparian guild assemblages in the Missouri and Columbia River basins were driven by abiotic and biotic drivers including reach elevation, sinuosity, stream gradient, forest cover, annual precipitation, as well as the occurrence of other guilds (Hough-Snee et al. 2015). Although several studies have described riparian guild distributions as a function of hydrologic and landscape condition, few have investigated the relationship between hydrologic condition, vegetation guilds and their traits, and specific ecosystem functions and services. Furthermore, the similarity of

relationships between vegetation guilds, hydrologic condition, and habitat provisioning have yet to be tested among rivers with varied environmental attributes.

### *Motivation*

Heightened demand for water resources will force land managers to address how increased water development and climate change will alter flow regimes, riparian vegetation, and habitat for sensitive bird species. Many of the proposed water projects occur on federal lands and managers will struggle to balance the economic, social, and environmental impacts of this development. Studies to assess the ecological water needs of riparian vegetation are often time consuming and costly and pressure for water development will push timelines for decision making that federal agencies cannot meet leaving riparian ecosystems without protections.

Ecological changes are commonly assessed using species distribution modeling along environmental gradients. In the last decade, efforts by riparian ecologists and hydrologists have provided regional frameworks to assess the range of ecological consequences from flow modification using species response curves (Poff et al. 2010). Ecological response curves may allow water managers to define flow standards across a wide range of rivers to conserve riparian vegetation and ecosystem functioning (Arthington et al. 2006). The transferability of this framework has been studied within regions across a range of flow metrics and biotic responses (Buchanan et al. 2013, McManamay et al. 2013). I explore the use of vegetation guilds to create meaningful ecological response curves within and between regions and assess if riparian plants are distributed similarly along hydrologic gradients.

I choose to work along three rivers within the Colorado River basin as the largest decreases in streamflow due to climate change are predicted within this watershed (Das et al. 2011). Water from the Colorado River is utilized for over 30 million people across seven western US states and Mexico and 70% of the water is used to irrigate croplands (Zielinski 2010). Water in the Colorado

River basin is over-allotted due to inaccurate predictions from an anomalous wet period in the historic record impacting users in seven basin states (Colorado, Wyoming, Utah, New Mexico, Arizona, Nevada, and California). Reductions in snowpack at elevations below 2500 m have been detected between 1978 and 2004, and the timing of spring runoff has shifted to occur two weeks earlier (Ray et al. 2008). Future changes in temperature and precipitation suggest an overall decline in runoff and a 20% decrease in annual Colorado River streamflows (Udall and Overpeck 2017). Reductions in the quantity and timing of surface water supplies will increase the pressure on groundwater resources that support river flows during dry summer months through baseflow (Webb and Leake 2006). In many Southwestern rivers, perennial flow has already significantly declined and may experience further de-watering if groundwater supplies continue to be depleted at current or elevated rates (Marshall et al. 2010).

## *Chapter 2: Using vegetation guilds to predict bird habitat characteristics in riparian areas*

In arid and semi-arid regions, riparian plants provide disproportionately important wildlife habitat compared to uplands and the percent of the landscape they occupy (Folliott et al. 2004). Diverse neotropical, migrant, and resident bird species use river corridors for a range of nesting, foraging, and breeding life stages (Donovan et al. 2002) with many species preferring native trees and shrubs. The study of bird diversity and abundance has commonly been connected to individual tree species, like *Populus* (cottonwood) and *Salix* (willow), but the use of vegetation guilds can link functional traits of species to the provisioning of preferred habitat for birds in riparian areas. In the first chapter I construct a bird habitat index using vegetation structure and environmental attributes at my three study reaches along the Verde River to test if heterogeneous vegetation predicts bird abundance and diversity. I delineate woody and herbaceous vegetation guilds using seven functional traits to define ranges of adaptive strategies to flood disturbance and water availability along the

Verde River in Arizona. Using defined vegetation guilds, I test whether vegetation guilds with distinct functional traits predict high quality bird habitat defined by the vegetation index.

*Chapter 3: Distribution of riparian vegetation guilds across gradients of groundwater and fluvial disturbance on a river in a semi-arid landscape*

In the third chapter I measure the connectivity of surface and subsurface water, growing season groundwater depths and diurnal fluctuations, and flood exceedance probability on geomorphic surfaces along the Verde River in Arizona. The Verde River is federally designated as Wild and Scenic and flow recommendations are necessary to maintain ecological values including riparian vegetation and wildlife populations. Using defined vegetation guilds from chapter 2, I model their distribution as a function of floodplain groundwater depth and flood exceedance probability. Using guild distribution models, I aim to quantify hydrologic thresholds where plant species are more likely to establish and persist. Hydrologic thresholds are important in determining these recommendations as water development in the upper watershed threaten to reduce summer baseflows, floodplain groundwater depths, and alter the presence and cover of riparian guilds that provide high quality bird habitat. Using groundwater and flood exceedance probability maps, I simulate changes in these conditions to assess how riparian communities might respond to altered flows.

*Chapter 4: Modeling riparian vegetation guild response to hydrologic change along rivers in the Colorado River basin*

Processes behind riparian plant assembly have mostly been described for larger alluvial rivers, where hydrogeomorphic processes of overbank flooding, scour, and deposition filter plant species (Katz et al. 2009, Merritt and Cooper 2000, Stella et al. 2013). Generalizations of plant response may be especially difficult between river systems where plant distributions are governed by large-scale watershed factors such as climate, geology, flow regime as well as reach-scale factors such as channel morphology, flood disturbance frequency, sediment size and hydraulic conductivity, and

groundwater-surface water dynamics. Environmental processes structuring riparian plant communities of low-order, high elevation streams have been described less frequently. Although riparian plant species have evolved similar functional traits to persist and reproduce in riparian environments we question if vegetation guild distributions can be predicted by depth to groundwater and flood exceedance probability among rivers of differing flow regimes, climate, and elevation. In the final chapter, I define vegetation guilds along the San Miguel and Dolores Rivers in Colorado and compare trait composition and guild membership to guilds described along the Verde River. I explore how vegetation guilds in each region are distributed along hydrologic gradients and discuss how differences in groundwater dynamics and climate effect relationships and the transferability of ecological responses. Finally, I simulate lowered groundwater levels and reduced flood frequencies and model the expansion and contraction of vegetation guilds to assess the magnitude of change for woody riparian guilds.

#### *Format and Contributions*

This dissertation is written in a manuscript style with Chapter 2 published in Wetlands and Chapters 3 and 4 slated for future publication. I conducted the vegetation surveys, collected and analyzed groundwater and streamflow data, and constructed 1D hydraulic models for each of my study reaches. For the second chapter, I collaborated with Dr. Heather Bateman to develop a bird habitat index and Kristan Godbeer conducted bird surveys. I worked with Dr. David Merritt and Dr. Chris Holmquist Johnson to conduct topographic surveys of Verde River study reaches and Dr. Chris Holmquist Johnson performed 2D hydraulic models for Chapter 3. Dr. David Merritt, Dr. Heather Bateman, Dr. Chris Holmquist Johnson, and Dr. David Cooper contributed to experimental design, methodology, synthesis, and editing.

## 2 Using vegetation guilds to predict bird habitat characteristics in riparian areas

### 2.1 Introduction

Water development projects and climate changes are altering river flows throughout the world, resulting in shifts of riparian vegetation. These changes are most significant in arid regions where water is scarce (Palmer et al. 2009; Döll et al. 2009). Riparian areas typically support the only deciduous forests in these regions providing critical wildlife habitat and landscape-scale connectivity (Selwood et al. 2017). Shallow water tables and frequent floods in riparian areas support greater vegetation biomass than adjacent uplands, and riparian forest canopies can moderate extreme daytime temperatures and relative humidity (Naumburg et al. 2005). Riparian ecosystems enhance local and regional species richness and provide refugia from the surrounding desert heat for birds, mammals, amphibians, and insects (Selwood et al. 2015; Ramey and Richardson 2017, Bateman and Merritt 2020). These ecosystems will become increasingly important as temperatures rise, droughts increase in intensity and duration, and such oases become scarcer (Sabo et al. 2005; Capon et al. 2013; Selwood et al. 2017).

Gradients of water availability and flood disturbance control the distribution and abundance of riparian plant species, influencing habitat quality for wildlife (Lite and Stromberg 2005; Merritt and Bateman 2012). Fluvial disturbance and associated scouring and deposition of sediment create and support heterogenous vegetation structure and composition (MacArthur 1964; McElhinny et al. 2005; Kissling et al. 2008). Reductions in flood frequencies and increased depth to groundwater can lead to stress on riparian trees, mortality, and subsequent forest collapse with the homogenization of riparian vegetation, encroachment of upland species, and terrestrialization within the riparian zone (Merritt and Cooper 2000; Cooper et al. 2003, Williams and Cooper 2005; Horner et al. 2009). Groundwater depletion decreased the proportion of obligate riparian trees (*Populus fremontii* and *Salix*

*gooddingii*) and increased non-native woody species (*Tamarix* spp.) with a subsequent decline in canopy-nesting birds including Arizona Bell's Vireo (*Vireo bellii* ssp. *arizonae*) and Abert's Towhee (*Melospiza aberti*) on the San Pedro River in Arizona (Brand et al. 2011). Changes in stream flow may also promote the invasion of non-native plant species such as giant reed (*Arundo donax*) and saltcedar (*Tamarix* spp.) which have been attributed to declines in migratory and resident bird communities (Hunter et al. 1988; Postel and Richter 2003; Fleishman et al. 2003; van Riper et al. 2008). *Tamarix* stands have been shown to provide habitat for the federally listed (endangered) Southwestern Willow Flycatcher (*Empidonax traillii* spp. *extimus*) (Sogge et al. 2008) and are used by birds during fall migration (Walker 2008). Some have referred to *Tamarix* as a functional equivalent to native riparian species in the United States (Stromberg 1998), while others suggest that it does not support the same biotic communities as native riparian woodlands (Bateman and Ostoja 2012; Bateman et al. 2013).

Perennial stream flow that supports productive woody riparian vegetation creates vital breeding, nesting, and foraging habitat for resident and migratory birds (Bottorff 1974; Carothers et al. 1974; Brand et al. 2010). However, habitat selection can differ between breeding and stopover migratory birds (Moore et al. 1995) as well as between individual species (Hostetler and Holling 2000). At a local scale, habitat selection may be based on resource needs with breeding birds requiring safe nesting and foraging sites while stop-over migrants select habitat for food availability (Hutto 1985). Forest cover was positively correlated with arthropod abundance and predicted insectivorous migrant distributions near the Mississippi Coast (Buler et al. 2007). Loss of native vegetation and structure can negatively influence both breeding and migratory bird populations (Hennings and Edge 2003).

Since bird species are sensitive to riparian vegetation structure and composition, they are good indicators of ecological condition and many scientists and land managers use bird species diversity as measurable targets for ecosystem restoration and conservation (Fleishman et al. 2003;

Vaughan et al. 2007; van Riper et al. 2008). The relationship of bird abundance, richness, and diversity to habitat is typically assessed using individual plant species. Higher bird species diversity and richness was found at sites with complex vegetation structure on Cherry Creek in Arizona and variability in bird habitat was explained by individual deciduous trees including *Populus fremontii* and *Salix gooddingii* (Merritt and Bateman 2012).

Plant species composition has been used along rivers to describe habitat quality, but the use of functional groups may provide an approach that is transferable within and between river basins. Riparian plant species are distributed along gradients of water availability and disturbance due to traits that allow them to tolerate environmental stressors of seasonal flooding and limited water availability (Merritt et al. 2010). Groups of plant species with similar sets of traits that allow them to disperse, survive, and reproduce in response to specific stream flow and soil water conditions are termed flow response guilds (Merritt et al. 2010). The use of guilds can facilitate the development of a more generalizable framework to predict changes in riparian habitat in response to altered flow patterns and water availability.

Riparian flow response traits and guilds have been identified for many rivers in the western United States, Spain, Portugal, Sweden, and Australia where they are used to quantify the effects of hydrologic alteration, climate, and land use (Bejarano et al. 2012; Lawson et al. 2015; Stromberg and Merritt 2016; Diehl et al. 2017; Aguiar et al. 2018). Many plant traits have been used to construct riparian guilds, however, Laughlin (2014) proposed that no more than 8 traits including leaves, stems, roots, and flowers be used as a higher number of traits has not improved explanations of guild differences. Our approach is to select traits for differentiating species based on their tolerance of disturbance, drought, and inundation as well as their competitive ability in fluvial settings. Few studies of riparian ecosystems have examined how vegetation guild composition and guild richness affect vegetation structure and wildlife habitat. The range of traits within a guild can help

explain how similar plant species contribute to vegetation structure and complexity that can support more avian species compared to homogeneous vegetation (MacArthur 1964; Kissling et al. 2008). We investigated the relationship between riparian vegetation guilds, vegetation structure, and bird community metrics along a free-flowing segment of the Verde River, in Arizona. We relate the cover of riparian flow response guilds to the ecosystem function of bird habitat and address the following questions:

- (1) What are the defining traits of riparian vegetation flow response guilds on the Verde River?
- (2) To what degree can vegetation structure and environmental attributes be used to characterize bird habitat to adequately predict land bird abundance, richness, and diversity?
- (3) What are the individual and combined influences of vegetation guilds on bird habitat?

## **2.2 Methods**

### *Study Area*

The Verde River in Arizona is one of the largest mostly free-flowing perennial rivers in the Colorado River basin. It originates at Sullivan Lake (a reservoir) in the Chino Valley at 1295 m elevation and continues southeast for 306 km before terminating at its confluence with the Salt River near Phoenix, Arizona (Brown 1982). The region is characterized by low annual rainfall, very high summer temperatures, periodic winter precipitation, a spring drought, late summer monsoon driven precipitation, and a fall drought (Ffolliott and Davis 2008). Winter storms arrive from the Pacific Ocean; whereas, summer monsoons originate in the Gulf of California and Mexico.

The Verde River supports some of the most extensive riparian gallery forests (*Salix gooddingii*, *Populus fremontii*, *Platanus wrightii*) in Arizona as well as mesquite (*Prosopis* spp.) and desert willow (*Chilopsis linearis*) shrublands. The riparian corridor provides habitat for more than 50 threatened, endangered, sensitive, and special status animal species and over 60 percent of the regional vertebrate species. Sixty-five km of the Verde River is federally designated as Wild and Scenic.

Upstream demands for water to support agriculture and urban development have altered summer river baseflows and analytical models predict future flow decreases of 0.11 to 0.14 cubic meters per second (cms) from 2005 to 2110 due to human water extraction (Garner et al. 2013). Increased water use in the basin for agriculture and urban development could be detrimental to riparian forests and invertebrate, bird, reptile, amphibian, and mammal species that rely on the Verde River.

We worked along three reaches on land managed by the U.S. Forest Service (Figure 2.1): Beasley Flat (425500E, 3815635N), Childs (435625E, 3801102N), and Sheep Bridge (434697E, 3771403N; UTM (SI) coordinates, zone 12N, WGS 84, NAVD88 vertical datum). All study reaches are downstream from the town of Camp Verde.

### *Vegetation Sampling*

We sampled vegetation in 100 m<sup>2</sup> plots (10 x 10 or 5 x 20 m in size) placed systematically along transects oriented perpendicular to the river. Within each plot we visually estimated total percent canopy cover of each vascular plant species as well as cover in four height classes (0-1.5, 1.6-4.0, 4.1-9.0, and > 9.0 m) using Braun-Blanquet cover classes (Braun-Blanquet 1965). We sampled 112 plots across the three river reaches (Beasley n = 37, Childs n = 37, Sheep Bridge n = 38). To quantify vegetation structure related to avian habitat we measured percent canopy cover using a spherical densiometer, basal area of woody plants, and quadratic mean diameter, and foliage height diversity (Shannon Diversity Index) (Curtis and Marshall 2000). Foliage height diversity (Shannon Diversity Index) and mean vegetation canopy cover were measured in four height classes (0-1.5, 1.6-4.0, 4.1-9.0, and > 9 m) as described by Carothers (1974). Percent cover of litter, downed wood, gravel, sand/silt, bedrock, and bryophytes was visually estimated and recorded. Plants were identified to species using Kearney & Peebles (1960) and nomenclature was updated using ITIS (2019). A common tall grass species that occurs along the Verde River was never found flowering.

Based on herbarium collections from the Verde River we identify this species as *Phragmites australis* but acknowledge that *Arundo donax* has also been found and may be present in our study sites.

We interpolated depth to groundwater for vegetation plots using a grid of groundwater monitoring wells (Beasley Flat n = 11, Childs n = 8, Sheep Bridge n = 8) and used groundwater depth on July 1<sup>st</sup>, 2018 to represent water availability during low flow conditions. Average depth to groundwater and standard error of the mean was calculated for plots that had greater than 10% vegetation guild cover.

#### *Bird Habitat Index*

To characterize bird habitat, we used ecologically relevant vegetation structure and environment variables to create a bird habitat index. We produced a principal component analysis (PCA) and selected variables with high factor weighting. Orthogonal variables were ranked by the product of their eigenvectors and the percent of variation explained by the principle component axes. We added values for each variable from all the PCA axes to determine final rank and selected a subset of variables that had the most explanatory power to reduce redundancy and collinearity. A habitat index was created for each plot by standardizing each retained variable and summing them. The summed plot value was normalized to obtain the final measure of the habitat index ranging from 0 to 1 for each sampled plot (Figure 2.2). Final variables describe habitat complexity across our vegetation and avian plots (Table 2.1).

#### *Vegetation Flow Response Guilds*

Commonly used traits in plant functional analysis studies include height, specific leaf area (SLA), and seed mass (Verheijen et al. 2016). Height is of global relevance and highlights the trade-off between access to light and the energetic cost of woody stems (Falster and Westoby 2003). SLA differentiates competitive and stress tolerant species (Westoby 1998) and highlights a trade-off between the rapid or slow return on investment (leaf economic spectrum, *sensu* Wright et al. 2004).

Leaves with short life spans have higher nutrient concentrations, higher rates of gas exchange, are thinner and less dense, and the plants can withstand longer periods of root submergence (Reich et al. 1997; Mommer et al. 2006). Leaves with greater longevity are smaller, thicker, more drought tolerant and conserve resources through time (Ackerly 2004). Seed mass reflects a trade-off between longevity, dispersal ability, and fecundity. Species that produce smaller seeds have low maternal investment, but typically produce high numbers of seeds that may readily germinate on disturbed, moist surfaces. In riparian ecosystems, average seed mass in plants across the floodplain increases from the active channel to the upland with larger seeds being able to remain dormant and survive conditions unsuitable for germination and survival (Stromberg and Boudell 2013).

Additional traits that increase plant resilience to environmental stressors across floodplains include the ability to re-sprout after disturbance, tissue density, deep rooting depth, and leaf  $^{13}\text{C}:^{12}\text{C}$  ratio, an indicator of water use efficiency. High tissue density confers resistance to drought and water loss and species with high tissue density are more likely to resist cavitation and grow taller (Hacke et al. 2001). Rooting depth influences how plants access water resources and many riparian trees in arid regions have deep-roots to access alluvial groundwater during summer months when rainfall is minimal and stream flow is at its lowest (Stromberg 2013). Root traits have been underutilized as a flow response trait due to limited information on root architecture and rooting depth (but refer to Stromberg 2013), however it is important for water and nutrient acquisition strategies and response to disturbance. Leaf uptake of  $\text{CO}_2$  results in water vapor loss and plants must balance C assimilation for growth and reproductive success with desiccation and xylem cavitation. Plants differ in their water-use efficiency and  $\text{CO}_2$  gained vs. water lost through transpiration. This can be measured using leaf  $^{13}\text{C}:^{12}\text{C}$  ratio (O'Leary 1988). During photosynthesis plants discriminate against the heavier stable isotope  $^{13}\text{C}$ , but when stomata are closed, the fraction of

leaf  $^{12}\text{C}$  decreases and becomes more enriched in  $^{13}\text{C}$  (Farquhar et al. 1989; Perez-Harguindeguy et al. 2016).

Plant trait values for specific leaf area, tissue density, diameter at breast height (DBH), height, and  $^{13}\text{C}:^{12}\text{C}$ , a proxy for water use efficiency were collected at our three study reaches on individuals that represented local growing conditions. Three individuals of each species were sampled, and trait values averaged across study reaches and species. For herbaceous and graminoid species, we used life cycle (annual vs. perennial) instead of growth form and excluded tissue density and DBH. Plant growth form, life cycle, and re-sprout capability were obtained from the USDA plants database (2019) and maximum potential rooting depth was determined from the literature. Seed mass (grams per 1000 seeds) was obtained from Kew Gardens Seed Information Database (Royal Botanic Gardens Kew 2019).

Using a hierarchical cluster analysis and traits for each plant species as the input data, species were grouped using a Gower dissimilarity matrix. This matrix can incorporate combinations of categorical, ordinal, and numerical data (Legendre and Legendre 1998). Groups were determined by assessing natural breaks in the hierarchical cluster analyses and non-metric multidimensional scaling (NMDS) ordinations of species in multivariate space. Correlated traits were removed from the final matrix to group species. To comply with assumptions of statistical tests we log transformed seed mass, tissue density, and height.

Average trait values for each guild were normalized and scaled separately for woody and herbaceous flow response guilds. To determine inundation tolerance, we summed scaled values for root depth (woody only), tissue density (woody only), and  $^{13}\text{C}:^{12}\text{C}$ . To assess a guilds' tolerance to disturbance we summed average trait values for re-sprout capability and SLA. For guild competitive ability we summed average trait values for seed mass and height. The final calculations were scaled across all guilds to determine if they place low or high (0-1) on inundation disturbance tolerance and

competitive ability. The scaled sums were reclassified into three ordinal groups of low (0-0.33), medium, (0.33-0.66), and high (0.66-1.0). To build the trait guild name we used the reclassified levels to assign names for inundation tolerance (prone, inter, tolerant), fluvial disturbance tolerance (prone, inter, tolerant), and competitive ability (inferior, subdominant, and dominant). Growth form was included in the final name. For instance, a tree guild with high (0.66-1) inundation tolerance, disturbance tolerance, and competitive ability was named “hydro-tolerant-dominant tree.” We gave each guild a trait short name which is used in the text.

### *Avian Community Measurements*

Bird occurrence and abundance were sampled in 6 to 8 plots at each reach that span the range of computed habitat index values. Bird sample plots were stratified across habitat scores of high, medium, and low. Bird count plots were separated by at least 60 meters to avoid overlap and inclusion of other vegetation types similar to Bibby et al. (1985). To validate the vegetation habitat index, bird surveys were conducted in May 2018 in 24 plots spanning the range of habitat index values. Surveys used a 20-m fixed radius point centered in the middle of each vegetation plot to calculate abundance and richness of bird species. Standard procedures suggest using a 25-m radius (Hutto et al. 1986); however, we used a smaller radius to increase detecting all birds in a smaller area and avoid the risk of counting birds associated with adjoining vegetation as the riparian zone was narrow at some of our study reaches (methods similar to Merritt and Bateman 2012). Surveys were conducted two consecutive mornings at each plot. Bird counts began within 30 minutes of dawn and one observer counted birds seen and heard for 10 minutes at each plot. We calculated per-point bird abundance, diversity (Shannon diversity Index), and richness for each plot. Three plots were removed from the final analysis due to river noise that reduced the detection of bird species within the 20 m radius.

### *Statistical Analysis*

To calculate the percent cover of flow response guilds in each plot, each species was assigned the mid-point of a Braun-Blanquet cover class. We then summed the species cover within a plot to obtain cover for each guild. We did not use relative cover as we wanted to characterize the complexity of coverage that exists in riparian forests. For example, *Salix gooddingii* may have 100% cover in the canopy and other species may occupy the understory or mid-canopy. We also calculated the presence and absence of flow response guilds in each plot to determine guild richness.

The relationships between avian community measurements, habitat indices, vegetation structure, and guild cover and richness were identified using general linear regressions. To compare highly ranked structure variables describing habitat quality between vegetation guilds we assigned plots a woody guild based on dominant guild cover and used non-parametric Kruskal-Wallis rank-sum tests with Bonferroni adjustments for multiple hypothesis tests. Analyses were performed in R 3.5.2 (R Core Team 2018). To analyze the relationship between guild cover and habitat index we used a best subsets model in the MuMin package to find the best fit from all possible models using AICc criteria (Barton 2018). Hierarchical cluster analysis was performed using the flexible beta method. In addition to identifying guilds using a cluster analysis, we confirmed our groups of species by plotting them in multidimensional space (NMDS).

Permutational multivariate analysis of variance (PERMANOVA) was used to test for multivariate differences between guilds by examining P values assessed using Monte Carlo (MC) tests due to the low number of unique permutations for many of the group comparisons using PRIMER-E version 7 (Clark and Gorley 2015). To identify differences between guilds we calculated mean trait values for each group to visualize in radial plots. Random forest, a non-parametric classification technique, was used to identify which traits had high rank in determining the flow response guilds. Multiple decision trees generated from bootstrapped samples from the original data

(Breiman 2001) were compiled to assess how losses of vegetation guilds would relate to high ranked variables used in the creation of the bird habitat index.

## 2.3 Results

### *Vegetation Flow Response Guilds*

We identified five woody and seven herbaceous riparian vegetation flow response guilds (Table 2.2) using dendrograms created from cluster analysis (Figure 2.3) and NMDS ordinations (Appendix Figure 1). On the woody species dendrogram we initially choose the dissimilarity of 0.4 to separate guilds (Figure 2.3), but merged *Brickellia floribunda* and *Gutierrezia sarothrae* with the generalist shrub guild as there was no statistically significant difference in trait composition between the two groups (PERMANOVA  $P > 0.05$ ). The final five woody guilds had significantly different trait compositions (PERMANOVA  $P < 0.001$ ) of maximum rooting depth, growth form, re-sprout capability, tissue density, specific leaf area (SLA), seed mass, and  $^{13}\text{C}$ : $^{12}\text{C}$ . We removed diameter at breast height (DBH) from the final trait matrix as it was highly correlated with height (Spearman correlation  $R = 0.97$ ,  $p < 0.001$ ). Based on our random forest model, traits with the highest importance in delineating woody flow response guilds were height, maximum rooting depth, tissue density, and re-sprout capability. Species within the tall tree and flood tolerant shrub guilds are riparian pioneers with small seeds and the ability to re-sprout following disturbance once established, but differ in growth form, height, and specific leaf area (Figure 2.4). The two species in the short tree guild (*Fraxinus velutina* and *Morus alba*) have lower tolerance to disturbance lacking the ability to re-sprout but are good competitors with dense wood. The drought tolerant shrub guild includes four species that are inundation intolerant, disturbance tolerant, with deep roots, high water use efficiency, large and heavy seeds indicating strong competitive ability, dense wood, and the ability to re-sprout (Table 2.2, Figure 2.4). The generalist shrubs guild contains seven species that are

disturbance intolerant, have medium tolerance to inundation with low competitive ability and are distinguished by dense wood and high water use efficiency (Figure 2.4).

Herbaceous species formed seven guilds using re-sprout capability, annual/perennial growth form, SLA, height, seed mass, and  $^{13}\text{C}:^{12}\text{C}$  (Table 2.2, Figure 2.3). The most important traits in identifying groups were seed mass, annual/perennial growth, water use efficiency (leaf  $^{13}\text{C}:^{12}\text{C}$ ), and SLA. Height was not highly ranked. Large seeded herbs and high specific leaf area (SLA) herbs were not statistically different (PERMANOVA  $P > 0.05$ ), but we choose to keep them separate based on the dendrogram (Figure 2.3) with a natural break at height 0.25 and plotted distance on the NMDS (Appendix Figure 1). All other herbaceous guilds had significantly different trait composition. Short wetland herbs included species with small seeds, low SLA, low water use efficiency while tall wetland herbs had low water use efficiency, small seeds and SLA, and lacked the ability to re-sprout (Figure 2.5). The ruderal perennial herb guild includes short species with small seeds and medium SLA while ruderal annual herbs includes short annuals with medium SLA, small seeds, and low water use efficiency. Drought tolerant herbs are short annuals with high water use efficiency and small seeds indicating they are disturbance intolerant, tolerant of mid-level inundation, and are poor competitors. Large seeded herbs and high SLA herbs can both re-sprout and have low water use efficiency with member species of large seeded herbs tending to be annuals indicating disturbance intolerance. Traits of large SLA herbs indicate tolerance to disturbance and inundation (Figure 2.5).

#### *Bird Habitat Index and Bird Communities*

A total of 225 birds, representing 45 species were recorded in our study plots (Table 2.3). Neotropical migrant warblers were the most common species observed, with Yellow Warbler (*Setophaga petechia*), Wilson's Warbler (*Cardellina pusilla*), Lucy's Warbler (*Oreothlypis luciae*), and Common Yellowthroat (*Geothlypis trichas*) being most abundant. Several bird species were associated

with mesquite woodlands, including Bell's Vireo (*Vireo bellii*), Ash-throated Flycatcher (*Myiarchus cinerascens*), and the Dusky Flycatcher/Hammond's Flycatcher (*Empidonax oberholseri*/*E. hammondi*). A significant positive relationship existed between bird habitat and bird diversity ( $R^2 = 0.30$ ,  $P = 0.006$ ), richness ( $R^2 = 0.27$ ,  $P = 0.009$ ), and abundance ( $R^2 = 0.22$ ,  $P = 0.019$ , Figure 2.6). There were no significant differences in bird metrics or habitat indices among the three river reaches. The plot with the highest bird abundance had 17 individuals of 7 species and the vegetation was dominated by *Prosopis velutina* with an understory of the non-native grasses *Bromus diandrus* and *Bromus rubens* with high litter cover. The highest avian richness occurred in a plot at Beasley Flat with 12 species and the vegetation had 65% canopy cover of trees and shrubs dominated by *Salix gooddingii* and *S. exigua* with mixed ground cover of litter and gravel. This plot was characterized by a mixed understory consisting of the non-native grass, *Sorghum halepense* and the native bulrush, *Schoenoplectus americanus*. The lowest avian abundance and richness occurred in plots at Childs and Sheep Bridge that had no canopy cover.

Vegetation structure and environmental variables that were highly ranked in their contribution to bird habitat heterogeneity included canopy cover, species richness, average cover in height class 2 (1.6-4.0 m), average cover in the top height classes (4-9 m and > 9 m), percent graminoid, percent tree, foliage height diversity, and woody basal area ( $\text{cm}^2/\text{plot}$ ). The variables percent groundcover of wood, litter, sand/silt, and bedrock, quadratic mean diameter of woody species, distance from the river, percent cover of forbs, and foliage hits throughout the forest canopy were removed to create the final bird habitat index that accounted for 74.0 % of the structural and environmental variation in plots (Table 2.1). Variables with lower explanatory power were percent gravel, average cover in height class 1 (ground to 1.6 m), and percent cover of shrubs. Values for the habitat structure index ranged from 0 to 1 with the highest value at Sheep Bridge in a plot with 98% canopy cover, 98% tree cover, 18 plant species, high vegetation cover in all vertical

height classes, high tree basal area, high groundcover of litter and wood, and low cover of shrubs and graminoids. The plot with the lowest habitat index value had 0.16% canopy cover, low overall vegetation cover, high cover of bare gravel, and was located at Sheep Bridge. Overall, plots of low, medium, and high vegetation structure indices had measurably different vegetation structure and environmental components (Figure 2.2).

### *Vegetation Guilds and Bird Habitat*

The percent cover of seven vegetation flow response guilds were positively related to bird habitat and the relationship between habitat index and cover was strong ( $R^2 = 0.72$ ,  $P < 0.001$ ). Bird habitat indices were higher in plots with increased cover of the tall tree guild dominated by *Populus fremontii* and *Salix gooddingii* ( $P < 0.001$ , Figure 2.7), short trees including *Fraxinus velutina* and *Morus alba* ( $P = 0.023$ ), flood tolerant shrubs including *Salix exigua* and *Baccharis salicifolia* ( $P < 0.001$ ), and drought tolerant shrubs including *Celtis reticulata*, *Prosopis velutina*, *Chilopsis linearis*, and *Tamarix ramosissima* ( $P < 0.001$ ). For herbaceous guilds, tall and short wetland herbs as well as ruderal perennial herbs were positively related to bird habitat ( $P < 0.001$ , Appendix Figure 2). The relationship between habitat heterogeneity and tall trees was different depending on the cover of ruderal perennial herbs ( $P = 0.025$ ). In plots with low cover of tall trees the relationship between ruderal perennial herb cover and habitat index is stronger than in plots with high cover of tall trees. Plot functional guild richness, the number of guilds in each plot, was positively related to habitat index ( $R^2 = 0.03$ ,  $P = 0.04$ ).

In plots where tall tree cover was dominant, canopy cover, cover in height class 3 and 4 (4.0 to  $> 9.0$  m), basal area, percent cover of trees, and foliage height diversity were higher than in plots dominated by drought tolerant and generalist shrubs (Figure 2.8,  $P < 0.001$ ). Percent graminoid was significantly higher in plots dominated by drought tolerant shrubs compared to tall trees ( $P = 0.003$ ) and flood tolerant shrubs ( $P = 0.01$ ). Percent canopy cover, foliage height diversity, basal area, and

cover in height class 2 (1.6-4.0 m) was lower in plots where generalist shrubs dominated compared to drought tolerant shrubs ( $P < 0.05$ , Figure 2.8). In plots with greater than 10% guild cover, average depth to groundwater during low flow (July 1<sup>st</sup>) was -1.31 m ( $\pm 0.09$ ) for the tall tree guild, -1.19 m ( $\pm 0.10$ ) for the short tree guild, -1.08 m ( $\pm 0.13$ ) for flood tolerant shrubs, and -3.24 m ( $\pm 0.28$ ) for drought tolerant shrubs. For short wetland herbs average depth to groundwater during low flow was -1.60 m ( $\pm 0.25$ ), -1.06 m ( $\pm 0.11$ ) for tall wetland herbs, and -3.36 m ( $\pm 0.42$ ) for ruderal herbs.

## 2.4 Discussion

Woody and herbaceous flow response guilds can be defined along the Verde River using a suite of plant traits including seed mass, height, water use efficiency, specific leaf area, and tissue density. Bird habitat is positively related to the abundance of four woody and three herbaceous guilds and plots with high guild richness. The strongest predictor of bird habitat is the tall tree guild (dominated by *Populus fremontii* and *Salix gooddingii*) followed by drought tolerant shrubs (dominated by *Prosopis velutina* and *Chilopsis linearis*) highlighting the need to conserve vegetation communities with contrasting structure. We validate a bird habitat index created from vegetation structure, composition, and environmental variables where heterogeneous vegetation habitat supports higher bird abundance, richness, and diversity. As future climate change and anthropogenic water extraction threatens to alter stream flow, the fate of riparian vegetation will determine whether bird species that historically have been residents or migrants can continue to use these floodplain habitats. Our modeling of habitat quality using flow response guilds can be generalized within regions where plant species may differ and will be useful to assess temporal changes in environmental conditions (Lytle et al. 2017).

### *Vegetation Flow Response Guilds*

Height, maximum rooting depth, tissue density, and re-sprout capability are the most important traits distinguishing woody guilds at our study reaches. This is consistent with research on

low-order streams in the interior Columbia and upper Missouri River basins where rooting depth, canopy height, and the potential to re-sprout were delineating traits for guilds (Hough-Snee et al. 2015). Eleven woody riparian guilds were identified along rivers elsewhere in Arizona compared with our five woody and seven herbaceous guilds (Stromberg and Merritt 2016). We used several traits distinct from those chosen by Stromberg and Merritt (2016) such as re-sprout capability,  $^{13}\text{C}:^{12}\text{C}$  ratio, growth form, and SLA that reflect species strategies to withstand flood inundation, drought, disturbance, and competition. Our drought tolerant shrub guild was dominated by *Chilopsis linearis*, *Celtis reticulata*, *Tamarix ramosissima*, and *Prosopis velutina* while Stromberg and Merritt (2016) placed these species into four different guilds. High variation in reported maximum rooting depth exists for species in our drought tolerant shrub guild, with *Prosopis velutina* roots up to 14 m deep (Stromberg 2013), *Chilopsis linearis* to 1.6 m (DePree and Ludwig 1978), *Tamarix ramosissima* to 8 m, and *Celtis reticulata* to 5 m (Stromberg 2013).

Differences in guild composition between studies may be attributed to the choice of hierarchical clustering methods, tests of significance, and trait selection. For instance, we included *Acer negundo* in the tall tree guild with *Salix gooddingii* and *Populus fremontii* due to similar tissue density, ability to re-sprout, and height, despite it having heavier seeds. Stromberg and Merritt (2016) grouped *Acer negundo* with *Fraxinus velutina* due to its high seed mass, small leaf area, and low average height, compared to *Salix gooddingii* and *Populus fremontii*. We grouped *Fraxinus velutina* with *Morus albus*, another species with heavy seeds in the short tree guild. *Acer negundo* was included in a guild with *Populus fremontii* on the Yampa River in Colorado using morphological plant traits such as height, root depth, and stem rigidity (Diehl et al. 2017).

Height was not an important discriminator of herbaceous guilds as there was low variability between species. Among other things, height determines a species' ability to compete for light (Falster and Westoby 2003), which may be important in forest understories. However, variation in

seed mass and annual or perennial life history may be more important traits for structuring herbaceous guilds on dryland rivers. In Central European grasslands, seed mass and propagule pressure predicted plant establishment success, but traits related to competition became more important after three years of growth (Kempel et al. 2013). Herbaceous plants should be included in future studies as they are more diverse than woody species in dryland regions, respond on shorter timescales, and are more sensitive to soil moisture, flood disturbance, and grazing pressure (Stromberg and Boudell 2013; Stromberg and Merritt 2016). Furthermore, we only sampled traits from mature species but suggest that future studies examine traits for juveniles and adults to evaluate trait variation across a species' life cycle.

#### *Bird Habitat Index Predicts Bird Communities*

Complex vegetation structure provides a range of food and nesting sites that facilitate resource partitioning and niche differentiation, increasing functional diversity within an ecosystem contributing to high bird diversity (Palmer and Bennett 2006; Kirkpatrick et al. 2009; Harrison et al. 2010). Although our study focused on bird use of habitat in May and our methods may have overlooked breeding birds arriving later in the season, we were able to validate a bird habitat index and relate it to measures of riparian vegetation. Similar to Cherry Creek, a small perennial stream in Arizona, our index relates high-quality habitat to tree-dominated vegetation supported by shallow alluvial groundwater and frequent flood disturbance (Merritt and Bateman 2012). The bird habitat index on Cherry Creek was positively related to native tree cover and diverse canopy layering but had no relation to nonnative tree and shrub cover. We also found canopy cover and measures of vegetation height diversity and size to be the strongest structural components describing variation in bird habitat along the Verde River. Birds chose complex vegetation structure along the Trinity River in California where their abundance could be predicted by canopy cover, height, understory shrub layers, and tree species richness (Rockwell and Stephens 2018). Vertical foliage height diversity was

more important in predicting bird abundance and diversity than horizontal structure in Yellowstone National Park (Baril et al. 2011). Both canopy height and heterogeneity are structure variables that describe niche differentiation allowing varied bird species to use different parts of the forest canopy (Seavy et al. 2009).

#### *Vegetation Flow Response Guilds and Bird Habitat*

Bird habitat was positively related to the cover of dominant tree, shrub, and herbaceous guilds with the tall tree guild having the strongest relationship with bird habitat complexity (Carothers et al. 1974; Strong and Bock 1990; Powell and Steidl 2002; Smith and Finch 2016).

*Populus fremontii* provided habitat for nine canopy nesting bird species, nine cavity dwelling bird species, and 19 bird species that nested in shrubs and subshrubs on the Gila River (Smith and Finch 2014). *Salix gooddingii*, *Acer negundo*, and *Platanus wrightii* ranked 2<sup>nd</sup> through 4<sup>th</sup> of trees with the greatest number of nesting bird species (Smith and Finch 2014). Observed differences in the number of nests and bird species in riparian trees may be due to varied tree abundance between rivers, but they appear to provide similar habitat for nesting birds (Smith and Finch 2014).

Drought tolerant shrubs also had a strong positive relationship with bird habitat heterogeneity. *Prosopis velutina*, a common species along arid rivers, forms woodlands on upper floodplain surfaces and historically had native herb understories that were later modified by cattle grazing. Current understories in these woodlands are dominated by nonnative grasses including *Bromus rubens* and *Bromus diandrus*. Birds like Phainopepla (*Phainopepla nitens*) and Bell's Vireo (*Vireo bellii*) prefer *Prosopis* shrublands over gallery forests (Repking and Ohmart 1977). Migrating birds preferred these shrublands when mesquite was flowering due to elevated insect biomass along the Colorado River in Arizona (McGrath et al. 2009). An earlier study on the Verde River identified 19 species and 244 pairs of breeding birds in *Prosopis* shrubland on the Lower Verde River (Stamp 1978) highlighting its importance as habitat on the reach scale. *Prosopis* woodlands along southwestern

rivers provide an intermediate habitat for bird species and should be prioritized for conservation along with *Populus* spp. and *Salix* spp.-dominated forests.

We explored whether combinations of overstory and understory guilds predicted heterogenous bird habitat. Herbaceous guild A has a stronger relationship to bird habitat when the cover of tall trees (e.g., *Salix gooddingii*) was lower. Much of the riparian forest understory was dominated by the non-native grass, *Schedonorus arundinaceus* (guild A) suggesting that herbaceous understory is more important to bird habitat heterogeneity at low canopy cover.

#### *Loss of Vegetation Flow Response Guilds*

Woody traits including tall canopy cover, vegetation cover in 1.6 to 9 m height classes, diverse foliage heights, and woody basal area were positively related to habitat heterogeneity and bird abundance, richness, and diversity. Foliage height diversity has been shown to drive bird abundance and richness along other rivers (Baril et al. 2011; Rockwell and Stephens 2018) and canopy cover is an important variable for migratory birds (Buler et al. 2007). The loss of woody guilds with these structural attributes and traits include tall and short trees, flood tolerant shrubs, and drought tolerant shrubs. Establishment and persistence of species within the tall tree guild will depend on spring flows to create suitable mineral soil seed beds that are matched by the timing of seed release, precipitation, soil moisture in initial years, connection to shallow groundwater, and shear stress and erosion from late-season floods (Shafroth et al. 2000; Rood et al. 2003). How will other species in the guild contribute to habitat structure if *Salix gooddingii*, the most abundant tall tree in our study reaches, decreases? Boxelder (*Acer negundo*) is more drought-tolerant and more likely to survive low flow periods (Dewine and Cooper 2008). The endangered Southwestern Willow Flycatcher preferred to nest in boxelder along the upper Gila River in New Mexico and dense foliage in the understory, high herbaceous groundcover, and high canopy cover predicted bird use (Stoleson and Finch 2003). Along low-to mid-elevation rivers in xeric landscapes, reductions in

canopy cover and composition may reduce food availability, one of the most important factors shaping migrant bird stopover habitat and foraging habitat for breeding birds (DeLong et al. 2005).

Large branches of species in our tall and short tree guilds support nesting raptors and other large birds, including the common Black Hawk, listed as threatened in Arizona, (Sadoti 2008) and cavity nesting woodpeckers (Li and Martin 1991). Lowered abundance of bird predators may affect food web structure by altering top-down control of forest vertebrates and invertebrates (Patten and Bolger 2003; Zanette et al. 2003; Mäntylä et al. 2011). Secondary cavity nesting opportunities for birds like Ash-throated Flycatchers may decrease without cavity building birds, like woodpeckers (Martin et al. 2004). Both the tall and short tree guilds were distributed where depth to groundwater averaged -1.19 and -1.31 m during low flow conditions indicating that lowering the water table below those depths could degrade habitat. Depth to groundwater in plots with *Prosopis* was -4.09 m during low flow. Loss of drought tolerant and flood tolerant shrub guilds that have average heights of 2.5 and 4.4 m may lead to degradation of habitat and affect birds that prefer to nest or utilize habitat below the canopy including Song Sparrow (*Melospiza melodia*) or ground-nesting Abert's Towhee (*Melospiza aberti*). Both species nest on the ground or in low shrubs preferring habitat with horizontal patchiness, dense foliage, and a diversity of foliage height (Meents et al. 1981). A reduction in foliage cover may alter nest-site selection and increase the risk of nest predation (Larison et al. 2001).

At the river reach scale, a mosaic of different habitat patches creates complex structures that can collectively accommodate more species. Hydrologic variables including depth to groundwater, interannual variability in flow, extreme flow events, and flood frequency will be important factors in determining the distribution and cover of flow response guilds in the future (Lawson et al. 2015). Areas with high guild richness may be more resilient to extreme events, like floods and droughts, as

well as disease due to the partitioning of resources and the differential resistance or tolerance of sympatric guilds to different disturbances.

### *Conclusion*

The increasing human demand for water combined with future climate changes will result in altered river flow patterns and riparian vegetation. The Verde River is one of the few perennial rivers in Arizona, but projected climate change and ongoing water development by humans may alter stream flows and floodplain groundwater levels causing riparian tree stress, dieback, and/or mortality (Williams and Cooper 2005). Increased flow intermittency can reduce canopy cover and height if tall riparian species are replaced with low-statured upland shrubs and annual herbs (Stromberg et al. 2010) and affect which bird species use the Verde River for nesting and migration. Although mesquite and other shrubs provide habitat for birds that nest at lower heights, the homogenization of canopy height and stand structure may reduce bird abundance, richness, and diversity along arid rivers.

The persistence of Verde River riparian forests and shrublands requires perennial flow including summer baseflow and flood flows that allow the establishment of tree species that can resist upland encroachment (Merritt and Poff 2010; Merritt and Bateman 2012). Prolonged periods of drought may cause contraction of riparian forests and loss of high-quality habitat (DeSante and George 1994). Human perturbations such as grazing, land conversion for agriculture, forest clearing, and fire will continue to modify vegetation and resource availability for Western birds (Moore et al. 1995) and other riparian obligate wildlife. Our understanding of bird habitat selection aids conservation efforts as decreases in the proportion of suitable habitat make migrant and resident bird populations highly vulnerable to environmental changes.

Table 2.1 Bird habitat variables used to create the bird habitat index and describe vegetation heterogeneity on the Verde River, Arizona, USA (n=112). Height class 1= 0-1.5 m, height class 2 = 1.6-4.0, height class 3 and 4 = 4.1-9.0 m and > 9 m)

| Variable                                       | Mean    | Standard Deviation |
|------------------------------------------------|---------|--------------------|
| Basal area (cm <sup>2</sup> /plot)             | 1229.29 | 2093.98            |
| Canopy cover (%)                               | 61.74   | 34.81              |
| Foliage height diversity (H')                  | 1.63    | 0.38               |
| Mean vegetation cover height class 1 (%)       | 9.56    | 8.11               |
| Mean vegetation cover height class 2 (%)       | 25.06   | 19.63              |
| Mean vegetation cover height class 3 and 4 (%) | 22.68   | 26.71              |
| Percent graminoid cover (%)                    | 49.57   | 44.86              |
| Percent gravel (%)                             | 17.67   | 28.70              |
| Percent shrub cover (%)                        | 18.99   | 28.67              |
| Percent tree cover (%)                         | 59.69   | 40.96              |
| Plant species richness                         | 14.36   | 5.46               |

Table 2.2 Riparian vegetation flow response guilds on the Verde River, Arizona

| Guild        | Trait-Derived Name                                                                                                                                                                                                  | Long Name                                               | Short Name              |
|--------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------|-------------------------|
| <b>T1</b>    | Hydro-tolerant-dominant trees                                                                                                                                                                                       | Inundation and disturbance tolerant tall trees          | Tall trees              |
| <b>T2</b>    | Hydro-prone-dominant trees                                                                                                                                                                                          | Disturbance intolerant inundation tolerant short trees  | Short trees             |
| <b>S1</b>    | Hydro-tolerant-inferior shrubs                                                                                                                                                                                      | Flood and disturbance tolerant short shrubs             | Flood tolerant shrubs   |
| <b>S2</b>    | Xero-tolerant-dominant shrubs                                                                                                                                                                                       | Drought tolerant, disturbance tolerant, tall shrubs     | Drought tolerant shrubs |
| <b>S3</b>    | Meso-prone-inferior shrubs                                                                                                                                                                                          | Disturbance intolerant generalist shrubs                | Generalist shrubs       |
| <b>A</b>     | Hydro-prone-inferior short herbs                                                                                                                                                                                    | Inundation tolerant, disturbance intolerant short herbs | Short wetland herbs     |
| <b>B</b>     | Hydro-prone-inferior tall herbs                                                                                                                                                                                     | Inundation tolerant, disturbance intolerant tall herbs  | Tall wetland herbs      |
| <b>C</b>     | Meso-prone-inferior herbs                                                                                                                                                                                           | Inundation and disturbance intolerant perennial herbs   | Ruderal perennial herbs |
| <b>D</b>     | Meso-prone-inferior herbs                                                                                                                                                                                           | Inundation and disturbance intolerant annual herbs      | Ruderal annual herbs    |
| <b>E</b>     | Xero-prone-inferior herbs                                                                                                                                                                                           | Drought tolerant, disturbance intolerant herbs          | Drought tolerant herbs  |
| <b>F</b>     | Hydro-tolerant-dominant herbs                                                                                                                                                                                       | Inundation and disturbance tolerant, large seeded herbs | Large seeded herbs      |
| <b>G</b>     | Hydro-tolerant-inferior herbs                                                                                                                                                                                       | Inundation and disturbance tolerant, large SLA herbs    | High SLA herbs          |
| <b>Guild</b> | <b>Species</b>                                                                                                                                                                                                      |                                                         |                         |
| <b>T1</b>    | <i>Populus fremontii</i> , <i>Salix gooddingii</i> , <i>Platanus wrightii</i> , <i>Acer negundo</i>                                                                                                                 |                                                         |                         |
| <b>T2</b>    | <i>Fraxinus velutina</i> , <i>Morus alba</i>                                                                                                                                                                        |                                                         |                         |
| <b>S1</b>    | <i>Salix exigua</i> , <i>Baccharis salicifolia</i>                                                                                                                                                                  |                                                         |                         |
| <b>S2</b>    | <i>Celtis reticulata</i> , <i>Prosopis velutina</i> , <i>Chilopsis linearis</i> , <i>Tamarix ramosissima</i>                                                                                                        |                                                         |                         |
| <b>S3</b>    | <i>Gutierrezia sarothrae</i> , <i>Brickellia floribunda</i> , <i>Amorpha fruticosa</i> , <i>Senegalia greggii</i> , <i>Mimosa aculeaticarpa</i> , <i>Ambrosia monogyra</i> , <i>Baccharis sarothroides</i>          |                                                         |                         |
| <b>A</b>     | <i>Bromus marginatus</i> , <i>Solanum elaeagnifolium</i> , <i>Amauriopsis dissecta</i> ,<br><i>Schedonorus arundinaceus</i> , <i>Apocynum cannabinum</i> , <i>Mentha spicata</i> , <i>Schoenoplectus americanus</i> |                                                         |                         |
| <b>B</b>     | <i>Equisetum hymenale</i> , <i>Typha domingensis</i> , <i>Schoenoplectus acutus</i> , <i>Phragmites australis</i>                                                                                                   |                                                         |                         |

|          |                                                                                                                                                                                                               |
|----------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <b>C</b> | <i>Bromus diandrus</i> , <i>Ambrosia psilostachya</i> , <i>Erodium cicutarium</i>                                                                                                                             |
| <b>D</b> | <i>Chenopodium fremontii</i> , <i>Hordeum murinum</i> , <i>Ambrosia trifida</i> , <i>Bromus tectorum</i> ,<br><i>Croton texensis</i> , <i>Bromus rubra</i> , <i>Avena barbata</i> , <i>Mellilotus indicus</i> |
| <b>E</b> | <i>Cynodon dactylon</i> , <i>Sorghum halepense</i> , <i>Setaria parviflora</i> , <i>Salsola tragus</i>                                                                                                        |
| <b>F</b> | <i>Datura wrightii</i> , <i>Lactuca serriola</i> , <i>Xanthium strumarium</i> , <i>Sonchus asper</i>                                                                                                          |
| <b>G</b> | <i>Vitis arizonica</i> , <i>Hydrocotyle verticillata</i> , <i>Rumex</i> sp.                                                                                                                                   |

Table. 2.3 List of bird species and abundance present at study reaches. Habitat index shows the range (minimum and maximum) or single value where (plot) the species was detected.

| Common name                   | Scientific name                        | Abundance | Habitat index |
|-------------------------------|----------------------------------------|-----------|---------------|
| Yellow Warbler                | <i>Setophaga petechia</i>              | 27        | 0.00-0.98     |
| Chipping Sparrow              | <i>Spizella passerina</i>              | 18        | 0.28-0.98     |
| Wilson's Warbler              | <i>Cardellina pusilla</i>              | 16        | 0.16-0.98     |
| Lucy's Warbler                | <i>Oreothlypis luciae</i>              | 13        | 0.36-0.79     |
| Common Yellowthroat           | <i>Geothlypis trichas</i>              | 11        | 0.44-0.98     |
| Song Sparrow                  | <i>Melospiza melodia</i>               | 11        | 0.00-0.98     |
| Black-chinned Hummingbird     | <i>Archilochus alexandri</i>           | 10        | 0.21-0.98     |
| Bell's Vireo                  | <i>Vireo bellii</i>                    | 9         | 0.19-0.98     |
| Northern Rough-winged Swallow | <i>Stelgidopteryx serripennis</i>      | 8         | 0.21-0.79     |
| Summer Tanager                | <i>Piranga rubra</i>                   | 7         | 0.21-0.98     |
| Yellow-breasted Chat          | <i>Icteria virens</i>                  | 7         | 0.35-0.85     |
| Bewick's Wren                 | <i>Thryomanes bewickii</i>             | 4         | 0.52-0.87     |
| Brown-headed Cowbird          | <i>Molothrus ater</i>                  | 4         | 0.21-0.87     |
| Gila Woodpecker               | <i>Melanerpes uropygialis</i>          | 4         | 0.52-0.76     |
| Ash-throated Flycatcher       | <i>Myiarchus cinerascens</i>           | 3         | 0.21-0.85     |
| Black-headed Grosbeak         | <i>Pheucticus melanocephalus</i>       | 3         | 0.19-0.76     |
| Ladder-backed Woodpecker      | <i>Picoides scalaris</i>               | 3         | 0.51-0.85     |
| Verdin                        | <i>Auriparus flaviceps</i>             | 3         | 0.51-0.85     |
| Black Phoebe                  | <i>Sayornis nigricans</i>              | 2         | 0.21-0.59     |
| Black-throated Gray Warbler   | <i>Setophaga nigrescens</i>            | 2         | 0.16-0.52     |
| Bullock's Oriole              | <i>Icterus bullockii</i>               | 2         | 0.85-0.98     |
| Dusky/Hammond's Flycatcher    | <i>Empidonax oberholseri/hammondii</i> | 2         | 0.60-0.87     |
| House Finch                   | <i>Haemorhous mexicanus</i>            | 2         | 0.28-0.76     |
| MacGillivray's Warbler        | <i>Geothlypis tolmiei</i>              | 2         | 0.52-0.98     |

|                          |                                 |   |           |
|--------------------------|---------------------------------|---|-----------|
| Marsh Wren               | <i>Cistothorus palustris</i>    | 2 | 0.44-0.73 |
| Red-winged Blackbird     | <i>Agelaius phoeniceus</i>      | 2 | 0.73-0.87 |
| Townsend's Warbler       | <i>Setophaga townsendi</i>      | 2 | 0.21-0.87 |
| Western Tanager          | <i>Piranga ludoviciana</i>      | 2 | 0.52-0.60 |
| Western Wood-Pewee       | <i>Contopus sordidulus</i>      | 2 | 0.36      |
| Abert's Towhee           | <i>Melospiza aberti</i>         | 1 | 0.98      |
| Blue-gray Gnatcatcher    | <i>Polioptila caerulea</i>      | 1 | 0.52      |
| Broad-tailed Hummingbird | <i>Selasphorus playacensis</i>  | 1 | 0.60      |
| Brown-crested Flycatcher | <i>Myiarchus tyrannulus</i>     | 1 | 0.76      |
| Cliff Swallow            | <i>Petrochelidon pyrrhonota</i> | 1 | 0.00      |
| Cooper's Hawk            | <i>Accipiter cooperii</i>       | 1 | 0.73      |
| Costa's Hummingbird      | <i>Calypte costae</i>           | 1 | 0.35      |
| Gray Flycatcher          | <i>Empidonax wrightii</i>       | 1 | 0.21      |
| Gray Vireo               | <i>Vireo vicinior</i>           | 1 | 0.60      |
| Green-tailed Towhee      | <i>Pipilo chlorurus</i>         | 1 | 0.73      |
| House Wren               | <i>Troglodytes aedon</i>        | 1 | 0.76      |
| Hutton's Vireo           | <i>Vireo huttoni</i>            | 1 | 0.60      |
| Orange-crowned Warbler   | <i>Oreothlypis celata</i>       | 1 | 0.52      |
| White-crowned Sparrow    | <i>Zonotrichia leucophrys</i>   | 1 | 0.70      |
| White-winged Dove        | <i>Zenaida asiatica</i>         | 1 | 0.59      |



Figure 2.1 Map of the Verde River watershed in Arizona and the three study reaches, Beasley Flat, Childs, and Sheep Bridge

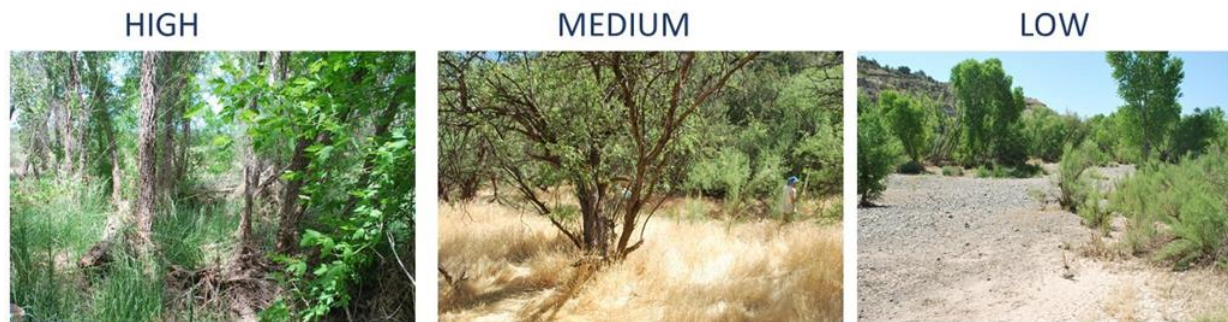


Figure 2.2 Visualization of riparian vegetation structure across a range of habitat index values from high (willow/cottonwood forest, 0.87), medium (mesquite forest, 0.46), and low (open cobble bar, 0.00). High habitat index values are characterized by complex structure with high canopy cover in multiple height classes, basal area, and foliage height diversity. Low habitat index values have less canopy cover and complexity of cover in the understory. The dominant guilds in the high index plot included tall trees, short trees, and short wetland herbs (guild richness = 8). In the medium indexed plot, dominant guilds included drought tolerant shrubs and ruderal perennials (guild richness = 4). In the low habitat index plot, the drought tolerant shrub guild was present, but had very low cover

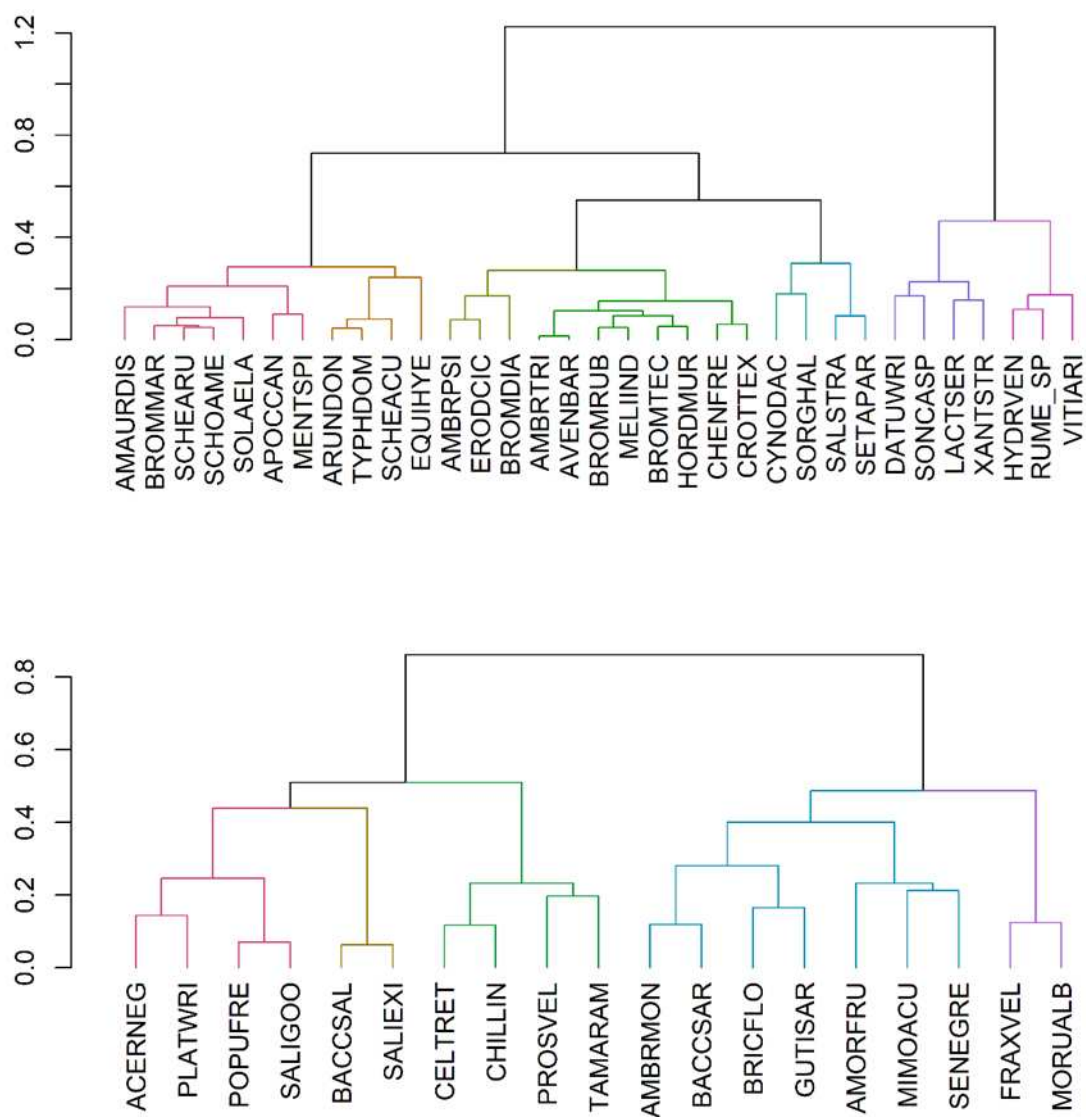


Figure 2.3 Dendrogram from hierarchical cluster analysis for woody (top) and herbaceous and graminoid species (bottom).

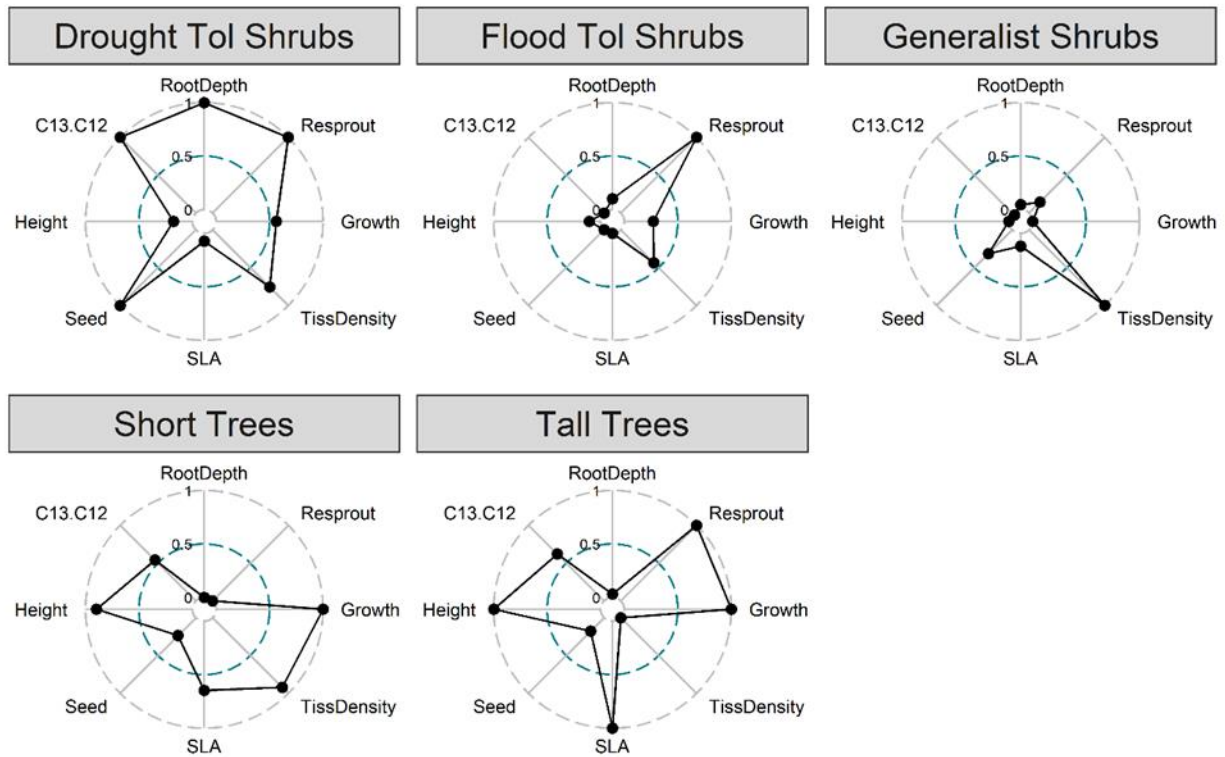


Figure 2.4 Radar plots for mean trait values for woody guilds along the Verde River, Arizona. Ability to resprout is ordinal with values of 0 or 1 (no or yes), growth form ranges from subshrub to tree, root depth (m), tissue density ( $\text{g}/\text{cm}^3$ ), SLA, Seed mass (grams/1000 seeds), Height (m), and  $^{13}\text{C}:^{12}\text{C}$  are continuous variables scaled between 0 and 1.

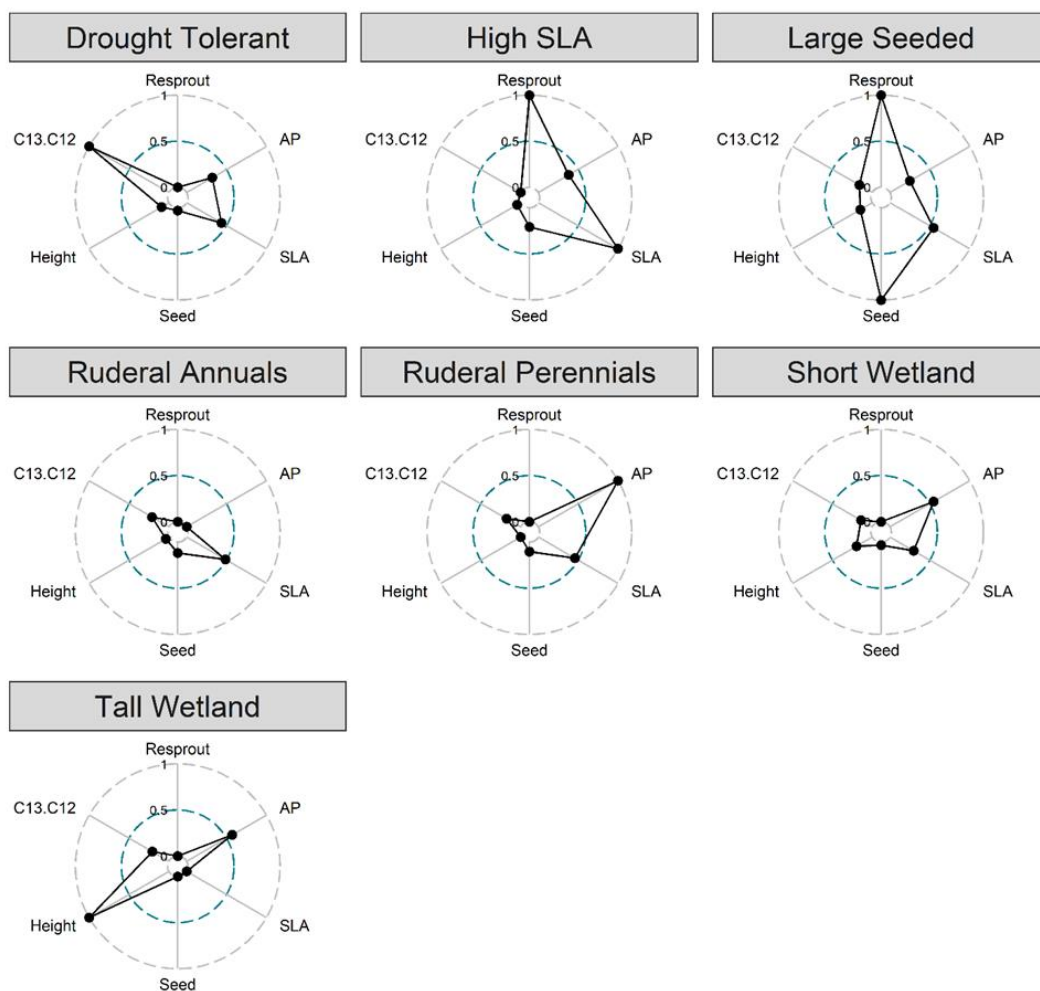


Figure 2.5 Radar plots detailing the trait profile of each herbaceous guild along the Verde River, Arizona. Ability to resprout is ordinal with values of 0 or 1 (no or yes), AP is ordinal and indicates whether the guild is annual or perennial (0 or 1), SLA (specific leaf area), Seed mass (log transformed), Height (m), and  $^{13}\text{C}:^{12}\text{C}$  are continuous variables that have been scaled.

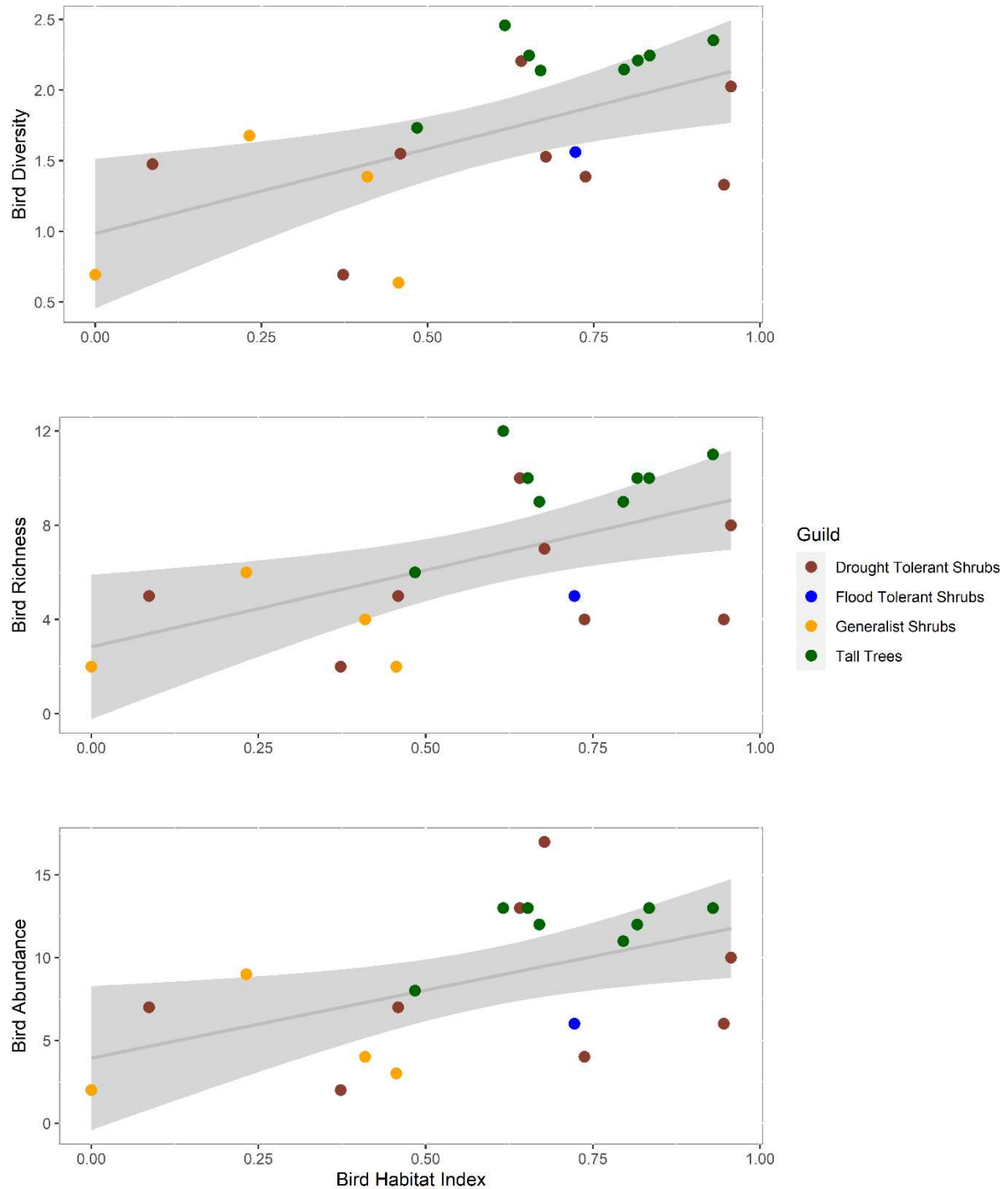


Figure 2.6 Bird Habitat Index related to a) bird abundance ( $R^2 = 0.22$ ,  $P = 0.019$ ) b) bird species richness ( $R^2 = 0.22$ ,  $P = 0.009$ ) and c) bird diversity (Shannon Diversity Index,  $R^2 = 0.30$ ,  $P = 0.006$ ) at three study reaches on the Verde, River, Arizona. Shaded regions represent the 95% confidence interval. Dominant woody guild is indicated by color with blue = S1 (flood tolerant shrubs), red = S2 (drought tolerant shrubs), orange = S3 (generalist shrubs), dark green = T1 (tall trees)

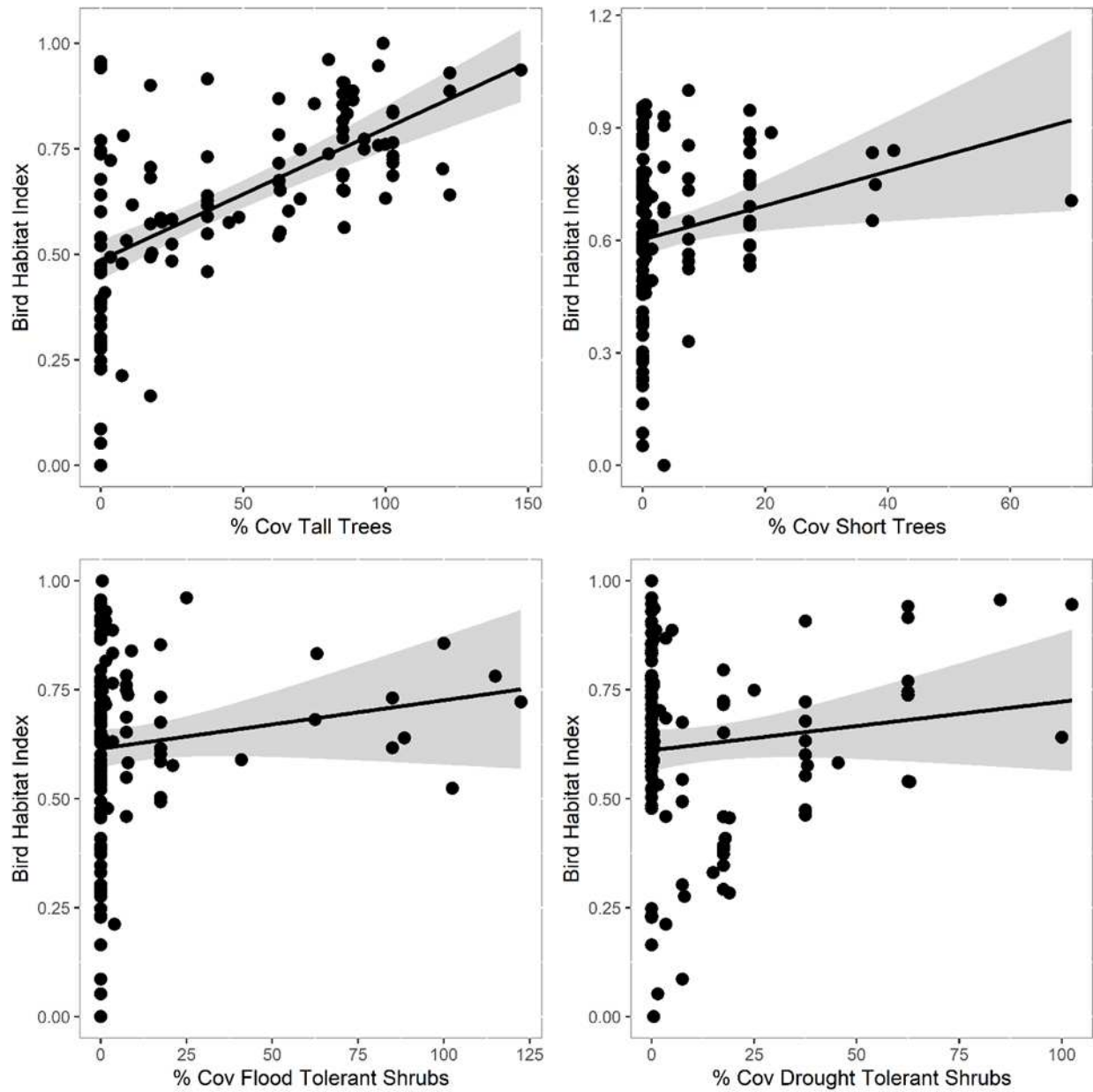


Figure 2.7 Relationship between the cover of woody flow response guilds and riparian habitat at three study reaches on the Verde River, Arizona

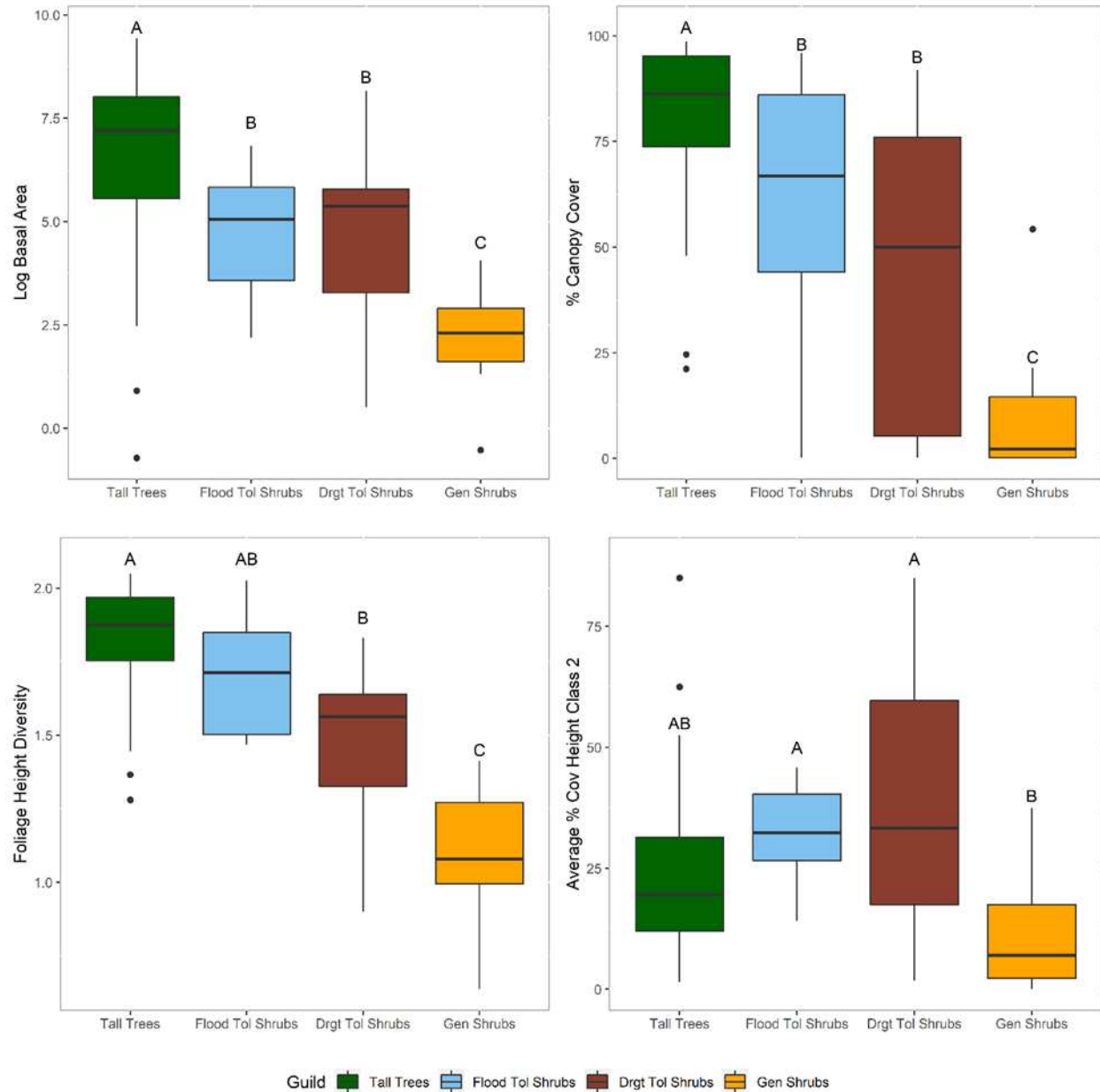


Figure 2.8 Boxplots for four of the top ranked structure variables including log basal area, percent canopy cover, foliage height diversity, and average percent cover in height class 2 (1.6 -4.0 m) between plots dominated by woody guilds (> 10% cover). Plots represent the median, 25<sup>th</sup> and 75<sup>th</sup> percentiles, and the 95<sup>th</sup> percentiles (end of the whisker). We tested if structure variables differed between vegetation guilds using non-parametric Kruskal-Wallis tests with Bonferroni adjustment for multiple comparisons. Different letters at the top denote significant differences between woody guild structure.

### **3 Distribution of riparian vegetation guilds across gradients of groundwater and fluvial disturbance on a river in a semi-arid landscape**

#### **3.1 Introduction**

Riparian plants have evolved morphological, physiological, and life history traits that allow them to persist in habitats with seasonally variable groundwater availability and fluvial stressors (Cornelissen et al. 2003). Different traits may influence the spatial distribution of plant species along gradients of groundwater depth and flood frequency producing distinct zonation between riparian and upland plant communities (Arthington et al. 2010; Merritt and Poff 2010; Gonzalez-Sanchis et al. 2012; Sommer and Froend 2014; Yin et al. 2015). Riparian ecosystems are sensitive to anthropogenic water development and climate changes that alter hydrologic regimes and result in changes in plant distributions and abundance (Barnett et al. 2008; Pittock and Connell 2010; Pyne and Poff 2017). The structure and composition of vegetation along rivers determines the habitat quality for birds, invertebrates, and herpetofauna. Key habitat for birds, such as deciduous trees, are particularly scarce in arid landscapes (Grimm et al. 1997; Lite et al. 2005; Bornette et al. 2008).

Riparian plants have hydrologic requirements for survivorship and recruitment (Stromberg et al. 1996; Lytle and Merritt 2004) and in arid and semi-arid regions may be partially or completely dependent on groundwater, especially during periods of low rainfall and drought (Eamus et al. 2006). Riparian trees, some of which are phreatophytes, use shallow groundwater and respond to water level declines with reductions in canopy cover, branch dieback (Scott et al. 1999), and mortality when a threshold of groundwater depth and duration is reached (Horton et al. 2001; Cooper et al. 2003; Kath et al. 2014). Lateral flow from the river to alluvial aquifers beneath floodplains is one connection between the aquatic and terrestrial riparian environment (Hauer et al. 2016). Alluvial

groundwater resources can be driven by patterns of streamflow with high flows facilitating groundwater recharge.

Seasonal variation in groundwater levels may follow the patterns of stream stage if it is supplied by lateral flow from the river, but other variations can occur on daily or sub-daily timescales (Gribovszki et al. 2010). Evapotranspiration (ET) by riparian vegetation rooted into the water table or saturated zone (capillary fringe) create diurnal water table fluctuations during the growing season (White 1932; Troxell 1936). Water table declines during the day are driven by ET and recovery each night occurs with stomatal closure and xylem filling as water flows from areas of higher to lower hydraulic head. Solar radiation, air temperature, relative humidity, and wind determine the rate and total daily riparian ET with early morning maximum and afternoon minimum groundwater levels. The daily groundwater elevation can slowly decline if the ET rate exceeds the recharge rate (Loheide 2005). Predictions of increased temperatures and longer growing seasons in coming years could increase evapotranspiration by riparian plants resulting in lowered groundwater tables if nightly recharge volumes exceed vegetation withdrawals (Roulet et al. 1992).

Overbank high flows that flood and scour riparian landforms remove plant biomass and facilitate the recruitment of key pioneer species (Mahoney and Rood 1998). Many riparian plants have adapted functional traits like flexible stems to withstand mechanical stress and extended periods of inundation, but upland plants lacking these traits may be excluded from areas that are frequently flooded (Puijalon et al. 2011). Low flows are another key component of natural hydrographs, serving a maintenance function of extant forests and riparian shrublands. As these two flow components change in magnitude and duration, predictable changes in riparian structure and function will occur. Lowered groundwater levels and altered flood frequency can lead to the invasion of upland and/or non-native species and mortality of native vegetation (Bendix 1994; Merritt and

Cooper 2000; Stromberg et al. 2010). Drought has already resulted in the loss of sensitive species with perennial flow loss on some arid rivers (Williams et al. 2015).

Changes in riparian plant composition in arid and semi-arid regions has large-scale implications in the provisioning of ecosystem services and functions (Bejarano et al. 2012). Increased cover of upland plant species may reduce the ecological functioning of river ecosystems by altering their food web structure, wildlife habitat, and rates of nutrient cycling (Naiman et al. 2005b; Kominoski et al. 2013). Understanding hydrologic thresholds for species turnover informs predictions of how changes in flow regimes and groundwater level could change plant species distributions and ultimately, ecosystem functioning (Merritt et al. 2010; Lozanovska et al. 2018). Riparian ecosystem research has focused on understanding the response of individual species to hydrologic patterns and processes (Stromberg et al. 2010; Smith and Finch 2016; Perry et al. 2020), but functional groups or guilds may provide an approach that is applicable within and between watersheds (Merritt et al. 2010). Groups of plant species with similar adaptations to fluvial disturbance and water availability can be classified into guilds and define the range of traits and strategies of riparian vegetation (Cornelissen et al. 2003; Merritt et al. 2010; Lawson et al. 2015; Stromberg and Merritt 2016). Riparian guilds have been used to study the response plants downstream from hydropower dams (Bejarano et al. 2012) and land use change in Europe (Aguiar et al. 2018). A classification of guilds was developed for ephemeral, intermittent, and perennial rivers in Arizona (Stromberg and Merritt 2016) and along the Colorado River through Grand Canyon (McCoy-Sulentic et al. 2017; Palmquist et al. 2018) describing the distribution of functional traits along hydrologic gradients.

Surface water in the arid southwestern United States is used by humans for agriculture, industry, and municipal water supplies. Perennial streamflow has declined in Arizona as a result of groundwater pumping, dams, and water diversions (Webb et al. 2007) and future water demand will

likely have to be met by increased groundwater pumping (Reclamation 2016). Alluvial groundwater levels along rivers across the world have declined due to flow regulation and groundwater extraction (Margat and Van Der Gun 2013; Chen et al. 2015; Jansson et al. 2019). Climate change may further decrease streamflow and groundwater availability (Catford et al. 2014, Rivaes et al. 2014) with reduced surface and sub-surface hydrologic connectivity (Seager et al. 2013; Reynolds et al. 2015).

Climate warming within the last 50 years have reduced streamflow by 5-10% in the Colorado River basin (Vano et al. 2012; Woodhouse et al. 2016) and streamflow is predicted to decline by 20% by the mid-21st century which could drastically affect riparian plant communities (Udall and Overpeck 2017). Reductions in the occurrence and areal extent of plant species is predicted to be more dramatic along rivers with large hydrologic changes (Jansson et al. 2019). An increased understanding of riparian vegetation hydrologic thresholds and responses is required to predict changes in essential ecosystem services and functions. We investigated the connection between streamflow, floodplain groundwater, and riparian vegetation guilds along two river reaches of the Verde River that are federally designated as Wild and Scenic. We quantify riparian guilds distributions as a function of floodplain groundwater depth and inundation exceedance probability and define hydrologic thresholds of dominant riparian guilds. Specifically, we answer the following questions:

- 1) What are the sources of floodplain groundwater along the Verde River and what maintains shallow water tables?
- 2) Does riparian vegetation, streamflow in the river, and shallow groundwater interact?
- 3) Can riparian vegetation guild probability of occurrence be predicted by groundwater depth and inundation exceedance probability?
- 4) Do vegetation guild or individual species models more accurately predict plant occurrences across the riparian zone?

- 5) How could the occurrence of riparian vegetation guilds change along the Verde River under scenarios of lowered groundwater tables and reduced flooding?

## **3.2 Methods**

### *Study Area*

The Verde River, a 359 km long tributary of the Colorado River drains a watershed of 16,027 km<sup>2</sup> and traverses the Colorado Plateau and Mogollon rim before flowing in the Sonoran Desert. Perennial flow in the headwaters is generated by groundwater discharge fed by the Big and Little Chino aquifers and streamflow increases downstream with additional groundwater and tributary inflows. The watershed is characterized by low annual rainfall, high summer temperatures, and some winter nights below freezing. The Verde River watershed has a bimodal precipitation regime with approximately half of its annual precipitation falling in winter and half during late summer monsoon rains generated by storms from the Gulfs of California and Mexico (NOAA 2004). The river can be divided into upper, middle, and lower segments. The lower segment is classified as Wild and Scenic upstream from a dam that forms Horseshoe Reservoir at km 201 above its confluence with the Salt River. Two representative reaches were selected in the lower segment of the river downstream from the town of Camp Verde at Beasley Flats (425500E, 3815635N UTM coordinates) and Childs (435625E, 3801102N) on land administered by the U.S Forest Service (Figure 3.1).

Between 1910 and 2005 groundwater discharge and Verde River baseflow decreased by approximately 10% due to surface water diversions and groundwater pumping (Garner et al. 2013). Diversions to support irrigated agriculture during the summer dried segments of the river (Haney et al. 2008). A proposed project within the City of Prescott groundwater management area (GMA) would extract water from the Big Chino Aquifer to support urban development and is predicted to influence Verde River streamflow. Increases in groundwater pumping and water diversion for

irrigated agriculture in the upper river segment could reduce stream flows and threaten downstream water rights, including the Salt River Project (SRP) that provides water for the city of Phoenix. Annual low flows on the Verde River occur in the month of June with an average discharge of 1.89 cms with the 7-day streamflow minimum occurring during the first week of July with an average discharge of 1.33 cms. High flows occur mainly in February with an average discharge of 26.93 cms with the highest magnitude flow occurring 2/22/1993 at 3369.70 cms. During the 2017-2018 water year the highest mean daily discharge was 143.28 cms in mid-January and the lowest was 1.14 cms during the first week of July. Between May 2018 and May 2019, the Verde River experienced several floods driven by late summer monsoons (July-October) and large winter storms (January-March) (Figure 3.2).

#### *Vegetation Sampling and Analysis*

We analyzed vegetation in 1 m<sup>2</sup> plots placed systematically along transects oriented perpendicular to the river from the edge of the baseflow channel to the upland. Within each plot we estimated percent canopy cover of all vascular plant species using Braun-Blanquet cover classes (Braun-Blanquet 1965). Plant species were identified using Kearney and Peebles (1960) and nomenclature updated using the integrated taxonomic information system (ITIS 2019). A total of 177 1m<sup>2</sup> plots (Beasley n = 90, Childs n = 87) were sampled. The study reach at Beasley Flat was divided into two segments that were separated due to wildlife and archeological considerations. Riparian vegetation guilds were developed and used to model guild occurrence across hydrologic gradients. We used seven traits to group 52 plant species into 5 woody and 7 herbaceous guilds (Table 3.1, Chapter 2). Plots, wells, and study reach topography was surveyed using real-time kinematic GPS (RTK-GPS) in 2018 with Trimble R6 receivers using real-time kinematic positioning (RTK). Data were recorded in UTM coordinates in zone 12N with the WGS84 horizontal datum.

#### *Hydrologic Data*

Groundwater monitoring wells were installed in a grid in the spring of 2017 and 2018 at each study reach (Beasley  $n = 11$  wells, Childs  $n = 8$ ). All wells were installed with steel drive points and outfitted with HOBO loggers that recorded water level and temperature every 15 minutes (Model U20L-04 and U20-001-01). Groundwater wells were not installed on upper floodplain surfaces due to archeological considerations. A barometric pressure logger was installed at each reach to correct groundwater loggers for atmospheric pressure. Groundwater depth was also measured manually each time a study reach was visited and used to verify logger data. Real Time Kinematic (RTK) surveyed elevations of plots and groundwater wells allowed us to calculate the groundwater elevation at each plot and construct groundwater profiles and maps ( $\pm 2$  cm). We used groundwater depth on July 1<sup>st</sup>, 2018 to represent low flow conditions (4 pm, lowest daily groundwater) and thin plate spline interpolation to create continuous water table elevation maps in R (Nychka et al. 2017). Depth to groundwater was deepest during this low flow period and may have the most impact on the distribution of plants within the riparian zone. We used data from the summer of 2018 as it had the most complete grid of wells.

A staff gauge equipped with a HOBO water level logger was installed in the Verde River upstream and downstream from each study reach (Beasley  $n = 4$  loggers, Childs  $n = 2$  loggers) to measure river stage. The Beasley Flat study reach had 4 in-stream pressure transducers as the site was divided into two segments. Using the detailed surveyed topography and UAS imagery we created digital elevation models (DEM) and triangular irregular networks (TIN) for each reach. Final TIN maps were converted to raster using the natural neighbor algorithm and point shape files for use in 2 dimensional (2d) hydraulic models in iRIC (International River Interface Cooperative; Nelson et al. 2016). 2D models were calibrated at specified discharges ( $1.18 \text{ m}^3/\text{s}$ - $1560 \text{ m}^3/\text{s}$ ). Roughness values varied as a function of discharge and final values resulted in minimum RMSE between observed water surface elevations from pressure transducers and modeled water surface

elevation. Using the calibration models, 2D models at each reach were run over the entire range of historical flows ( $0.50 \text{ m}^3/\text{s}$ - $2000 \text{ m}^3/\text{s}$ ) and future flow scenarios.

Mean daily flow records from 1989-2019 from USGS gage #09506000 (Camp Verde) were used to create rating curves to determine discharge at any river stage. Daily exceedance probability (EP) was calculated with Weibull plotting position ( $EP = m/N + 1$ ) where  $m$  is the rank of the discharge and  $N$  is the number of discharges in the scenario (USGS Bulletin 17-B). Daily EP was recalculated for each flow scenario in the 2D hydraulic models. Maps of inundating discharge were generated for each study reach to create digital inundation maps with a grid of cells indicating the discharge where a cell's water depth is greater than zero. Each study reach inundating discharge map was re-classified using EP for the modeled discharges and plot level EP was extracted (Appendix Figure 3).

### *Statistical Analysis*

We performed logistic regression using 10-fold cross validation with the caret package in R (Kuhn 2019). Data were divided into training (70%) and testing subsets (30%). We reported model performance using receiver operating curve analysis (ROC) and area under the curve (AUC). An AUC less than 0.5 indicates that the model does not predict better than chance (Swets 1988). We only used models that had  $AUC > 0.7$  and accurately predicted at least 65% of guild presence. We calculated probability thresholds for vegetation guilds by maximizing the sum of model sensitivity and specificity with the coords function in R (Baddeley 2013). Confusion matrices were used to calculate the overall accuracy and Cohen's kappa. From our models, we created flow response curves to characterize the relationship between the distribution of riparian vegetation as a function of depth to groundwater and flood exceedance probability.

We choose three climate-based scenarios that correspond to predictions of future flows to model changes in riparian vegetation and used the past 30 years of the daily flow record to construct

future flows. In scenario 1 we decreased summer flows below  $2.69 \text{ m}^3/\text{s}$  (25<sup>th</sup> percentile) from May-middle July by 10% but left flood peaks alone. In scenario 2, we increased the magnitude of winter storms in the 1<sup>th</sup> quartile ( $> 107.81 \text{ m}^3/\text{s}$ ) by 20% and those in the 10<sup>th</sup> quartile ( $13.5 \text{ m}^3/\text{s}$ ) by 10% while simultaneously reducing summer low flows by 10% (Trenberth et al. 2007; Wang and Zhang 2008; Maurer et al. 2017). In our final scenario we decreased winter flood magnitudes above the 10<sup>th</sup> quartile by 10% and reduced summer low flow by 10%. To model the response of riparian vegetation guilds to changes in groundwater we imposed lowered groundwater levels (0.25, 0.50, and 1.00 m) to our interpolated groundwater surface in ArcGIS using spatial analyst (ESRI, Redlands, California, USA). Model parameters from significant logistic models calculated the probability of occurrence of guilds at lowered groundwater scenarios.

### **3.3 Results**

#### *River Stage and Groundwater Levels*

Groundwater levels in monitoring wells were highly correlated with river stage in all study reaches. Wells within 5 to 15 meters of the river had the highest correlations to river stage (Spearman rank  $r > 0.90$ ) compared to wells farther from the river (Spearman rank  $r = 0.71 - 0.86$ ) when analyzed over the study timeframe (June 2017-May 2019). Wells closer to the river responded more quickly to changes in river stage while wells farther from the river had longer lags of response. Maps of groundwater elevation (Figure 3.3) illustrate that the Verde River is losing water to the floodplain alluvium at flows below bankful stage including those analyzed at 0.82, 4.93, and 69.94 cms. Thus, the Verde River is the dominant source of water to the riparian zones in our study reaches. Groundwater and river elevations were highly correlated during the winter ( $r > 0.86$ ), summer monsoon ( $r > 0.91$ ), ascending flood limbs ( $r > 0.99$ ), and descending flood limbs ( $r > 0.99$ ) demonstrating high connectivity between the river and alluvial groundwater throughout the year (Figure 3.4).

Between May 2018 and May 2019 groundwater levels varied by 4.17 to 5.46 m at Childs, and 5.45 to 6.84 m at Beasley Flat. Most of this variation occurred during a very large flood on February 15<sup>th</sup>, 2019 that produced a river stage increase of 5.6 m at the upper Beasley study reach over approximately 7 hours. The flood covered the entire floodplain and submerged all groundwater wells. From May 2017 to May 2018 no floodplain inundating floods occurred, and groundwater levels ranged from 1.09 to 2.33 m at Beasley Flat and 1.02 to 1.69 m at Childs. Maximum depth to groundwater across vegetation plots during the 2018 growing season ranged from 0.18 to 7.49 m at Beasley Flat and 0.09 to 5.25 m at Childs. Groundwater levels were the most variable in plots at lower Beasley Flat (2.41 m) a floodplain area with large cobble and sediments. Differences in summer groundwater level variability appears to be attributed to differences in channel morphology, sediment grain size distribution, and watershed position.

The correlations between river stage and groundwater level did not account for a temporal lag in the groundwater response to changes in river stage, and lag times were dependent on flood magnitude. Wells farther from the channel had longer response lags than wells closer to the channel. For example, a flash flood on July 11<sup>th</sup>, 2018 increased the flow from 1.38 to 19.45 cms and increased river stage at Beasley Flat by approximately 0.40 m over a 9-hour period. Wells within 10 m of the channel responded rapidly to the rising stage with little to no lag and groundwater level rise matched river stage rise. However, wells 20-50 m from the channel had lags ranging from 6 to 12 hours and groundwater level increased only ~20 cm, half of river stage change. During a larger flood on October 3rd, 2018, the river rose rapidly to a discharge of 70.23 cms with wells within 10 m of the river experiencing almost no lag while wells on the outer edge of the floodplain at Beasley Flat experienced a short 30-minute lag.

Water level records during the growing season (April-October) clearly show diurnal changes driven by riparian vegetation evapotranspiration (Figure 3.5). This groundwater variation creates

lower correlations (Spearman rank correlation  $r < 0.90$ ) between stream stages and well water level. Daily variation was greatest May-July coinciding with the highest average monthly temperatures, low relative humidity, and high vapor pressure deficit. Larger diurnal variations occurred in wells farther from the channel compared to wells within 15 m of the channel (Figure 3.5). Between 7 am and 4 pm plant water use exceeded the rate of groundwater recharged from the river and the alluvial groundwater level declined. After 4 or 5 pm, transpiration slowed and groundwater levels increased until equilibrium, around midnight. The rate of groundwater recharge slowed from midnight till 6 am due to a decrease in hydraulic gradient between the river and alluvial groundwater. At the Upper Beasley reach, groundwater and river elevations were highly correlated at 6 am ( $r > 0.96$ ) following nighttime recharge, but correlations were lowest around 5:00 pm when groundwater depths were at the daily low. At Lower Beasley and Childs, well and river stage correlations were still high ( $r > 0.90$ ) at 5:00 pm on summer days with both sites exhibiting large diurnal groundwater variation.

#### *Distribution of Riparian Vegetation Guilds along Hydrologic Gradients*

Depth to groundwater and exceedance probability were highly correlated (Spearman rank  $r > 0.90$ ,  $P < 0.001$ ) and we explored the variable that best predicted our 12 vegetation guilds along the Verde River (Table 3.2). The most frequently occurring vegetation guilds included tall trees (47% of plots), drought tolerant herbs (29%), tall wetland herbs (27%), drought tolerant shrubs (22%), ruderal annual herbs (22%), generalist shrubs (17%), and flood tolerant shrubs (16%). Logistic regression models with depth to groundwater predicted our tall tree guild in areas where groundwater levels were between -0.38 to -2.50 m during low flow periods (86.8% accuracy, Table 3.2, Figure 3.6). Prediction of tall trees using exceedance probability was also high (81.0%) with tall trees more likely to be found where exceedance probability ranged from 1 to 75%. Short trees were more likely to occur where groundwater was shallower than -1.44 m during low flow periods (70.9 % accuracy,

Figure 3.7), but the variability in short tree occurrence was not explained by exceedance probability ( $P > 0.05$ ).

Depth to groundwater predicted the individual tree species, *Populus fremontii*, and had similar classification accuracy (84.6% correctly classified, Table 3.2, Figure 3.6) compared to the tall tree guild model. However, groundwater depth only correctly classified 71.8 % of plots with *Salix gooddingii* compared to the tall tree guild model (86.8% correctly classified). The occurrence of flood tolerant shrubs was significantly predicted by depth to groundwater (AUC = 0.71, 69.6%, Figure 3.7) and species were found where groundwater was less than ~ 0.90 m from the floodplain surface. *Salix exigua*, a member of flood tolerant shrubs, was correctly classified in 77.9% of plots (AUC = 0.84) and occurred where groundwater was shallower than 0.70 m (Appendix Table 1).

Drought tolerant and generalist shrub guild occurrences were predicted by both exceedance probability and depth to groundwater during low flow (Table 3.2). The drought tolerant shrub guild was more likely to occur on higher elevation floodplain surfaces where daily flood exceedance probabilities were less than 3% and where groundwater was deeper than -1.84 m (Appendix Table 1, Figure 3.9). Generalist shrubs occurred on surfaces where groundwater was deeper than -2.18 m and daily flood exceedance probability less than 2.0% (Figure 3.7). Individual species models for members of the drought tolerant shrub and generalist shrub guilds had 6-12% higher accuracy than guild models (Table 3.7). *Ambrosia monogyra*, a member of the generalist shrub guild, was accurately classified in 89.1% and 91.3% of plots using exceedance probability and depth to groundwater, respectively.

Groundwater depth and study reach predicted the occurrence of short wetland herbs (Table 3.2), however, upper Beasley Flat was the only reach where groundwater depth predicted guild occurrence (AUC = 0.98, 92.7% balanced accuracy). Groundwater depth (AUC = 0.88) and exceedance probability (AUC = 0.87) predicted tall wetland herbs and an individual model for tall

wetland herb member species *Phragmites australis* resulted in similar prediction accuracy (Table 3.1). Both tall and short wetland guilds were found in areas with shallow groundwater (Appendix Table 1) compared to other herbaceous guilds that occurred in plots with greater depth to groundwater (Figure 3.9). The variability of ruderal annual herbs (Guild D) was explained by depth to groundwater while exceedance probability explained drought tolerant herb variability (Guild E), however, models had poor fit and predictive ability (Table 3.2). An individual species model for *Cynodon dactylon* (Guild E, non-native grass) also had poor fit and predictive ability (AUC < 0.70). Depth to groundwater predicted the occurrence of *Melilotus indicus*, a non-native clover in the ruderal annual herb guild (Guild D), in areas where groundwater was less than -2.0 m (AUC = 0.67, 71.2% balanced accuracy). Although herbaceous species grouped together due to similar functional traits, many species within guilds spanned the hydrologic gradients measured. For example, within the ruderal annual herb guild, *Melilotus indicus* only occurred where groundwater was less than -2.0 m while other species like *Bromus rubens* occurred in plots where groundwater exceeded -6.0 m. We were not able to model the effect of groundwater depth and exceedance probability on two guilds, large seeded (F) and high SLA (G) herbs due to low occurrences in our sample plots.

#### *Simulated changes in floodplain groundwater levels and flooding*

A simulated floodplain groundwater lowering of 1.00 m predicted to decrease the occurrence of tall and short trees between 1-34% along the Verde River (Table 3.3). A 0.50 m decrease in groundwater predicted a small (<2%) increase of tall and short trees at Childs on floodplain areas. Flood tolerant shrubs were predicted to decrease the most along the Verde River. Simulations of groundwater decline at Childs and Beasley Flat indicate an almost complete loss of this guild on current floodplain surfaces. Simulations of lowered groundwater increased the occurrence of both drought tolerant and generalist shrubs (Table 3.3). The areal extent of tall and short wetland herbs

fell by 8.7-10.4% across our study reaches with predicted presence of less than 2% with a 1.00 m decrease in groundwater.

Simulated increases in winter flood magnitudes increased tall tree occurrence by ~1% and reduced winter flood magnitudes decreased occurrence by ~ 1% (Table 3.4). Tree and shrub guild occurrences did not change under scenarios of lowered summer flow since those flows did not go over bank and inundate plots. Decreased winter flows and summer flow predicted small (1-7%) increases of drought tolerant shrubs and generalist shrubs while increased winter flows decreased the occurrence of both guilds (0.3-5% decrease, Table 3.4). Tall wetlands herb occurrence increased by ~2 % with simulated increased winter flood magnitudes and decreased ~2 % with simulated decreases in winter floods.

### **3.4 Discussion**

Our findings highlight the connection between surface flow, alluvial groundwater, and riparian vegetation along the Verde River in Arizona and the dependency of shallow alluvial groundwater on streamflow. Surface and groundwater are highly connected, and groundwater is controlled by changes in streamflow and stage. Therefore, changes in flow of the Verde River will directly influence groundwater depth. Groundwater within two meters of the floodplain surface was shown to be essential for maintaining species within the tall and short tree guilds and groundwater less than one meter is needed to support flood tolerant shrubs near the channel edge. We were able to predict tall and short tree guilds with comparable accuracy as individual species models suggesting that species within these guilds occupy similar hydrologic niches due to their functional traits. Shrub guilds had good prediction accuracy and model fit, but models using individual member species tended to have better classification accuracy. The occurrence of tall riparian trees and upland shrubs were predicted by both depth to groundwater and exceedance probability, but simulations of hydrologic change demonstrate that the lowering of alluvial groundwater levels will have a larger

effect on riparian plant communities than altered flooding. The maintenance of guild diversity that includes both riparian and drought tolerant guilds in the riparian landscape is essential in the provisioning of habitat for resident and migratory birds along the Verde River and contraction of riparian forests and species within the tall tree, short tree, and drought tolerant shrub guilds could reduce bird diversity and abundance (Cubley et al. 2020).

### *Alluvial Groundwater Dynamics*

Our study reaches along the Verde River are losing reaches, however, losing and gaining reaches may be spatially variable along rivers. Sections of river in the upper Verde River watershed may be gaining groundwater from regional sources with river flow doubling over certain river segments (Beisner et al. 2018). However, the floodplains in the Wild and Scenic segment of the Verde River occur in bedrock valleys with limited or little if any groundwater input from the uplands and are largely or completely dependent on the Verde River for water. Temporally, river reaches can switch between gaining and losing with flow magnitude and river stage, but groundwater dependent vegetation along losing reaches of the Verde River depend on surface flows during the growing season as their groundwater sources.

The response of groundwater to flow events was explained by both flow magnitude and distance from the channel. Wells farther from the river have a lower amplitude and slower response than those closer to the channel. Differences in groundwater lag times and variability across the floodplain may be due to sediment texture variation in channel and floodplain influencing hydraulic conductivity in horizontal and vertical directions (Chen 2007). At lower Beasley Flat, groundwater stage was more correlated to river stage than other reaches due to the abundance of large cobble and responded more quickly to river stage changes. Hydraulic conductivity of the floodplain subsurface and riverbed also controlled the rate of nightly groundwater recharge during the growing season

when groundwater levels vary by ~5-10 cm per day as a result of evapotranspiration (Zhu et al. 2011; Loheide et al. 2005).

Diurnal groundwater variation along the Verde River begins during mid-April leaf-out and is at its maximum in May through July but becomes less distinctive with the commencement of summer monsoonal storms. This is distinctly different than other rivers where groundwater variations increase through the growing season (Butler et al. 2007). However, our findings are consistent with another study on the San Pedro River in Arizona where the amplitude of daily variations was strongest in June and early July before monsoon rain driven storms create small flood peaks and alluvial groundwater rises (Goodrich et al. 2000). Inflow to the alluvial aquifer throughout the day and especially at night replaces groundwater transpired during the day along the Verde River, confirming the connectivity between the river and floodplain groundwater. Decreases in river stage due to potential climate changes and/or water extraction could influence the rate of groundwater recharge (Zhu et al. 2011). We found that evapotranspiration did not deplete groundwater leading to a lowering of the floodplain water table, however, it is unclear how a reduction of summer flows might affect the rate of recharge. Steepening hydraulic gradients may increase the rate of exchange between the river and alluvial groundwater but shrinking the stream wetted perimeter could reduce the area of exchange and limit groundwater recharge affecting riparian plants (Cognac and Ronayne 2020).

Differences in the amplitude of diurnal groundwater variation across the floodplain may be influenced by vegetation type ET rates, soil properties and their hydraulic conductivity and water hold capacity, temperature, windspeed, and humidity. Higher rates of ET have been reported for riparian trees compared to shrubs, herbs and grasses (Schilling 2007; Satchithanatham et al. 2017). Larger variations were observed in areas dominated by wetland plants and more uniform subsurface sediment texture in a Wyoming watershed (Lautz 2008). Although comparisons of ET rates between

vegetation types was not within the scope of this study, compositional shifts along the Verde River could alter local alluvial groundwater levels, regional water budgets, and downstream water yields and water quality.

#### *Vegetation Guilds Along Hydrologic Gradients*

The dominant vegetation species on the Verde River are included in the tall tree guild with the most abundant being *Salix gooddingii* (willow) followed by *Populus fremontii* (cottonwood). We found that flood exceedance probability and depth to groundwater were useful in explaining the distribution of tall trees, short trees, drought tolerant shrubs, generalist shrubs, and tall and short wetland herbs. Depth to alluvial groundwater was also a stronger predictor of riparian plant distributions than flood exceedance probability on Cherry Creek in Arizona (Merritt and Bateman 2012). Tall trees were less likely to occupy areas where groundwater was deeper than 2.55 m at our study reaches on the Verde River similar to groundwater depth thresholds for *Populus fremontii* and *Salix gooddingii* along the San Pedro River in Arizona ( $< 2.6$  m, Lite and Stromberg 2005), Cherry Creek ( $< 2.0$  m, Merritt and Bateman 2012), and other rivers in the Sonoran Desert (Horton et al. 2001; Stromberg et al. 1991).

Our study included both woody and herbaceous guilds as herbaceous species outnumber woody species and may be more responsive to environmental changes on short timescales. In general, woody guilds were more likely to be predicted by hydrologic variables than herbaceous guilds, similar to a study in Sweden where almost half of graminoid and forb species were impactive to flow regulation (Bejarano et al. 2020). We used the same functional traits to group woody and herbaceous species into guilds, but we may have excluded traits more relevant in determining herbaceous hydrologic niche, such as aerenchyma tissue and root/shoot ratios (Pan et al. 2020). Variation in herbaceous species presence/absence may be driven by different hydrologic variables like intra-annual flow fluctuation and low flow duration (Bejarano et al. 2020). The assembly of

herbaceous communities may also be affected by a combination of hydrology and other environmental variables such as land-use, nutrient availability, soil moisture, and light availability (Angiolini et al. 2017). Forbs and graminoids had the greatest decreases in species richness along rivers in Sweden in response to river regulation (Bejarano et al. 2020) stressing the need to further assess the response of these growth habits alongside trees and shrubs. We modeled vegetation guilds across a gradient of groundwater at low flow, however, we acknowledge that species may require a range of conditions throughout their lifecycle for establishment, growth, and survival on floodplain surfaces. Uncertainty in hydrologic conditions and our focus on depth to groundwater during the lowest part of the growing season was useful to explain the distribution of plants with a wide range of life history strategies, but different groundwater scenarios likely play a role in the persistence of seedlings and juveniles, particularly for species within the tall tree guild.

#### *Hydrologic Scenarios and Shifts in Riparian Guilds*

Reductions in floodplain groundwater levels could drastically decrease the occurrence of species within the tall and short riparian tree and flood tolerant shrub guilds. If groundwater levels drop by 1.00 m, flood tolerant shrubs may disappear from current floodplain surfaces due to its shallow groundwater threshold (0.90 m). Riparian specialist species also fared the worst in response to scenarios of hydrologic change along the Vindel River in Sweden with large reductions predicted for those species occupying narrow ranges of inundation tolerances (Jansson et al. 2019). Riparian forests and willow shrubs were also projected to lose the most species based on climate change scenarios with species losses ranging from 1-13% (Ström et al. 2012). Rapid changes in groundwater depth may disconnect riparian phreatophytes from water sources and result in reduced canopy cover and tree dieback. Tree root extension may not be able to keep pace with groundwater drawdown (Williams and Cooper 2005).

Our simulations of alterations to winter floods and summer flows had less of a predicted effect on the areal coverage of guilds compared to simulations of groundwater decrease. Tall tree areal coverage was predicted to change by only 0.7-1.1% in response to altered winter flood magnitudes. Our results show an 0.3-7% increases in drought tolerant and generalist shrubs with decreases in large winter flood magnitudes. Others, however, have demonstrated more dramatic shifts away from disturbance-adapted riparian (tall) trees and replacement of riparian obligates with upland drought-adapted guilds from decreases in flood frequency (Lytle et al. 2017; Tonkin et al. 2017). Changes in hydrology have contributed to an increase of mesquite (*Prosopis velutina*), a member of our drought tolerant shrub guild, of more than 300% since 1972 along the Upper San Pedro River in Arizona (Williams et al. 2006) and encroachment of gallery forests by this species is predicted to increase within the next 100 years (Dixon et al. 2009). Although mesquite provides essential habitat for migratory birds (McGrath et al. 2008), loss of riparian trees will be detrimental for other birds that preferentially use tall trees for nesting, foraging, and breeding (Smith and Finch 2014). Increased flood frequency may also lead to a shift toward younger trees (Stromberg et al. 2010) with reductions in forest stand basal area and woody stem densities, important factors for the provisioning of bird habitat (Cubley et al. 2020). Many of the riparian trees in our study reaches are mature and we have observed little recruitment.

Our scenario of changes in streamflow does not account for an increase in the prevalence of drought, which may occur more frequency and severely, further decreasing streamflow past our projections (Serrat-Capdevila et al. 2013). Changes in monsoonal precipitation will also influence flood frequency, but future patterns are uncertain although limited evidence suggests that summer storms will occur later in the year with more severity (Cook et al. 2013; Serrat-Capdevila et al. 2013). Our 2D hydraulic models also assume stationary channel and floodplain geometry, but high flows

that either scour surfaces or deposit large amounts of sediment could change the vegetation plot elevations.

### *Conclusion*

Arid regions of the world are expected to experience increased precipitation variability with severe droughts that lead to hydrologic stress (Pyne and Poff 2017). Climate change in the American Southwest is predicted to increased temperature and evapotranspiration rates and totals (Garfin et al. 2014) with reduced precipitation as snow that will lower summer streamflow (Seager et al. 2013). In the Verde River basin, perennial flowing portions of the river network are predicted to diminish 8-20% during the spring and early summer months (Jaeger et al. 2014) which could result in lower groundwater recharge along losing reaches. Hydrologic changes are expected to be exacerbated where flow is jointly affected by climate change (Woo et al. 2008) and human water development (Palmer et al. 2009). Upstream of our study reaches, Yavapai County is one of the fastest growing rural areas in the United States and demand for water resources is rapidly increasing (Blasch et al. 2006). Riparian forests along the Verde River are highly dependent on groundwater resources during periods of drought and low streamflow with many trees unable to persist where groundwater is deeper than 2 m.

Monitoring schemes using guilds or cornerstone species have been proposed to maintain ecosystem functioning along rivers (Jansson et al. 2019) and we demonstrate the applicability of vegetation guilds that occupy distinct hydrologic niches on floodplains. The delineation of vegetation guilds and their hydrologic thresholds can assist managers in efforts to preserve and maintain the outstandingly remarkable scenic, fish and wildlife, and historic, and culture values of the wild and scenic segments of the Verde River. Perennial flow and natural flood regimes are essential for the conservation of diverse riparian habitats along the Verde River that include species within our tall tree, short tree, flood tolerant shrub, and drought tolerant shrub guild.

Table 3.1 Vegetation guilds along the Verde River, the number of member species, and the dominant species within each guild. Guilds previously defined in chapter 2.

| <b>Guild Name</b>       | <b>Guild Code</b> | <b>Dominant Member Species</b>                                     | <b># of Species</b> |
|-------------------------|-------------------|--------------------------------------------------------------------|---------------------|
| Tall trees              | T1                | <i>Salix gooddingii</i> , <i>Populus fremontii</i>                 | 4                   |
| Short trees             | T2                | <i>Fraxinus velutina</i> , <i>Morus alba</i>                       | 2                   |
| Flood Tolerant Shrubs   | S1                | <i>Salix exigua</i> , <i>Baccharis salicifolia</i>                 | 2                   |
| Drought Tolerant Shrubs | S2                | <i>Prosopis velutina</i> , <i>Celtis reticulata</i> ,              | 4                   |
| Generalist Shrubs       | S3                | <i>Ambrosia monogyra</i> , <i>Baccharis sarothroides</i>           | 7                   |
| Short wetland herbs     | A                 | <i>Schedonorus arundinaceus</i> , <i>Schoenoplectus americanus</i> | 7                   |
| Tall wetland herbs      | B                 | <i>Phragmites australis</i> , <i>Typha domingensis</i>             | 4                   |
| Ruderal perennial herbs | C                 | <i>Bromus diandrus</i> , <i>Ambrosia psilostachya</i>              | 3                   |
| Ruderal annual herbs    | D                 | <i>Bromus rubra</i> , <i>Mellilotus indicus</i>                    | 6                   |
| Drought Tolerant herbs  | E                 | <i>Cynodon dactylon</i> , <i>Sorghum halepense</i>                 | 4                   |
| Large Seeded Herbs      | F                 | <i>Datura wrightii</i> , <i>Xanthium strumarium</i>                | 4                   |
| High SLA Herbs          | G                 | <i>Hydrocotyle verticillata</i> , <i>Rumex</i> spp.                | 3                   |

Table 3.2 Guild and individual species distribution models and metrics of model performance including area under the ROC curve (AUC), percentage of correct classifications (balanced accuracy using specificity and sensitivity), Cohen's kappa, and the threshold probability of occurrence (Prob). AUC values > 0.7 indicate a fair to high performing model.

| <b>Guild/Species</b>   | <b>Model</b>              | <b>AUC</b> | <b>Accuracy</b> | <b>Kappa</b> | <b>Prob</b> |
|------------------------|---------------------------|------------|-----------------|--------------|-------------|
| Tall Tree (T1)         | T1 ~ EP + EP <sup>2</sup> | 0.82       | 81.0%           | 0.62         | 0.41        |
| Tall Tree (T1)         | T1 ~ GW + GW <sup>2</sup> | 0.90       | 86.8%           | 0.74         | 0.38        |
| <i>POPUFRE</i>         | PF ~ GW + GW <sup>2</sup> | 0.86       | 84.6%           | 0.52         | 0.31        |
| <i>SALIGOO</i>         | SG ~ GW + GW <sup>2</sup> | 0.69       | 71.8%           | 0.39         | 0.41        |
| Short Tree (T2)        | T2 ~ GW + GW <sup>2</sup> | 0.83       | 70.9%           | 0.32         | 0.24        |
| <i>FRAXVEL</i>         | FV ~ GW + GW <sup>2</sup> | 0.84       | 78.3%           | 0.32         | 0.22        |
| Flood Tol. Shrub (S1)  | S1 ~ GW                   | 0.72       | 69.6%           | 0.19         | 0.22        |
| <i>SALJEXI</i>         | SE ~ GW                   | 0.84       | 77.9%           | 0.29         | 0.13        |
| Drgt Tol. Shrub (S2)   | S2 ~ EP                   | 0.82       | 84.6%           | 0.79         | 0.03        |
| Drgt Tol. Shrub (S2)   | S2 ~ GW                   | 0.86       | 82.2%           | 0.55         | 0.08        |
| <i>PROSVEL</i>         | PV ~ EP                   | 0.95       | 96.4%           | 0.82         | 0.05        |
| <i>PROSVEL</i>         | PV ~ GW                   | 0.95       | 90.9%           | 0.75         | 0.18        |
| Generalist Shrub (S3)  | S3 ~ EP                   | 0.89       | 80.5%           | 0.50         | 0.36        |
| Generalist Shrub (S3)  | S3 ~ GW                   | 0.86       | 84.5%           | 0.51         | 0.13        |
| <i>AMBRMON</i>         | AM ~ EP                   | 0.90       | 89.1%           | 0.45         | 0.08        |
| <i>AMBRMON</i>         | AM ~ GW                   | 0.92       | 91.3%           | 0.52         | 0.11        |
| Short Wetland Herb (A) | A ~ GW + Reach            | 0.71       | 71.3%           | 0.40         | 0.29        |
| <i>SCHEARU</i>         | SU ~ GW + Reach           | 0.90       | 88.3%           | 0.65         | 0.41        |
| A <sub>3</sub> Up Beas | A ~ GW                    | 0.98       | 92.7%           | 0.71         | 0.62        |
| Tall Wetland Herb (B)  | B ~ GW                    | 0.88       | 85.6%           | 0.61         | 0.34        |
| Tall Wetland Herb (B)  | B ~ EP                    | 0.87       | 72.6%           | 0.35         | 0.19        |
| <i>PHRAAUS</i>         | PA ~ EP                   | 0.78       | 77.7%           | 0.23         | 0.09        |
| <i>PHRAAUS</i>         | PA ~ GW                   | 0.79       | 84.3%           | 0.57         | 0.24        |

Table 3.3 Modeled proportional prevalence of vegetation guilds at study reaches along the Verde River, Arizona. We calculated the current prevalence along with changes in occurrence from simulated decreases in groundwater of 0.5 and 1.0 m.

| <b>Guild</b> | <b>Reach</b>  | <b>Current Occurrence (%)</b> | <b>0.50M GW (%)</b> | <b>1.00M GW (%)</b> |
|--------------|---------------|-------------------------------|---------------------|---------------------|
| T1           | Upper Beasley | 56.2                          | 48.9                | 36.8                |
| T1           | Lower Beasley | 53.8                          | 37.2                | 19.2                |
| T1           | Childs        | 46.5                          | 48.0                | 45.5                |
| T2           | Upper Beasley | 21.5                          | 5.3                 | 2.2                 |
| T2           | Lower Beasley | 8.8                           | 4.0                 | 1.3                 |
| T2           | Childs        | 16.6                          | 16.7                | 2.7                 |
| S1           | Upper Beasley | 9.6                           | 3.0                 | 0.4                 |
| S1           | Lower Beasley | 6.4                           | 1.5                 | 0.2                 |
| S1           | Childs        | 23.9                          | 4.3                 | 1.0                 |
| S2           | Upper Beasley | 52.8                          | 67.0                | 91.7                |
| S2           | Lower Beasley | 71.3                          | 86.5                | 100.0               |
| S2           | Childs        | 52.2                          | 59.3                | 83.8                |
| S3           | Upper Beasley | 38.5                          | 42.9                | 55.5                |
| S3           | Lower Beasley | 37.9                          | 52.8                | 72.6                |
| S3           | Childs        | 46.0                          | 49.0                | 52.4                |
| A            | Upper Beasley | 20.0                          | 4.3                 | 1.3                 |
| B            | Upper Beasley | 20.8                          | 4.5                 | 1.4                 |
| B            | Lower Beasley | 10.9                          | 2.8                 | 0.5                 |
| B            | Childs        | 36.1                          | 10.9                | 1.9                 |

Table. 3.4 Modeled proportional prevalence of vegetation guilds as a function of flood exceedance probability at study reaches along the Verde River. We calculated the proportional percent of guilds using exceedance probability from the last 30 years of record and three future flow scenarios. Scenario 1 = decrease in growing season flows (May- middle July) by 10%, Scenario 2 = increased winter storm magnitude and 10% decrease in low flows, Scenario 3 = decrease in winter storm magnitude and 10% decrease in growing season low flow. See methods section for more detailed description.

| <b>Guild</b> | <b>Reach</b>  | <b>Current % Occurrence</b> | <b>Scenario 1</b> | <b>Scenario 2</b> | <b>Scenario 3</b> |
|--------------|---------------|-----------------------------|-------------------|-------------------|-------------------|
| T1           | Upper Beasley | 58.8                        | 58.8              | 59.9              | 57.7              |
| T1           | Lower Beasley | 73.5                        | 73.5              | 74.4              | 72.8              |
| T1           | Childs        | 48.7                        | 48.7              | 49.7              | 48.0              |
| S2           | Upper Beasley | 70.9                        | 70.9              | 65.3              | 75.7              |
| S2           | Lower Beasley | 51.7                        | 51.7              | 48.9              | 58.5              |
| S2           | Childs        | 56.2                        | 56.2              | 55.6              | 57.1              |
| S3           | Upper Beasley | 37.6                        | 37.6              | 37.2              | 38.0              |
| S3           | Lower Beasley | 24.1                        | 24.1              | 23.8              | 24.4              |
| S3           | Childs        | 46.7                        | 46.7              | 46.5              | 47.0              |
| B            | Upper Beasley | 8.8                         | 8.8               | 9.7               | 8.3               |
| B            | Lower Beasley | 18.4                        | 18.4              | 20.4              | 16.5              |
| B            | Childs        | 26.4                        | 26.4              | 28.9              | 24.8              |

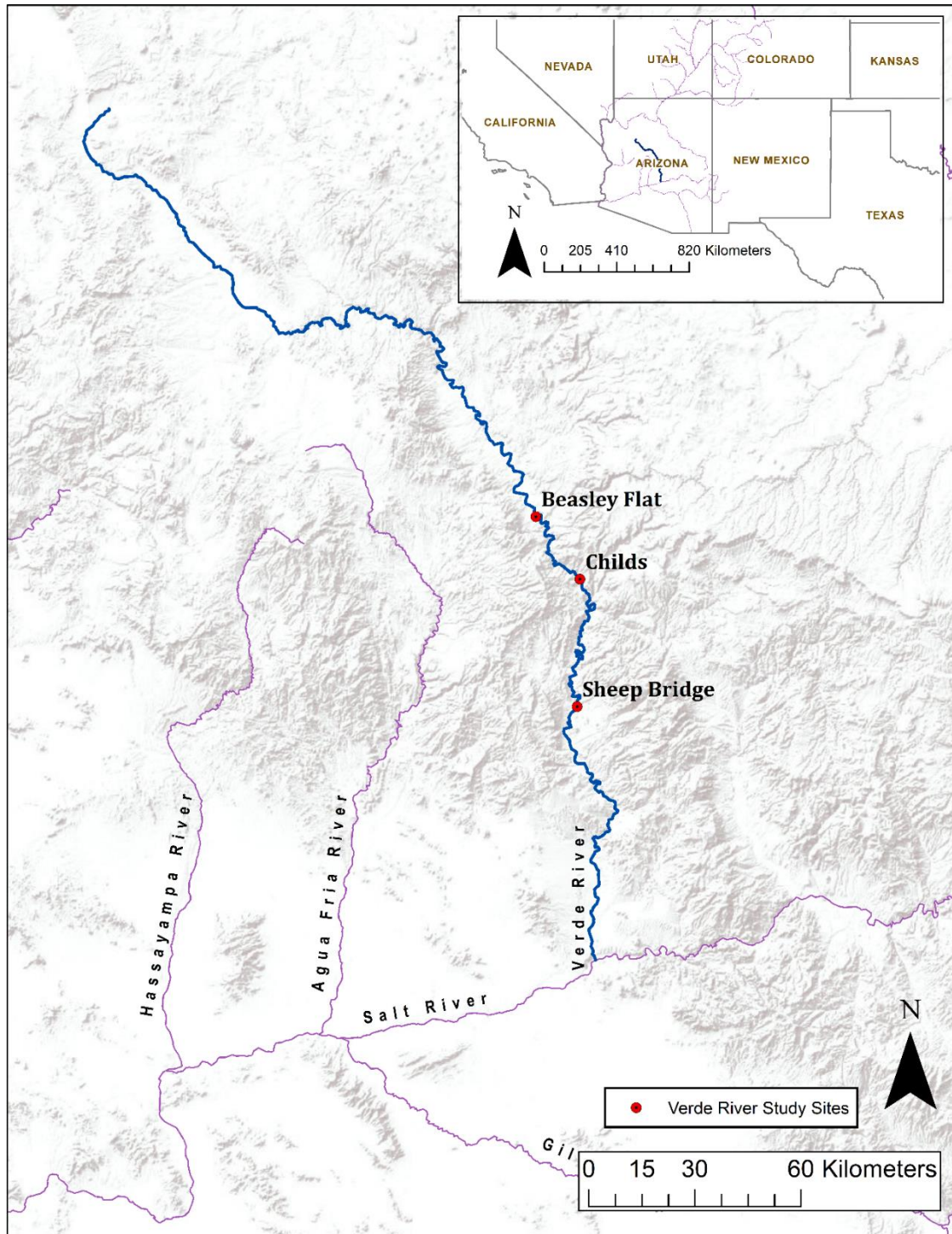


Figure 3.1 Location of study reaches along the Verde River in Arizona. Study reaches at Beasley Flat and Childs were used in this chapter.

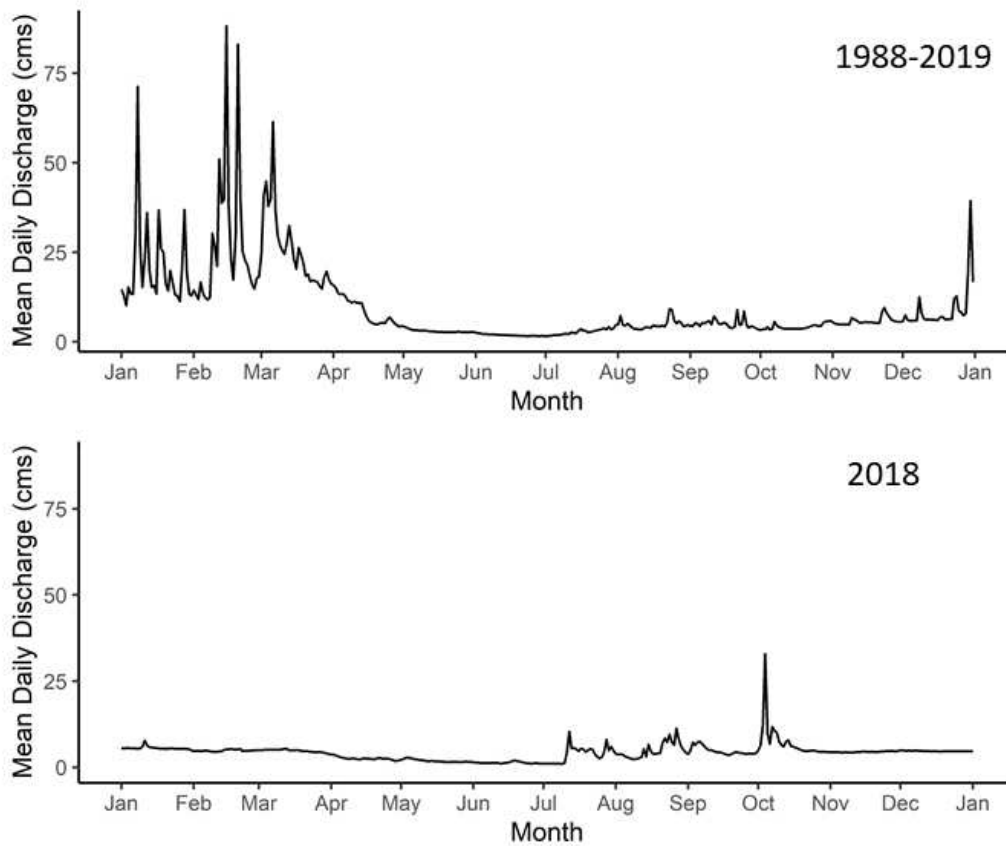


Figure 3.2 Mean daily discharge for period of record from 1988-2019 (top) and daily discharge ( $\text{m}^3/\text{s}$ ) January 2018-December 2018 using daily flow data from the Camp Verde gauge (USGS ##9506000) (bottom).

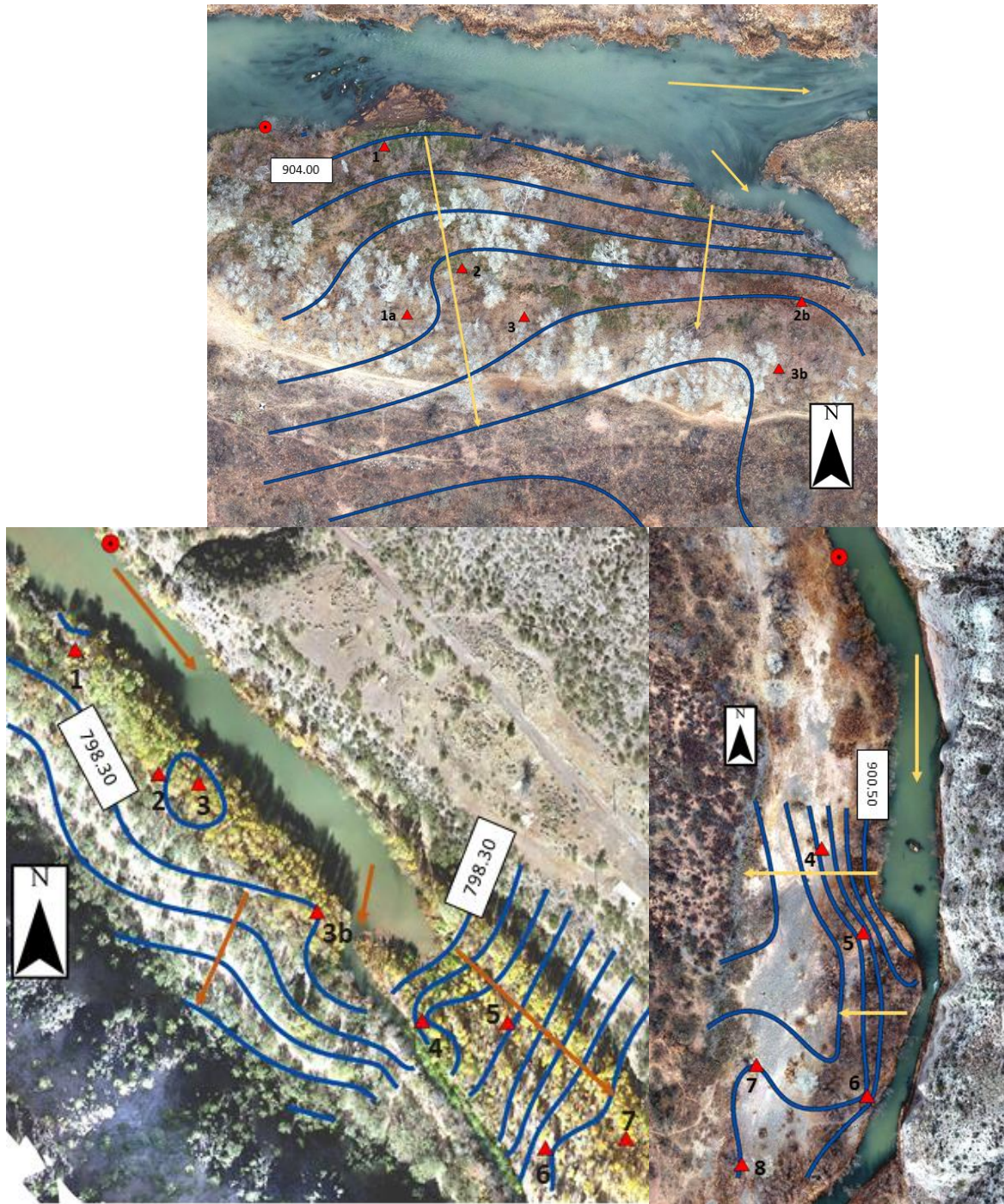


Figure 3.3 Water table contour map at upper Beasley Flat (top), lower Beasley Flat (bottom right), and Childs (bottom left) study area representing groundwater and surface water conditions on July 1, 2018 when Verde River flow was low and stable. Flow direction is illustrated by arrows. Elevations are represented as meters above sea level and the contour interval at upper Beasley Flat is 0.10 m, 0.25 m, at lower Beasley Flat, and 0.10 m at Childs. Red triangles represent monitoring wells and red circles indicate location of river staff gauges. Flow at time of interpolation was  $1.09 \text{ m}^3/\text{s}$  at the Camp Verde USGS gauge #9506000.

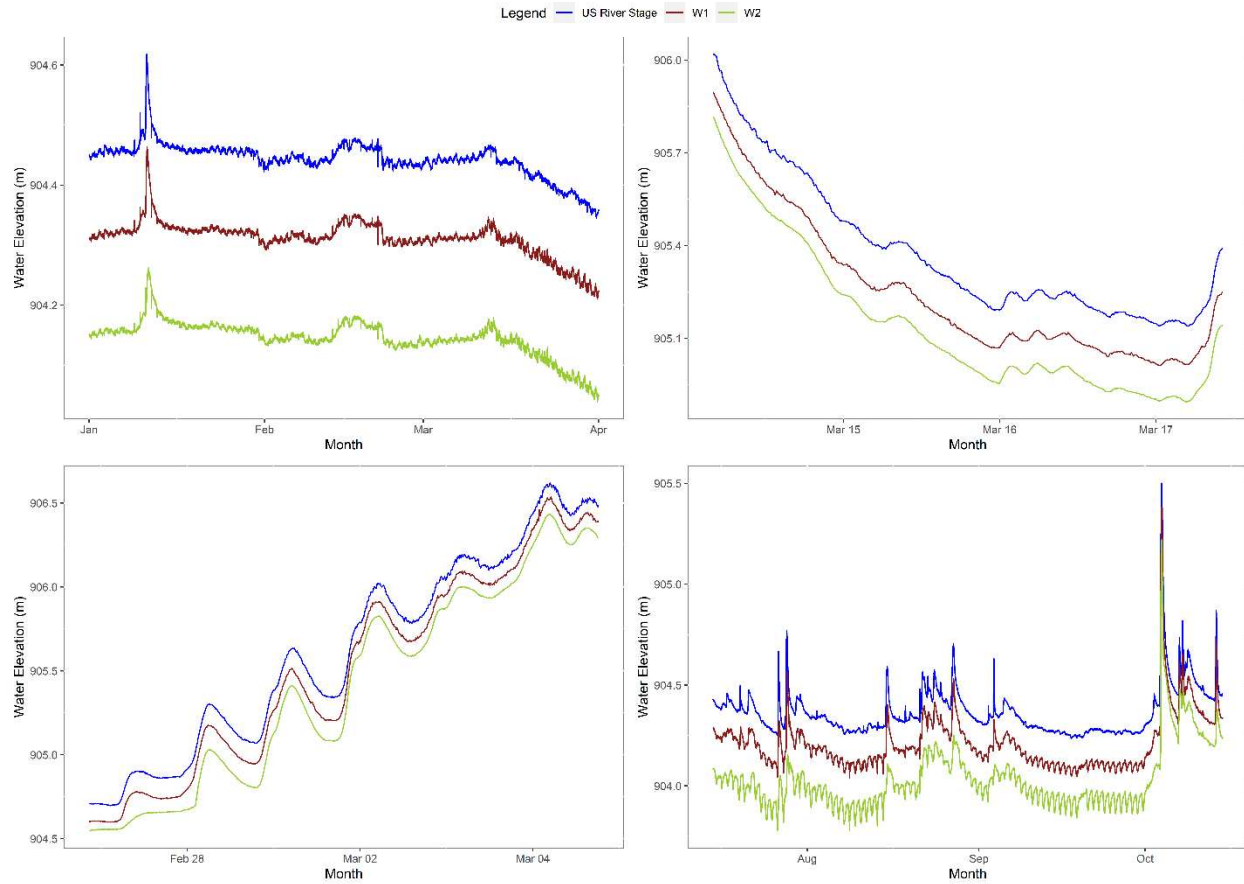


Figure 3.4 Stream and groundwater levels are highly correlated during stable winter periods (top left, W1 Spearman rank correlation  $r=0.97$ ,  $P<0.001$ , W2  $r=0.96$ ,  $P<0.001$ ), ascending flood limbs (bottom left, W1 and W2 Spearman rank correlation  $r=0.99$ ,  $P<0.001$ ), descending flood limbs (top right, W1 and W2 Spearman rank correlation  $r=0.99$ ,  $P<0.001$ ), and during a summer monsoon period (bottom right, W1 Spearman rank correlation  $r=0.98$ ,  $P<0.001$ , W2  $r=0.88$ ,  $P<0.001$ ) demonstrating high connectivity between the river and alluvial groundwater. Graphs shows upstream pressure transducer at the upstream Beasley Flat reach (US River Stage) and two groundwater wells, well 1 (W1) located closer to the river and well 2 (W2) located further into the riparian forest (see Figure 3.3).

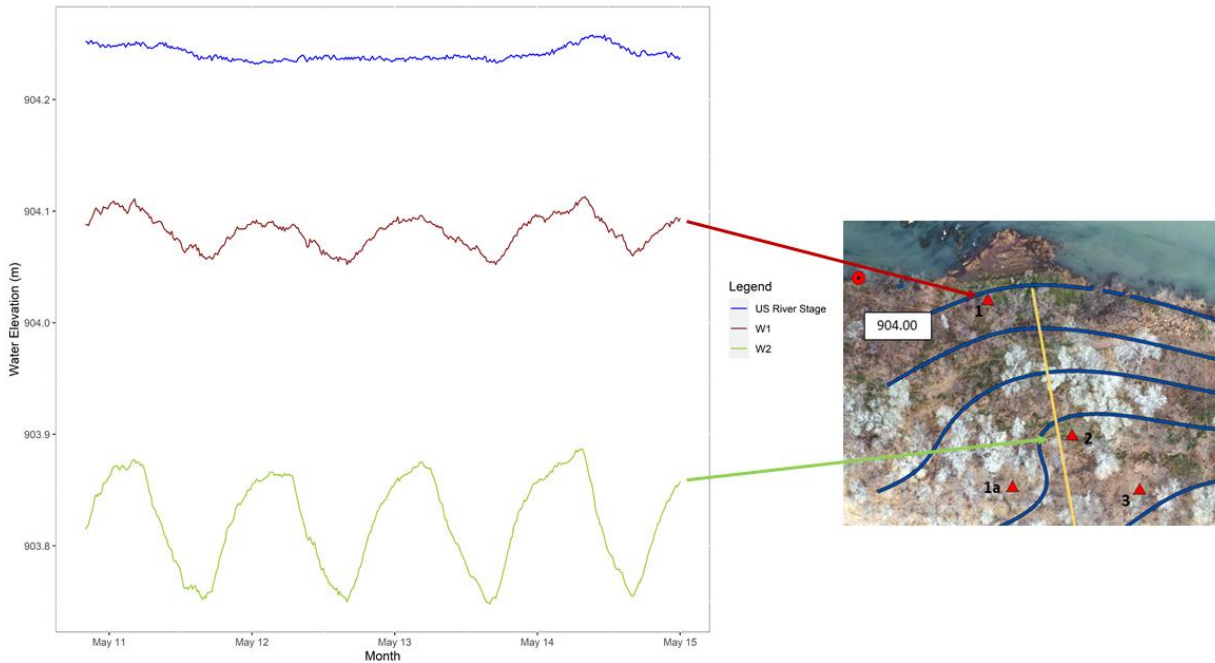


Figure 3.5 Stream and well elevations were not as highly correlated during summer months due to diurnal variations in groundwater levels from forest evapotranspiration. Graphs show the upstream pressure transducer at the upper Beasley Flat (US River Stage) and Well 1 (W1, Spearman rank correlation  $r = 0.97$ ;  $P < 0.001$ ) located 10 m from the river and Well 2 (W2,  $r = 0.87$ ;  $P < 0.001$ ), located 40 m from the river that has larger diurnal fluctuations from April to early July 2018.

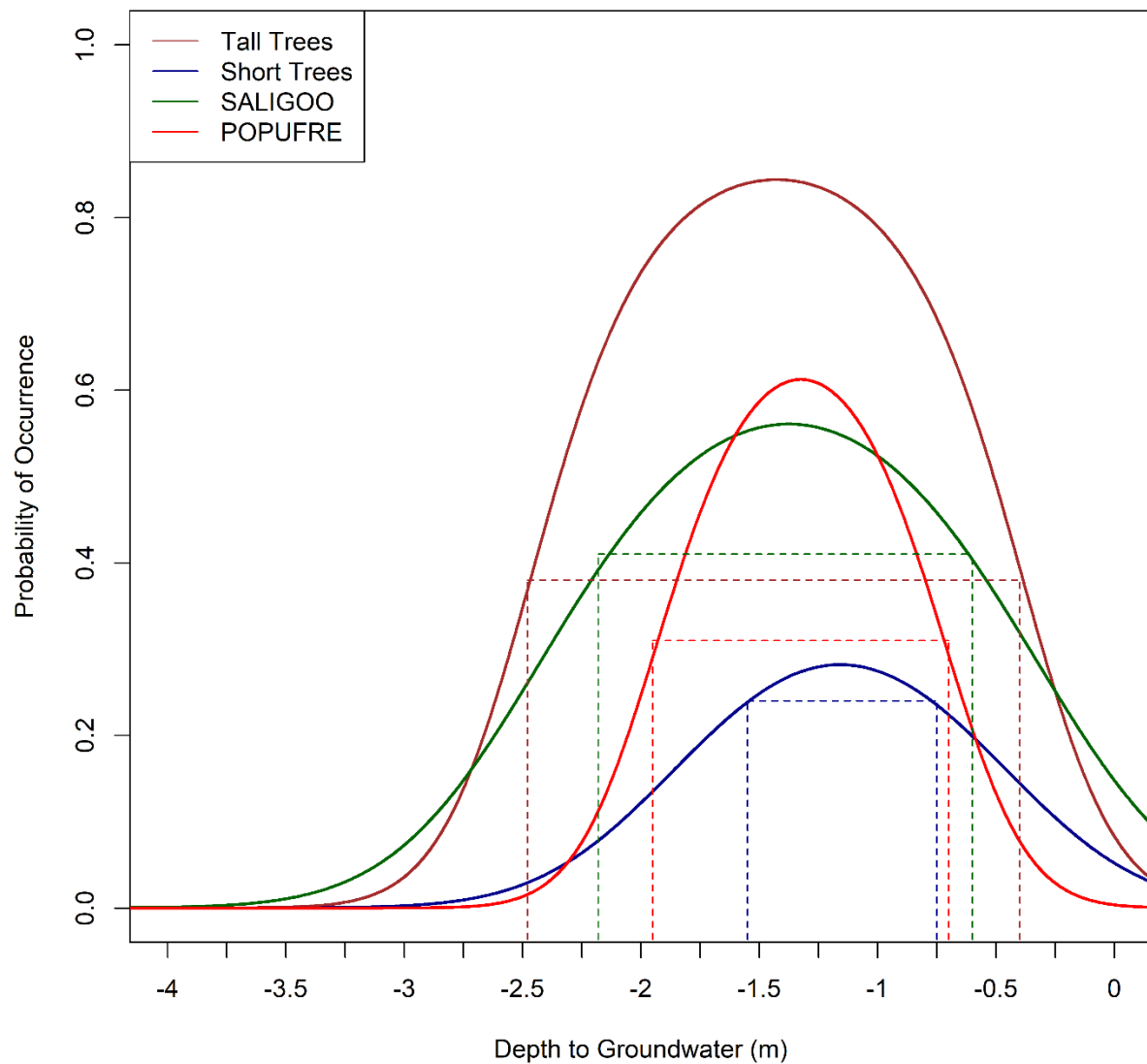


Figure 3.6 Predicted probability of occurrence of the tall tree guild (T1), short tree (T2), *Populus fremontii*, *Salix gooddingii* along a gradient of groundwater depth. Groundwater thresholds for guilds and species are shown with dashed lines. Tall trees were more likely to occur where groundwater depth was less than 2.50 m and greater than 0.4 m from the surface while short trees had a narrower hydrologic width (1.55 to 0.75 m).

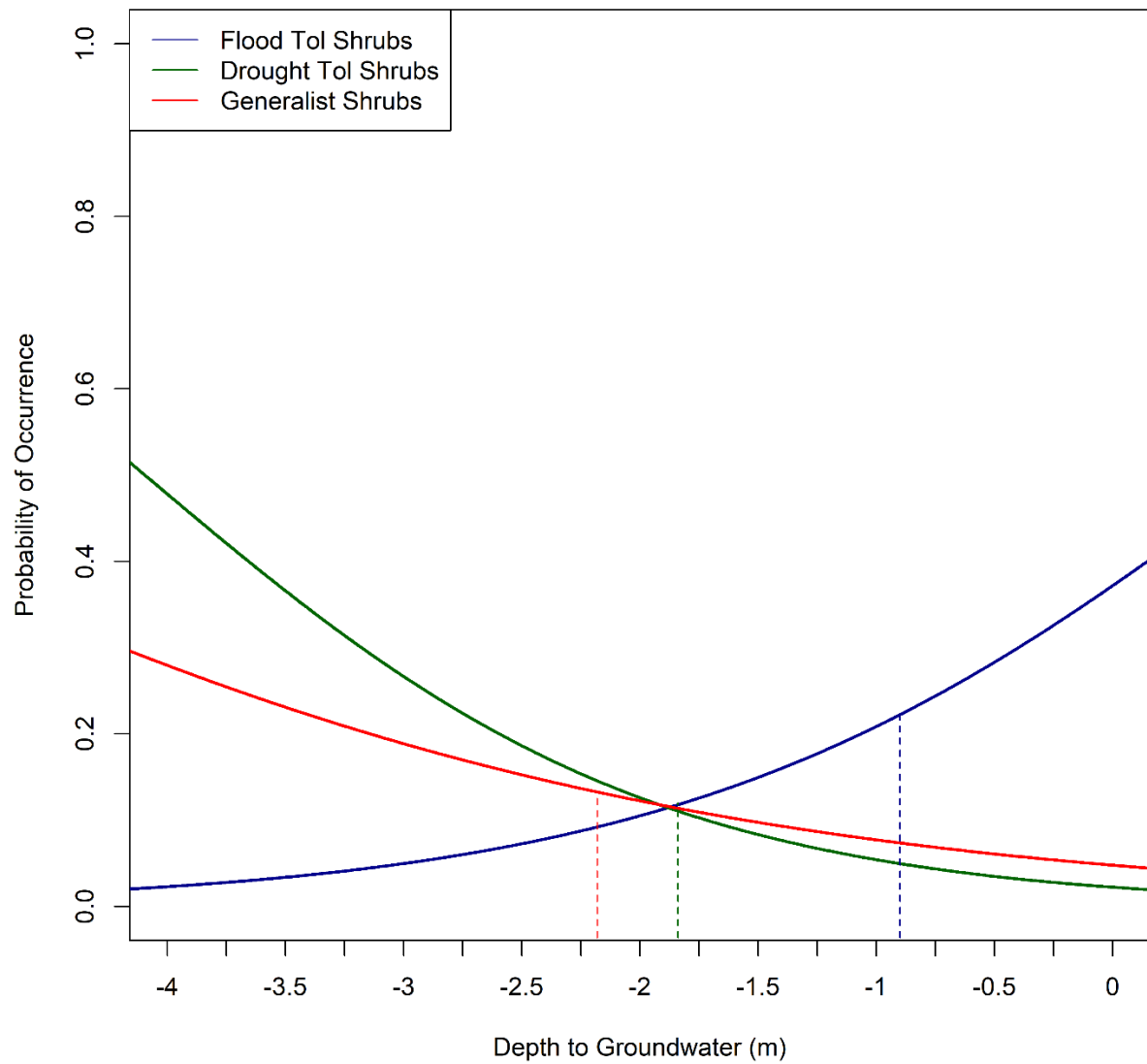


Figure 3.7 Predicted probability of occurrence of flood tolerant shrubs (S1), drought tolerant shrubs (S2), and generalist shrubs (S3) along a depth to groundwater gradient along the Verde River in Arizona. Hydrologic thresholds indicated for each guild by dashed lines S1 = 0.90 m, S2 = 1.84 m, S3 = 2.18 m.

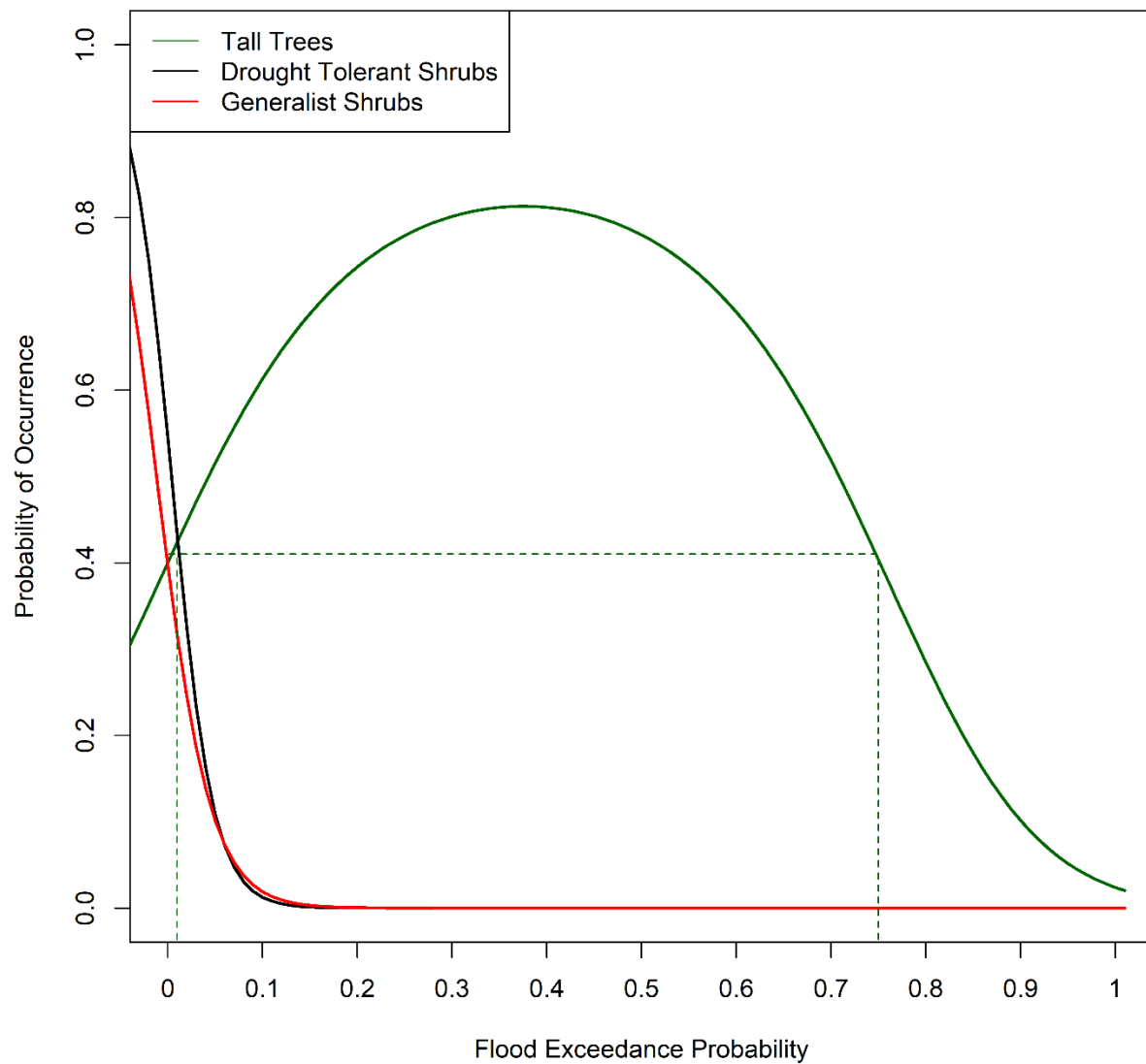


Figure 3.8 Predicted probability of occurrence of tall trees, drought tolerant shrubs, and generalist shrubs along a gradient of flood exceedance probability. Tall trees tolerant were more likely to occur where flood exceedance probability was between 1% to 75% while drought tolerant shrubs occurred in areas that were flooded less frequently (3%). Generalist shrubs had lower flood tolerance and occurred where exceedance probability was less than 2%.

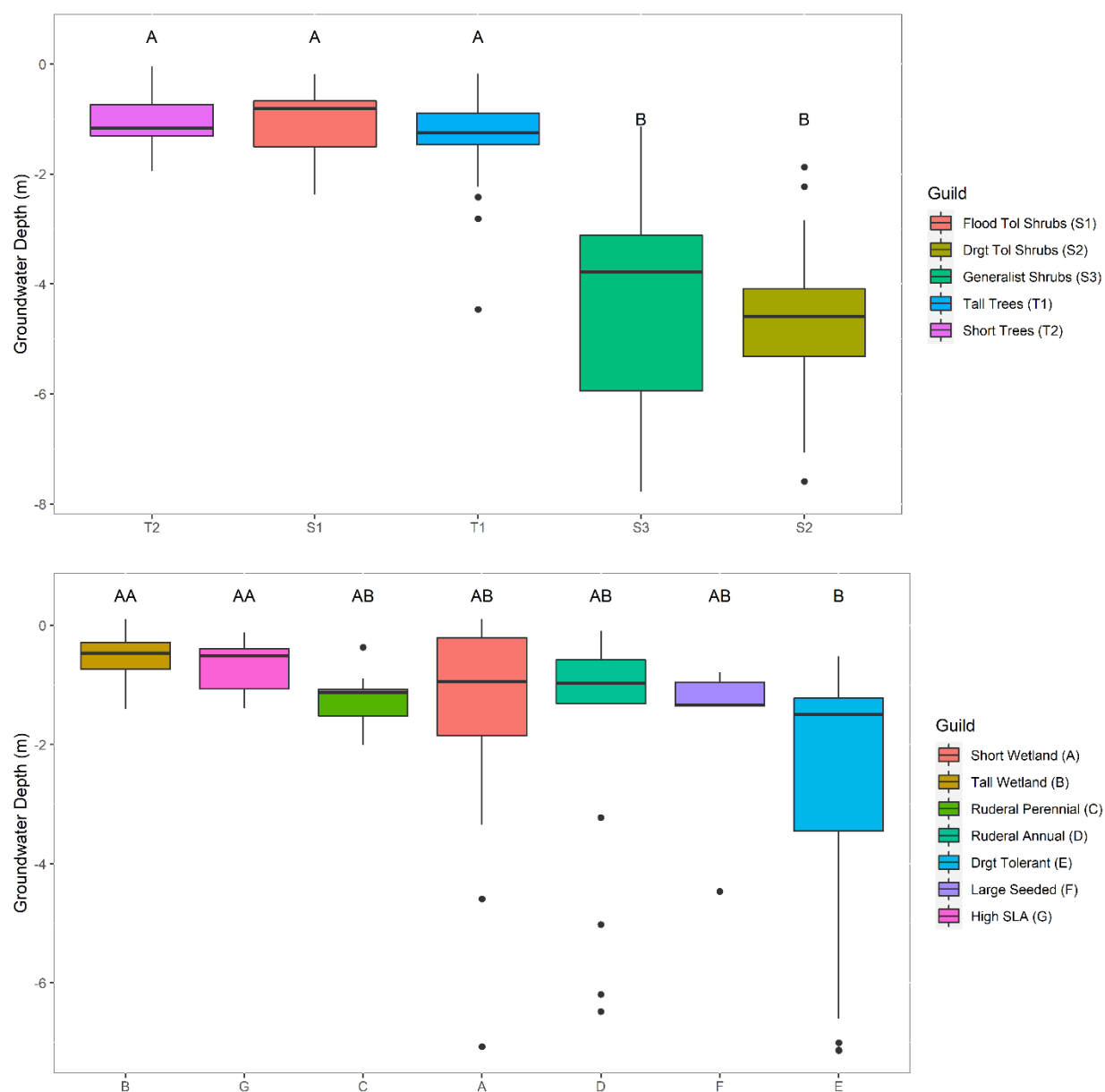


Figure 3.9 Depth to groundwater across plots with greater than 10% cover of woody (top) and herbaceous (bottom) vegetation guilds. Depth to groundwater was interpolated across plots on July 1, 2018, during the time period of the historical 7-day minimum flow.

## **4 Modeling riparian vegetation guild response to hydrologic change along rivers in the Colorado River basin**

### **4.1 Introduction**

Managers and scientists are challenged with quantifying river flows to maintain the ecological functions of riparian areas while simultaneously meeting society's growing water needs for urban, agricultural, and industrial uses (Arthington 2012). Dams, water storage, diversions, and groundwater pumping have altered the natural streamflow patterns of many rivers and increases in human water withdrawal will lead to a reduction in annual streamflow and lower alluvial groundwater levels (Rajagopalan et al. 2009; Palmer et al. 2008; IPCC 2014; Laizé et al. 2014). Understanding if reduced or otherwise altered streamflow results in shifts, directional or otherwise, in riparian ecosystems involves assessing the current distribution of biota along hydrologic gradients and quantifying likely changes in suitable habitat under different flow regimes. The response of each species to the same flow alteration could vary among watersheds with different climates, existing flow regimes, and geomorphologic settings (Keddy 1992; Palmer et al. 2009). Such predictions of vegetation and functional change in riparian areas can inform decision-making and, in some cases, assure that human water demands are met within acceptable changes in riparian and aquatic ecosystem functioning.

Changes in natural streamflow patterns can lead to a change in the presence, frequency, and abundance of native plant species, altering vegetation composition and ecosystem functioning (Friedman et al. 2005; Auble et al. 2005). In arid areas, lower summer flows and reduced flood frequencies contribute to riparian tree stress, dieback, and reduced recruitment to maintain populations given natural patterns of mortality (Stromberg et al. 2005). In arid and semi-arid regions of the world, changes in water availability and flow patterns are predicted to increase the dominance of drought-tolerant plant species (Webb and Leake 2006) and alter vegetation structure and the

provisioning of habitat for migratory and resident birds (Cubley et al. 2020) as well as mammals, insects, and herptiles (Selwood et al. 2015; Ramey and Richardson 2017). Maintenance of riparian vegetation requires an understanding of optimal hydrologic ranges that facilitate species establishment and persistence (Merritt and Poff 2010; Chen et al. 2015) and whether plant relationships to hydrologic conditions are similar within and across watersheds. Climate change is predicted to alter streamflow regimes and riparian plant responses may differ based on characteristics including elevation, annual precipitation, and watershed area (Null et al. 2010).

Vegetation distribution models can help scientists make predictions of the expansion and contraction of species under different climate and hydrologic scenarios (Cao et al. 2015). Similarities in vegetation response to flow alteration and water availability between rivers could reduce the need for data collection on every river of concern to support in-stream flows and identify rivers of high resource conservation value (Murray et al. 2011). The response of individual plant species may vary between rivers in different climate regions with varied flow patterns and generalizations may not be possible (Patten 1998; Shafroth et al. 2000; Lesica and Miles 2001). However, the use of functionally equivalent groups of species may provide an approach that is applicable between rivers for predicting plant response among and within river basins (Stromberg and Merritt 2015).

Plant species have evolved functional traits that allow them to tolerate or evade stressors including disturbance, inundation, and soil water variability (Snow and Vince 1984; Stromberg 1997). Experimental and observational studies demonstrate the segregation of plant species along groundwater depth and flood disturbance gradients (Auble et al. 1994; Araya et al. 2011). A riparian vegetation guild is an assemblage of plant species with similar ecological traits adapting them to resources and stressors along rivers (Merritt et al. 2010). A model of a riparian vegetation guild's distribution along hydrologic gradients may be useful for comparing that guild's distribution across

river reaches, rivers regions, and continents where floristic composition differs, but similar guilds occur (Merritt et al. 2010; Lytle et al. 2017).

The use of riparian vegetation guilds created with functional traits links species assembly to environmental filters (Westoby and Wright 2006). Functional trait-based approaches may provide different insights into patterns and relationships across gradients of disturbance compared to floristic studies alone (Mouillot et al. 2013). High species richness within vegetation guilds in theory indicate possible functional redundancy that could provide resilience against environmental perturbations (Naeem 1998; Laliberté et al. 2010). Trait-based predictions of riparian vegetation response to changes in streamflow and climate change may also be valuable for assessing possible changes in ecosystem functioning (Catford et al. 2013).

Understanding the magnitude and direction of vegetation response to perturbations across river basins can help in the development of predictions of altered composition of other biota (Chen and Olden 2018), food web structure, and rates of ecosystem processes (Ford and Vose 2007; Kominoski et al. 2013). The response of riparian vegetation guilds to hydrologic changes has been analyzed in Europe, North America, and Australia (Merritt et al. 2010; Lawson et al. 2015, Stromberg and Merritt 2016; Aguiar et al. 2018). However, few studies have examined whether riparian vegetation guilds within and across geographic regions currently occupy similar habitats and if they will occupy similar habitat under future flow conditions. Flow relationships supporting freshwater fish guilds in an area with high spring flows and summer monsoons were transferable within and across basins that had similar levels of flow alteration (Chen and Olden 2018). Guilds dependent on specific flow components were hypothesized to have narrower distributions than generalist guilds that can survive across wider environmental gradients (Freeman and Marcinek 2006).

Chen and Olden (2018) found that fish guild distributions were similar within and between rivers with similar flow regimes. However, we asked if riparian vegetation guilds and their habitat relationships would be similar along rivers and reaches at a larger regional scale with diverse climates and distinct flow regimes. In the western United States, the basin that is predicted to experience the largest reductions in streamflow is the Colorado River (Das et al. 2011). Therefore, analyzing the distribution of riparian vegetation guilds along hydrologic gradients on three rivers in the Colorado River basin could provide an important model of potential vegetation response to climate changes. Specifically, we addressed the following questions:

- 1) How do riparian vegetation guilds differ along rivers with distinct climate and hydrologic regimes?
- 2) How do groundwater depth and inundation duration-exceedance probability differ between study reaches and regions?
- 3) Can we use guild distribution models in one region and hydrologic setting to make inference to similar guilds in other regions? How transferable are guild distribution models?
- 4) Which ecoregional and riparian ecosystem types are most vulnerable to projected effects of climate change including lowered groundwater levels and/or reduced exceedance probability?

## **4.2 Methods**

We worked on three perennial rivers in the Colorado River basin; the Dolores and San Miguel Rivers in Colorado and the Verde River in Arizona (Figure 4.1). We selected reaches with similar valley confinement, although reach selection was limited on the Dolores River due to private land access and a prevalence of narrow canyons with constrained floodplains. Our study reach on the lower Dolores River differs from the other Colorado reaches in being largely unconfined and on private land. It is downstream from McPhee Dam and upstream from the confluence with the San

Miguel River near the town of Bedrock, Colorado (685623E, 4242832N). A second Dolores River reach is upstream from the dam, downstream from the town of Rico and upstream from Bear Creek on Forest Service-managed land (748809 E, 4162410N). The upper San Miguel study reach is downstream from Placerville, Colorado on land managed by the Bureau of Land Management (BLM) (753892E, 4213119N). The lower San Miguel River reach is upstream from Uravan, Colorado and is a Nature Conservancy preserve (700820E, 4245770N). Verde River study reaches are upstream from Horseshoe Dam and downstream from the town of Camp Verde within the section of river designated as Wild and Scenic as part of the National Wild and Scenic River System. We worked at three reaches, Beasley Flat (425500E, 3815635N), Childs (435625E, 3801102N), and Sheep Bridge (434697E, 3771403N). Reach-specific details can be found in Appendix Table 2.

The Verde River watershed is arid to semi-arid with an average of 18 inches of precipitation per year (Blasch et al. 2006) and large magnitude floods occurring following winter precipitation with smaller floods during the summer monsoon. Mean annual flow at the Camp Verde USGS gauge is  $9.74 \text{ m}^3/\text{s}$  over the last 30 years with the largest daily flow on January 8<sup>th</sup>, 1993 at  $1795 \text{ m}^3/\text{s}$ . Groundwater pumping and agricultural diversions in the Verde Valley have lowered water tables and streamflow (Wirt and Hjalmarson 2000).

The timing of high magnitude flows is more predictable on the Colorado Rivers with snowmelt dominated peak flows in May or early June (Figure 4.2, Smith and Finch 2016). Lower reaches of the San Miguel and Dolores Rivers experience late summer rainfall and 30% of the largest magnitude floods are in response to monsoon rain, not snow, and the intensity of summer rains decreases with elevation (Fleener 1997). Large differences in temperature and precipitation occur between the upstream and downstream study reaches in Colorado. Mean annual flow was  $13.04 \text{ m}^3/\text{s}$  on the lower Dolores River before construction of McPhee Dam in 1984, but now is  $6.01 \text{ m}^3/\text{s}$ . Downstream from the dam, a minimum flow standard limits “no flow” days, but annual peak

flows have been reduced by 60 %. The San Miguel River, a tributary of the Dolores River, has mean annual flow of 8.76 m<sup>3</sup>/s and only small diversions remove water from the river. Within the Colorado River basin, the San Miguel is one of the least regulated rivers.

### *Vegetation Analysis*

At each study reach (Verde River n = 3, San Miguel River n = 2, Dolores River n = 2) we established cross-valley transects perpendicular to the stream channel with 1 m<sup>2</sup> plots randomly located on each geomorphic surface. Percent canopy cover of each vascular plant species was determined by ocular estimate from the lowest extent of perennial vegetation to the upper edge of the riparian zone (Verde Beasley Flat 90 plots, Verde Childs 86 plots, Verde Sheep Bridge 89 plots, San Miguel Placerville 63 plots, San Miguel Uravan 79 plots, Dolores Bear Creek 71 plots, Dolores Bedrock 78 plots). Species nomenclature followed Ackerfield (2015) for the Colorado reaches and Kearney & Peebles (1960) for the Arizona sites updated using the integrated taxonomic information system (ITIS 2019).

Bird habitat quality was assessed in 100 m<sup>2</sup> plots in each study reach. We measured percent cover of litter, gravel, basal area of woody species, foliage height diversity, and mean vegetation canopy cover in four height classes (0-1.5, 1.6-4.0, and 4.1- > 9 m, Carothers 1974) to create a bird habitat index (Merritt and Bateman 2012). The bird habitat index was validated on the Verde River and high habitat index values predicted bird abundance, diversity, and richness (Cubley et al. 2020). We classified each vegetation plot based on the dominant woody vegetation guild to compare bird habitat index values across vegetation guilds, study regions, and reaches.

Plant traits were sampled in the field and collected from plant databases. For each species, we measured the height, specific leaf area, wood density, leaf <sup>13</sup>C:<sup>12</sup>C, and diameter at breast height (DBH) of three individual species at each reach. Collected trait information was averaged across river reaches within the study region to obtain a single trait value per dominant species. Methods for

the collection of specific leaf area and woody density follow protocols from Garnier et al. (2013). DBH was measured using calipers or a diameter tape and plant height was measured using a meter stick or clinometer. Seed mass, growth form, and resprout capability were taken from the USDA plant database (2018), Kew Royal Botanical Gardens (2016), or trait databases from studies on other western rivers. Vegetation guilds were previously classified along the Verde River (Cubley et al. 2020).

We used a Gower dissimilarity matrix as it allows for a combination of continuous, binary, and ordinal variables to group plants into guilds (Gower 1971; Legendre and Legendre 2012). Hierarchical cluster analysis generated dendrograms which were pruned using natural breaks to create vegetation guilds. Guild membership was tested using permutational multivariate analysis of variance (PERMANOVA) from a non-metric multidimensional scaling (NMDS) ordination in Primer-e v. 6.0 (Anderson 2014). Traits with non-normal distributions were log-transformed before analysis. We examined Spearman rank correlations and when two or more traits were correlated, and we removed the trait that had lower factor weighting in a principal component analysis (PCA). The final trait matrix for the Colorado study reaches included twenty-six species and eight traits. Final traits included rooting depth (ordinal), resprout capability, growth form, tissue density, height, specific leaf area, seed weight, and  $^{13}\text{C}:^{12}\text{C}$ . Functional richness was calculated as the number of woody guilds within each plot and functional redundancy as the number of species within each guild (Laliberté et al. 2010).

### *Hydrologic Analysis*

Groundwater monitoring wells were installed along the Verde River in 2017 and 2018, and in 2016 along the San Miguel and Dolores Rivers (Beasley  $n = 11$ , Childs = 8, Sheep Bridge  $n = 8$ , Placerville = 11, Uravan = 17, Bear Creek = 11, Bedrock = 8). Each well on the Verde River was equipped with a logging pressuring transducer (HOBO Model U20L-04 and U20-001-01) that

logged groundwater elevation every 15 minutes. On the San Miguel and Dolores Rivers one well per reach was equipped with a pressure transducer (In-Situ Model Rugged TROLL 200) and we measured depth to groundwater manually every two weeks for all wells during the summer of 2016. At all study reaches, a barometric pressure logger was used to correct pressure transducer data for atmospheric pressure. Depth to groundwater was interpolated for each vegetation plot during the growing season at a low flow period (mid-July 2017 in Colorado, early July 2018 in Arizona) as this period during low flow is the most stressful for riparian plants, particularly in arid landscapes. We used the thin plate spline method in the fields package of the statistical program R (Nychka et al. 2017). This interpolation method better represents the smooth surface and contour of groundwater compared to inverse distance weight interpolation where bulls' eyes are common with isolated data points (Franke 1982).

We conducted topographic surveys of vegetation transect including plots, channel morphology, and groundwater wells using real-time kinematic Global Positioning System (RTK-GPS) at each study reach. Data were recorded in the Universal Transverse Mercator (SI) coordinates in zone 12 using the WGS84 horizontal and NAVD88 vertical datum. One-dimensional step backwater hydraulic models were constructed to determine the inundating discharge and flood exceedance probability for each vegetation plot, a proxy for flood disturbance that can influence plant recruitment, loss of biomass, and plant survival (HEC-RAS, USACE 2005). Hydraulic models were calibrated using surveyed water surface elevations in 2017 and validated using water surface elevations from a subsequent survey in 2018 at Colorado study reaches (Appendix Table 3). No large changes in channel morphology were observed between 2016-2018. At the three Verde River study reaches, pressure transducers at the upstream and downstream end of each reach, recorded river stage every 15 minutes and were used to construct and validate 1-D hydraulic models across a

range of river discharge and stages (Appendix Table 3). Roughness coefficients were estimated using Coon (1998) and adjusted to calibrate measured and predicted water surface elevations.

Daily discharge data were obtained for each reach from USGS stream flow gages (Table 4.1) and exceedance probabilities were calculated using flow duration curves by fitting polynomial regressions (Richter 1996). On the Verde River we used mean daily flow from the last 30 years of the flow record, but at Colorado study reaches we used full records as floods were less frequent. We only used post-dam construction flow data at the Bedrock study reach (post-1986). Prior to dam construction the largest daily flow on the Dolores River at Bedrock occurred on April 30<sup>th</sup>, 1973 (230.8 m<sup>3</sup>/s) while post-construction the largest flow occurred May 26<sup>th</sup>, 2005 (148.4 m<sup>3</sup>/s). At Bear Creek reach the flood of record occurred on June 19<sup>th</sup>, 1952 at 51.25 m<sup>3</sup>/s.

#### *Data Analyses*

We determined if full species composition differed between reaches using non-metric multidimensional scaling (NMDS) with a Bray-Curtis dissimilarity matrix (McCune and Grace 2002). We removed plant species that were found in less than three plots and contributed to less than 5% of the relative vegetation cover within a plot. Additionally, we conducted an indicator species analysis (Dufrêne and Legendre 1997) to understand differences in full plant species composition between study reaches. We used logistic models to determine how depth to groundwater, exceedance probability of flooding, reach, and region influenced the distribution of riparian woody vegetation guilds. Logistic regression, a form of generalized linear models (GLM) was used as they have been shown to be more robust than machine learning models, with less overfitting that could limit generality (Meynard and Quinn 2007; Wenger and Olden 2012). Models with the lowest AIC were chosen, unless the difference in AIC was less than two, then models were not considered statistically different (Motulsky and Christopoulos 2004).

To evaluate logistic model performance, we divided data into training and testing matrices (70% / 30% split) and used receiver operating characteristic (ROC) analysis to report the area under the curve (AUC). Only models with AUC greater than 0.7 were retained as values above this indicate fair ( $> 0.70$ ) to excellent model fit ( $> 0.90$ ) (Swets 1988). Confusion matrices describing percentage of model specificity, the proportion of presence correctly identified, and sensitivity, the proportion of absence correctly observed were also used to evaluate model fit (Subhash 2019).

We determined hydrologic thresholds for vegetation guilds using the intersection point of the 95% confidence intervals from overlapping guild response curves (Lite and Stromberg 2005). At study reaches without overlapping guild distributions, we used ROC analysis to determine probability of occurrence thresholds for each guild model by maximizing the sum of model sensitivity and specificity (Manel et al. 2001; Robin et al. 2018). To compare reaches with similar hydrologic guild thresholds we conducted Kolmogorov-Smirnov tests (Arnold and Emerson 2011).

To model the response of guilds to changes in groundwater levels we simulated lower groundwater levels (-0.50 m and -1.00 m) in our models and recalculated flood exceedance probabilities with daily flows reduced by 5%, 10%, and 20% for each study reach. Within the Colorado River Basin studies suggest reductions in baseflow (Reynolds et al. 2015) and a 20% decrease in annual streamflows by 2050 (Udall and Overpeck 2017). Xiao et al. (2018) found that streamflows have declined 16.5% across the Colorado River basin with over half of the decrease attributed to reduced runoff from warmer temperatures and the other half attributed to reduced winter snowpack.

At each reach we calculated the change in potential habitat area of vegetation guilds to imposed lower groundwater levels and flood exceedance probability. To model changes in guild distribution at each study reach we split surveyed vegetation transects into 10 cm increments and calculated the inundating discharge for each increment using unique stage-discharge relationships

from our 1-D hydraulic models. Flood exceedance probability was calculated at every segment using flow duration curves from USGS gage records and for each altered flow scenario. In addition, depth to groundwater was linearly interpolated along transects at each 10 cm segment. Transects started at the vegetation plot closest to the water and extended to the most upland plot. Model parameters from significant logistic guilds models calculated guild probability of occurrence at each 10 cm increment using present and future scenarios of groundwater and flood exceedance probability. The proportion of guild presence was calculated for each reach using all transects and 10 cm segments.

### 4.3 Results

#### *Vegetation Guild Composition Across Regions*

One hundred and thirty-three plant species were found in the Arizona study reaches, and 144 in Colorado. 22 species in Arizona and 33 in Colorado are woody. Floristic species composition differed between the three rivers and between study reaches on the same river (PERMANOVA  $P < 0.01$ ). Along the Verde River, average similarity of species composition was 13.2% between Childs and Sheep Bridge, 9.96% between Sheep Bridge and Beasley Flat, and 9.28% similarity between Beasley Flat and Childs. In Colorado, the higher elevation reaches Bear Creek and Placerville had the highest average similarity, 9.18%.

Woody indicator species at Beasley Flat included *Ambrosia monogyra* and *Chilopsis linearis*, at Childs *Prosopis velutina*, *Populus fremontii*, and *Fraxinus velutina* and at Sheep Bridge *Salix gooddingii*, *Tamarix ramosissima*, *Baccharis salicifolia*, and *Platanus wrightii*. Indicator species at Bedrock included *Tamarix chinensis*, *Artemisia tridentata*, *Chrysothamnus viscidiflorus*, and *Ericameria nauseosa* and at Bear Creek *Populus angustifolia*, *Cornus sericea*, *Salix eriocephala*, *Populus tremuloides*, and *Picea pungens*. On the San Miguel River at Placerville, *Alnus incana*, *Betula occidentalis*, *Lonicera involucrata*, *Rosa acicularis*, and *Juniper scopulorum* were indicators while at the lower elevation Uravan reach *Forestiera pubescens*, *Toxicodendron radicans*, *Salix exigua*, and *Rhus aromatica* were indicators.

Five woody guilds were identified in each study region and different guilds occurred in the Arizona and Colorado study reaches (Table 4.1, Figure 4.3, Appendix Table 4). Tall trees (T1) and generalist shrubs (S3) had similar trait composition between study regions and occurred at all study reaches (Appendix Table 4). Species within these guilds had similar rooting depth, re-sprout capability, tissue density, and height, but there were large differences in seed mass, specific leaf area, and their C<sup>13</sup>:C<sup>12</sup> ratio (Table 4.2). Guilds with dissimilar trait composition between study regions included drought tolerant/mesic shrubs (S2) and flood tolerant shrubs (S1) (Figure 4.4, PERMANOVA  $P < 0.05$ ). Flood tolerant shrubs in Colorado were less clustered in an NMDS indicating greater variation in trait composition among members with deeper roots, height, specific leaf area, and seed weight (Figure 4.4, Table 4.2). The cluster analysis grouped *Acer negundo* with tall trees (T1) along the Verde River, but grouped *Acer glabrum* with flood tolerant shrubs (S1) along our Colorado study rivers. *Tamarix* was classified with flood tolerant shrubs along the San Miguel and Dolores Rivers while along the Verde River it clustered with drought tolerant shrubs (S2) with deep roots (Figure 4.4). Flood tolerant shrubs are more abundant in southwestern Colorado than along the Verde River and cover was highest at Bear Creek and Placerville (Appendix Table 4).

Mesic shrubs along the Dolores and San Miguel Rivers have shallow roots, low heights, high specific leaf area, and low seed weight (Table 4.2). Since drought tolerant/mesic shrubs and flood tolerant shrubs had different trait compositions along the Verde River and southwestern Colorado rivers we treated them as separate guilds. Verde River flood tolerant shrubs (S1) and southwestern Colorado mesic shrubs (S2) were not significantly different in trait compositions ( $P = 0.30$ , Figure 4.4). Short trees (T2) were found exclusively along the Verde River while coniferous trees (T3) were found along the San Miguel and Dolores Rivers. These two tree guilds had similar trait composition ( $P = 0.10$ ). Conifer trees, particularly *Picea pungens* (blue spruce), a facultative wetland species (USDA 2019), were found in high abundance of floodplains in the highest elevation reaches (Appendix

Table 4, Gage et al. 2016). No conifer species was dominant in the Verde River riparian zone, although *Juniperus scopulorum* was present in the riparian-upland transition.

Functional redundancy, or species richness within a guild, was lower in tall trees along the Dolores and San Miguel Rivers with only *P. fremontii* and *P. angustifolia* compared to the Verde River where four species were present in the tall tree guild (Table 4.1). The flood tolerant shrub guild along the Verde River had two species compared to nine along the San Miguel and Dolores Rivers (Table 4.1). Functional redundancy was similar in the generalist shrub guild with 7 species along the Verde River and 6 species along the Dolores and San Miguel Rivers. Guild richness was not different across study reaches ( $P = 0.16$ ). Bird habitat quality was predicted by study reach and dominant vegetation guild ( $P = 0.003$ ). Bird habitat was lower at Bedrock than the other reaches ( $P < 0.001$ ) and Uravan was lower than Placerville ( $P = 0.02$ ) and Childs ( $P = 0.02$ ). Bird habitat quality was highest in plots dominated by tall trees and conifer trees and lowest in plots dominated by generalist shrubs.

#### *Hydrologic Attributes*

Study reaches along the Verde River had wider ranges of exceedance probability in the riparian zone than study reaches along the Dolores and San Miguel Rivers (Appendix Figure 4). Higher elevation reaches on Colorado Rivers had narrow ranges of flood exceedance probability; Uravan on the San Miguel was the most similar to Verde River study reaches. Along the Verde River, vegetation plots at Childs were most likely to be flooded (Appendix Figure 4). Maximum plot flood exceedance probability was highest on unregulated reaches of the San Miguel and Dolores River, with Placerville EP = 32.3%, Uravan EP = 32.1%, Bear Creek EP = 49.5% compared to plot EP at Bedrock = 24.0%. Floodplain groundwater levels and water level variance differed between study reaches. During the 2018 growing season (April 14th-October 1st) maximum and minimum depth to groundwater at monitoring wells ranged from + 0.25 to -2.12 m at Childs, + 0.14 to -2.07

m at Sheep Bridge, +1.18 to -1.86 m at Upper Beasley Flat, and + 0.34 to -3.06 m at Lower Beasley Flat. Groundwater levels varied throughout the growing season from 0.58 to 1.26 m at Childs, 0.15 to 0.68 m at Sheep Bridge, 0.54 to 0.96 m at Upper Beasley Flat, and 1.36 to 3.23 m at Lower Beasley Flat. During the 2016 growing season in Colorado (May 1<sup>st</sup> to September 30<sup>th</sup>) minimum and maximum depth to groundwater ranged from -0.18 to -1.49 m at Placerville, -0.03 to -3.36 m Uravan, -0.15 to -1.23 m at Bear Creek, at + 0.63 to -4.11 m at Bedrock. Depth to groundwater varied 0.22 to 1.08 m at Placerville, 0.31 to 2.99 m at Uravan, 0.35 to 0.91 m at Bear Creek, and 0.58 to 2.28 m at Bedrock during the growing season. The slope of alluvial groundwater from the channel edge to upland transition zone during growing season low flow was greatest in Beasley Flat = 7.47 m/m, Childs = 5.21, Sheep Bridge = 5.16, and Bedrock = 4.3. By comparison groundwater slope along losing transects were lower at Bear Creek = 2.13, Placerville = 1.99, and Uravan = 2.64.

Stream stage at our study reaches along the Verde River was higher in elevation than the adjacent floodplain groundwater, indicating losing reaches with water flowing from the stream into the alluvial groundwater system. At Placerville and Bear Creek, hillslope groundwater contributed to the floodplain creating alluvial water tables that are higher than the adjacent stream during low flow. The processes of gaining and losing groundwater varied across the length of each study reach. For instance, groundwater is higher than the river at the upstream part of the Placerville reach but is lower than the river at the bottom end of the reach. This pattern is similar at Bear Creek where groundwater elevations are lower than the channel on the river left floodplain and higher than the river on the right floodplain. Bedrock and Uravan were losing throughout the reach. Exceedance probability and depth to groundwater were highly correlated in Arizona (Spearman rank  $r > 0.8$ ) but had a lower correlation in Colorado ( $r < 0.5$ ).

### *Vegetation Guilds Along Hydrologic Gradients*

#### *Tree Guilds*

Tall and short trees tree distributions were explained by depth to groundwater at three reaches along the Verde River ( $P < 0.001$ , Table 4.3). The tall tree guild was most common where the water table was less than 2.5 m deep during low flow periods and short trees were more likely in areas where groundwater was less than 1.5 m deep (Figure 4.5, overlap distribution with S2). Exceedance probability was also a good predictor of tall trees, but thresholds differed across reaches with Childs having tall trees in more frequently flooded areas. Tall trees were predicted by exceedance probability and depth to groundwater at Sheep Bridge, but model fit was poor (AUC  $< 0.70$ ). Depth to groundwater and flood exceedance probability ( $P = 0.05$ ) described variability of the tall tree guild at Uravan and exceedance probability at Bear Creek ( $P = 0.05$ ), but model fit was also poor (AUC  $< 0.70$ ).

#### *Shrub Guilds*

Depth to groundwater during low flow periods (AUC = 0.79) and exceedance probability (AUC = 0.73) predicted the presence of flood tolerant shrubs in Arizona and species were more likely to occur where groundwater was less than  $\sim 1.30$  m from the ground surface and flood exceedance probability was greater than 5.7%. Groundwater depth and reach (AUC = 0.85) interacted to predict flood tolerant shrubs in Colorado ( $P < 0.007$ ) and presence was accurately predicted in 84.7% and 87.0% of plots, respectively. Flood tolerant shrubs had higher likelihood of occurrence where groundwater was shallower than  $\sim 0.90$  m at Uravan ( $P < 0.001$ ) and where EP was greater than 2% ( $P < 0.001$ ) while at Bedrock flood tolerant shrubs were more likely to be found in areas with exceedance probabilities greater than 0.3% ( $P < 0.001$ ) and where groundwater was less than  $\sim 2.62$  m. Differences in thresholds for flood tolerant shrubs between Uravan and Bedrock were driven by the elevated presence of *Tamarix chinensis* at Bedrock and its inclusion in the guild. *Salix exigua* is the dominant species in the flood tolerant shrub guild at Uravan. An individual species model at Bedrock indicates that *Salix exigua* occurs in areas where groundwater is less than

~1.73 m about one meter above that of *Tamarix chinensis* at Bedrock and in areas where exceedance probability was greater than ~2%, similar to flood tolerant shrubs at Uravan.

Occurrence of flood tolerant shrubs was greatest in the higher elevation reaches in Colorado, but hydrologic conditions did not explain the variability in guild distribution at Placerville or Bear Creek ( $P > 0.05$ , Table 4.3). Members of the flood tolerant shrub guild at the higher elevation reaches; *Alnus incana*, *Betula occidentalis*, *Salix exigua*, *Salix eriocephala*, *Salix lasiandra*, and *Cornus sericea* were common on the floodplain, but members are found across a wide range of hydrologic condition which may explain the lack of a relationship. However, *Salix* spp. occurrence was predicted by groundwater depth at Placerville ( $P = 0.02$ , AUC = 0.76, 73.3% balanced accuracy) and was found in areas where groundwater was less than 0.56 m deep. Other species within the flood tolerant shrub guild at Placerville like *Betula occidentalis* and *Alnus incana* were found where groundwater was deeper, and they had wider hydrologic niches compared to *Salix* spp. At Bear Creek, depth to groundwater did not significantly predict *Salix* spp. occurrence ( $P = 0.07$ ) but it did predict the occurrence of *Alnus incana* ( $P = 0.01$ , AUC = 0.70, 70.8 % balanced accuracy), another dominant flood tolerant shrub guild member. Other species of the flood tolerant shrub guild at higher elevation reaches in Colorado were not predicted by hydrologic condition, models had poor fit, or species occurrence was  $< 10$  and we did not run logistic models.

Reach interacted with depth to groundwater (AUC = 0.84) and EP (AUC = 0.83) to predict the occurrence of drought tolerant shrubs along the Verde River. Overall, species within the drought tolerant shrub guild in Arizona were more likely to be found in plots where groundwater depth was deeper than -3.25 m (threshold derived from 95% interval overlap with guild T1, Figure 4.5) and exceedance probability was less than 2%. Drought tolerant shrubs were not well predicted at Sheep Bridge, but occurrence was lower than other reaches due to a narrower riparian zone and lack of upper terrace landforms (Appendix Table 4). In Colorado, EP and reach predicted mesic shrub

presence, but only exceedance probability predicted mesic shrubs at Bear Creek ( $P = 0.03$ ), but model fit was poor.

EP and reach ( $AUC = 0.78$ , no interaction) and groundwater depth and reach ( $AUC = 0.77$ , no interaction) significantly predicted the presence of the generalist shrub guild along the three rivers, but not study reaches (Table 4.3). In Arizona, generalist shrubs were more likely to be found in plots where groundwater was deeper than  $-2.57$  m, but threshold differed across study reach for EP and were more likely to be found where EP was less than  $0.7\%$  at Lower Beasley Flat,  $0.3\%$  at Childs, and  $7.7\%$  at Sheep Bridge. EP and groundwater depth predicted generalist shrubs at Uravan in Colorado ( $P < 0.001$ , Table 4.3) and this guild was more likely present where EP was less than  $0.6\%$  and groundwater was deeper than  $-1.64$  m. Generalist shrub model fit was poor at Bedrock ( $AUC < 0.70$ ) and generalist shrubs were not present on the floodplain at Bear Creek.

#### *Simulated Changes in Hydrology*

The magnitude of the change in guild occurrence was predicted to be higher for changes in groundwater levels than for decreases in exceedance probability for both riparian and upland guilds. Simulated decreases in groundwater depth during the low flow season resulted in a decreased presence of tall trees, short trees, flood tolerant shrub at our study reaches along the Verde River. With reductions in groundwater levels, tall tree occurrence was reduced by  $\sim 6$ - $27\%$  across reaches on the Verde River. Short trees and flood tolerant shrubs had narrower groundwater ranges than tall trees and their presence was predicted to decrease the most (Appendix Table 5). Simulations of less frequent flooding only decreased tall tree occurrences by  $\sim 1$ - $5\%$  at Beasley Flat and Childs. Flood tolerant shrubs were predicted to increase by  $1$ - $4\%$  at Sheep Bridge and Childs, respectively. However, flood tolerant shrubs decreased by  $\sim 6\%$  at Beasley Flat reaches. Both drought tolerant shrubs (S2) and generalist shrubs (S3) were predicted to expand with simulated drops in groundwater and reductions in exceedance probability. On the lower San Miguel at Uravan, flood

tolerant shrubs were virtually eliminated with a 1.00 m decrease in groundwater levels and presence decreased by  $\sim 4\%$  with a 20% decrease in daily flows (Appendix Table 5). At Bedrock, occurrence of flood tolerant shrubs also decreased by  $\sim 10\%$  with predictions of reduced exceedance probability. Overall, vegetation at the high elevation reaches on the San Miguel and Dolores Rivers was predicted to change the least compared with low elevation reaches and those along the Verde River.

#### 4.4 Discussion

Five woody vegetation guilds were identified in Arizona and Colorado study reaches using traits known to represent adaptations to stressors and resources associated with flood disturbance and varying water availability in the riparian zone (Aguiar et al. 2013; Stromberg and Merritt 2016). Trait composition was similar for the tall tree and generalist shrub guilds but differed for other woody guilds between the two study regions. Despite our delineation of similar guilds on the three study rivers our results imply that reach-scale geomorphic differences and hydrologic processes supporting them are different. In the Missouri and Columbia River basin, guild presence and absence also corresponded to reach scale attributes like elevation, channel sinuosity, stream gradient, buffer forest cover, buffer slope, and climate variables (Hough-Snee et al. 2015). Depth to groundwater thresholds for tall trees coincided with steep gradients of groundwater depth from the channel to the riparian zone in Arizona. Shallow groundwater depth and less frequent flooding in higher elevation reaches in Colorado resulted in less distinct zonation of riparian communities.

Some of the same riparian vegetation guilds were distributed in different habitats across study reaches suggesting that there may be limits to transferring guild distribution models developed in one region to another region. The free-flowing reaches on the San Miguel exhibited guild-environment relations most similar to reaches along the Verde River with flood tolerant shrubs and *Salix exigua* found in areas with groundwater within 1.0 m of the floodplain surface and generalist

shrubs at Uravan where flood probability was low and groundwater depth greater than 1.0 m.

Differences in vegetation guild habitat between Uravan and Bedrock suggest low transferability of vegetation-hydrologic relationships between free-flowing and regulated rivers, especially with the dominance of non-native species like *Tamarix* that was a member of our flood tolerant shrub guild at Bedrock.

Our simulations of changes in flow and groundwater availability demonstrate that riparian guilds with narrower hydrologic ranges would decrease the most under future hydrologic scenarios and the magnitude of change was greater in response to lowered groundwater levels compared to inundation exceedance probability. A complete loss of stream flow and recharge of alluvial groundwater from the river could be detrimental to the survival and reproduction of tall trees, short trees, and flood tolerant shrubs. Our results along the Verde River and the lower elevation reach on the San Miguel River supports other studies indicating that upland plant species are often excluded from riparian areas due to their intolerance of flooding and have affinities for uplands due to higher water use efficiency and less dependence on shallow groundwater. Our simulation of lowered groundwater levels predicted increased occupation of upland guilds that have traits to thrive in areas with low water availability. Higher elevation study reaches with shallow groundwater levels from hillslope contributions may be more resilient to changes in streamflow since the river is not the sole recharge source.

#### *Riparian Vegetation Guilds Across Study Rivers*

Species within our tall tree guild were the structural dominants along the Verde River while flood tolerant shrubs at high elevation reaches and tall trees, flood tolerant shrubs, and generalist shrubs were dominant at low elevation reaches along the San Miguel and Dolores Rivers. Variation in dominance across study reaches indicates that different guilds provide the foundation of biotic communities along rivers as a function of climate, elevation, and flow regimes. Identification and

conservation of dominant guilds that provide habitat structure will be an important component in managing riparian areas to maintain wildlife habitat, especially in arid landscapes (Cubley et al. 2020). We found that our habitat index to assess vegetation structural complexity for birds was lowest at the Bedrock study reach, indicating that flow regulation by the McPhee Dam may have degraded habitat for birds. Conservation of riparian forest habitats are important to maintain high bird richness and diversity (Selwood et al. 2017; Morissette et al. 2018; Cooke and Tauzer 2020).

We used the same functional traits between study rivers to objectively group species into guilds. Trait composition was similar for the tall tree and generalist shrub guild between the two study regions, but functional redundancy was lower for tall trees along Colorado reaches than Arizona study reaches. Functional redundancy within the flood tolerant shrub guild along the San Miguel and Dolores Rivers was higher, resulting in varied trait composition and dissimilarity to traits of the two species within flood tolerant shrub guild along the Verde River. Guild species membership strongly influenced relationships to hydrologic condition, especially at Bedrock where half of flood tolerant shrub occurrences were attributed to *Tamarix chinensis*. Although *T. chinensis* grouped with flood tolerant shrubs along the San Miguel and Dolores Rivers we show its relationship to flooding and groundwater depth differ from *Salix exigua* despite trait similarity. The grouping of *Picea pungens* with *Juniperus scopulorum* may also affect the conifer guild relationship to hydrologic attributes as they occur in different hydrologic niches along rivers with *P. pungens* occurring alongside *P. angustifolia* and *A. incana* (Carsey et al. 2003).

The selection of functional traits along with species clustering methodology can lead to large differences in riparian guild membership across studies. Stromberg and Merritt (2015) grouped *Tamarix chinensis* along Arizona rivers with species we identified as generalist shrubs including *Baccharis sarothroides*, *Ambrosia monogyra*, and *Ericameria nauseosa*. We used several distinct traits including re-sprout capability, specific leaf area, and  $^{13}\text{C}:^{12}\text{C}$  ratio, than Stromberg and Merritt (2016)

and excluded spinescence. In our study, *Tamarix* along the Verde River grouped with species within the drought tolerant shrub guild, dominated by *Prosopis velutina*, a deeply rooted leguminous shrub. Early methods to divide species into groups relied on *a priori* classification, but our study along with others (Hough-Snee et al. 2015; Diehl et al. 2017; Aguiar et al. 2018) have used objective statistical methods to delineate vegetation guilds. However, the field lacks consensus on a common suite of functional traits that could better facilitate comparison of riparian vegetation guilds among studies. Current databases for riparian species traits are few and guild membership differences may also be attributed to variable trait values driven by the method of trait collection, seasonal timing, age of selected species, and phenotype plasticity across rivers (Lechowicz and Blais 1988; Funk et al. 2007).

#### *Vegetation Guilds and Hydrologic Processes*

Our results support studies from other regions suggesting that the occurrence of riparian guilds corresponds with both reach scale hydrologic attributes as well as large-scale environmental filters such as climate and elevation (Hough-Snee et al. 2015). At Verde River study reaches, floodplain groundwater was supported by a hydrologically losing channel while on the San Miguel River, stable isotope analyses indicated that groundwater is supplied from both side slope groundwater sources and river water (Cooper and Conovitz 2000). Depth to groundwater thresholds for tall trees coincided with steep gradients of groundwater depth from the channel to the riparian zone in Arizona. Less steep groundwater gradients from the channel to the upland, hillslope groundwater contributions, and climate resulted in fewer predictive relationships for species and guilds at higher elevation reaches along the San Miguel and Dolores Rivers. Tall trees were less sensitive to groundwater levels in Colorado than Arizona where Verde River trees may be more reliant on shallow groundwater because evapotranspiration rates are so high (Cleverly et al. 2015) and groundwater is supplied only by the river and precipitation at the scale of our study reaches.

Riparian plant communities at higher elevations in Colorado (and in cooler, wetter climate worldwide) may be able to survive in landscape positions above the effect of flood waters due to greater water availability sources other than river driven sources, e.g., from precipitation (Webb and Brotherson 1988; Friedman et al. 2006). In a previous study, *Populus angustifolia* was distributed along a gradient of flood frequency on the San Miguel River, although it was dependent on tree age (Friedman et al. 2006). Young trees were found in areas with flood recurrence intervals less than 22 years, mature trees in areas with recurrence intervals longer than 22 years, and mixed ages were found on surfaces with varied flood recurrence intervals (Friedman et al. 2006). It is possible that the zonation of species within the tall tree guild was also related to hydrologic regime, but rather than species turnover along an elevation gradient, this zonation may be age or size-class related. Decreases in flooding and inundation with elevation may also be influencing guild distributions along the Dolores and San Miguel Rivers. Friedman et al. (2006) reported lower flood frequency in high elevation than low elevation reaches of the San Miguel River. These higher elevation riparian zones are more likely influenced by colluvial disturbance like landslides and debris flow than alluvial flooding. Although flood disturbance creates nursery sites for cottonwoods and willows, the establishment and persistence of cottonwoods may be reliant on rainfall instead of alluvial groundwater resources in more humid regions (Polzin and Rood 2006).

At the other low elevation reach, Bedrock, vegetation patterns appear to be influenced by an upstream dam and generalist shrubs have encroached onto lower floodplain surfaces. Groundwater dynamics were similar on the three Verde River reaches and the Bedrock reach due to its location in an unconfined valley and dampened groundwater recharge from the loss of high magnitude spring floods (Colbe and Kolb 2012). Sexual reproduction of *Populus* spp. has most likely been disrupted by alteration of the flow regimes and cattle grazing (Rood and Mahoney 1990; Samuelson and Rood

2004) and riparian floodplains lack distinct zonation between upland and riparian species (Aguilar et al. 2018).

The relationships between groundwater depth, exceedance probability, and vegetation guild presence was most similar between the lower elevation reaches on the San Miguel and Dolores Rivers and the Verde River reaches although predicted probability distributions were statistically dissimilar. Flood tolerant shrub and generalist shrub guild distributions were explained by groundwater depth and exceedance probability at Uravan. The climate and valley form at Uravan are more like study reaches along the Verde River, but groundwater levels were shallower and the riparian zone less frequently flooded. Models predicting presence of fish species within and between river basins were more transferable when hydrological conditions were similar (Chen and Olden 2018). However, environmental similarity does not necessarily equate to generalized species-environmental relationships across basins. Chen and Olden (2018) found that fluvial specialist fish guilds were the least transferable among basins suggesting these that these species have stronger dependencies on system-specific flow attributes. In a study predicting fish species presence, environmental predictors for fish species in five rivers were similar, but functional forms were inconsistent (Huang and Frimpong 2016). We found this to be true between study reaches where the effect of exceedance probability and groundwater depth differed across reach for flood tolerant shrubs, a fluvial specialist guild. Although hydrologic relationships for the flood tolerant shrub guild had the most commonality between study regions, this finding may be attributed to a shared common and abundant species, *Salix exigua*, that is present at all our study reaches.

Our attempt to objectively group species may account for the lack of guild-hydrologic relationships especially for speciose guilds like flood tolerant shrubs at high elevation reaches in Colorado. Although species within this guild have similar functional traits, we found that members were found across different hydrologic ranges. At Placerville, *S. exigua* occurred in areas where

groundwater was less than 0.5 m, but *Alnus incana* was found across a wider range of groundwater depths. Friedman et al. (2006) found *S. exigua* was restricted to wet sites with high flood exceedance probability while *A. incana* and *B. occidentalis* colonized recently disturbed areas on less frequent flooded surfaces. Although *A. incana* and *B. occidentalis* can reproduce asexually (USDA Plant Database 2019) they are less likely to form root sprouts than *S. exigua*. These species also differ in their timing of seed release with *A. incana* dispersing seeds in the fall and *S. exigua* in the spring and summer which may account for their distributions on the floodplain.

Our selection of traits for use in both study regions may not distinguish relationships at river reaches with varied environmental conditions and hydrologic attributes. Riparian communities within a particular biome may be better distinguished by suites of functional traits relevant to assembly within that particular climatic zone. For example, in the Mediterranean biome of Portugal, riparian woody plant communities were discriminated by canopy height, leaf area, rooting depth, and diaspore type (Stella et al. 2013; Aguiar et al. 2018) compared to stem flexibility, canopy height, leaf area, diaspore type, and dispersal and reproduction type in the boreal biome of Sweden (Bejarano et al. 2018). Future riparian trait-based approaches may benefit from the identification of region-specific traits to better distinguish plants occurrences in ecoregions where stressors on plant species may be dissimilar.

#### *Simulated changes in water table and exceedance probability*

We predict declines in dominant riparian vegetation guilds with lowered floodplain groundwater in both study regions, but not all study reaches. A water table decline of greater than 0.50 m could drastically decrease cover of the structural dominant trees in Arizona while in Colorado, Placerville, Uravan, and Bedrock flood tolerant shrub and *Salix exigua* occurrences will decrease with lowered groundwater levels. Loss of *Alnus incana*, a flood tolerant shrub member, has large implications for the aquatic flood web because roots support nodules of the nitrogen fixing

bacteria *Frankia* that increase leaf nitrogen and increase the value of leaves as food sources (Hieber and Gessner 2002). Overall, riparian guilds with narrower groundwater ranges were predicted to decrease the most including tall trees, short trees, and flood tolerant shrubs. Drought tolerant shrubs (S2) and generalist shrubs (S3) were predicted to expand with simulated drops in groundwater and reductions in flooding similar to others (Stromberg et. Al. 2010; Merritt and Bateman 2012).

Shallower water tables with low variation in the growing season at higher elevation reaches indicates more resiliency to future reductions in streamflow from climate changes. Another study that examined the distribution and vulnerability of invertebrate species to climate changes between ecoregions also found that colder and wetter regions were more buffered against warming and drying (Pyne and Poff 2017). Resiliency may be a function of both large and local scale factors. In California, higher elevation watersheds were more protected from climate warming effects than others on the western slope of the Sierra Nevada and a watershed with high groundwater input was the most resilient to low flow conditions (Null et al. 2010). River reaches in Sweden receiving groundwater discharge from uplands had 15-20% higher plant richness (Kuglerová et al. 2014) and cottonwoods were found to grow faster in gaining compared to losing stream reaches (Stanford 2003). Riparian areas with groundwater discharge may be more resilient to changes in summer flows and lowered spring flood peaks (Andréasson et al. 2004). However, reduced precipitation, shifts from snow to rain driven precipitation, and earlier snowmelt may increase spring runoff and reduce groundwater recharge in mountain areas (Huntington and Niswonger 2012). The magnitude of future hydrologic alteration along with regional species adaptations may drive differences in vegetation responses among river reaches (Lozanovska et al. 2020).

### *Conclusions and Management Implications*

Relationships between vegetation and hydrologic conditions vary between river basins as well as within basins where physical processes that effect riparian plant distributions change with

elevation and reach specific attributes. Hillslope processes influencing riparian zone groundwater may be more important in the assembly of riparian communities in high elevation river reaches and the focus of using streamflow metrics in these reaches may give an incomplete picture of riparian plant distributions (Friedman et al. 2006; Kuglerová et al. 2014). In areas with sharper hydrologic gradients, a complete loss of surface flow and recharge of alluvial groundwater from the river could be detrimental to the survival and reproduction of structural dominants including tall trees, short trees, and flood tolerant shrubs. Since climate and elevation influence river properties including streamflow, geomorphology, and seasonality, efforts have been made to characterize freshwater biomes to provide predictive frameworks at broad spatial scales (Dodd et al. 2019). The framework for freshwater biomes or others that account for elevation, climate, and reach-scale attributes may be more useful to generalizing riparian guild distributions among watersheds and ecoregions.

As the need to maintain ecosystem functions and services increases with climate change and human water development, ecological models are useful to predict potential future changes and target areas that may be less resilient (Arthington et al. 2010). However, uncertainty in the magnitude of hydrologic change in riparian zones influences the accuracy of future predictions of plant responses. Changes in riparian plant communities will most likely be dependent on factors including local geology and hillslope morphology affecting groundwater, patterns of precipitation and temperature, and streamflow regimes. Our research highlights the complexity of assembly processes along rivers and generalizing the assembly of plants into guilds between regions. The scope of guild transferability should be narrowed and explored within climate, flow and groundwater regimes, and valley geomorphic classifications to define the boundaries of guild transferability.

Table 4.1 Species composition of vegetation guilds in Colorado and Arizona. Vegetation guilds were identified with hierarchical cluster analysis using plant height, specific leaf area, wood density, leaf  $^{13}\text{C}:^{12}\text{C}$ , seed mass, resprout capability, and growth form. We tested whether guilds had distinct trait compositions using PERMANOVA.

| <b>Guild</b>                  | <b>Guild Name</b>       | <b>Arizona Guild Species</b>                                                                                                                                                                                                                           |
|-------------------------------|-------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| T1                            | Tall trees              | <i>Populus fremontii</i> , <i>Salix gooddingii</i> , <i>Platanus wrightii</i> , <i>Acer negundo</i>                                                                                                                                                    |
| T2                            | Short trees             | <i>Fraxinus velutina</i> , <i>Morus alba</i>                                                                                                                                                                                                           |
| T3                            | Coniferous trees        | -                                                                                                                                                                                                                                                      |
| S1                            | Flood tolerant shrubs   | <i>Salix exigua</i> , <i>Baccharis salicifolia</i>                                                                                                                                                                                                     |
| S2                            | Drought tolerant shrubs | <i>Celtis reticulata</i> , <i>Prosopis velutina</i> , <i>Chilopsis linearis</i> , <i>Tamarix ramosissima</i>                                                                                                                                           |
| S3                            | Generalist shrubs       | <i>Gutierrezia sarothrae</i> , <i>Brickellia floribunda</i> , <i>Amorpha fruticosa</i> , <i>Senegalia greggii</i> , <i>Mimosa aculeaticarpa</i> , <i>Ambrosia monogyra</i> , <i>Baccharis sarothroides</i>                                             |
| <b>Colorado Guild Species</b> |                         |                                                                                                                                                                                                                                                        |
| T1                            | Tall trees              | <i>Populus deltoides</i> , <i>Populus angustifolia</i>                                                                                                                                                                                                 |
| T2                            | Short trees             | -                                                                                                                                                                                                                                                      |
| T3                            | Coniferous trees        | <i>Juniperus scopulorum</i> , <i>Picea pungens</i>                                                                                                                                                                                                     |
| S1                            | Flood tolerant shrubs   | <i>Alnus incana</i> , <i>Betula occidentalis</i> , <i>Cornus sericea</i> , <i>Salix eriocephala</i> , <i>Salix exigua</i> , <i>Salix lasiandra</i> , <i>Tamarix chilensis</i> , <i>Acer glabrum</i> , <i>Acer glabrum</i> , <i>Populus tremuloides</i> |
| S2                            | Mesic shrubs            | <i>Lonicera involucrata</i> , <i>Symphoricarpos rotundifolius</i> , <i>Toxicodendron radicans</i> , <i>Rosa acicularis</i> , <i>Rhus aromatica</i>                                                                                                     |
| S3                            | Generalist shrubs       | <i>Artemisia tridentata</i> , <i>Chrysothamnus viscidiflorus</i> , <i>Forestiera pubescens</i> , <i>Ericameria nauseosa</i> , <i>Ribes inermis</i> , <i>Gutierrezia sarothrae</i>                                                                      |

Table 4.2 Average and stand deviation of traits for each riparian vegetation guilds in Colorado and Arizona. Root depth is ordinal from 1 to 4 (shallow to deep), resprout capability is ordinal 0 or 1 (no and yes), tissue density (gm/cm<sup>3</sup>), height (m), SLA (cm<sup>2</sup>/g), Seed mass (g/1000 seeds), and C13:C12 are continuous variables.

| Guild | Growth         | Root<br>Depth  | ReSprout | Tissue<br>Den    | Height           | SLA                | Seed<br>Mass     | C13:C12       |
|-------|----------------|----------------|----------|------------------|------------------|--------------------|------------------|---------------|
| S1-CO | shrub/tree     | 2.33 ±<br>0.50 | 1        | 0.57 ±<br>0.08   | 6.92 ±<br>5.47   | 153.64 ±<br>54.43  | 6.80 ±<br>13.41  | -28.47 ± 0.77 |
| S1-AZ | shrub/tree     | 1.50 ±<br>0.71 | 1        | 0.45 ±<br>0.0002 | 3.04 ±<br>0.05   | 126.98 ±<br>0.14   | 0.08 ±<br>0.04   | -28.96 ± 0.61 |
| S2-CO | shrub          | 1.20 ±<br>0.45 | 1        | 0.90 ±<br>0.64   | 1.20 ±<br>0.54   | 188.18 ±<br>55.56  | 15.57 ±<br>10.63 | -28.13 ± 1.41 |
| S2-AZ | shrub/tree     | 3.75 ±<br>0.50 | 1        | 0.70 ±<br>0.08   | 4.69 ±<br>0.24   | 130.60 ±<br>0.24   | 54.09 ±<br>59.61 | -28.06 ± 1.89 |
| S3-CO | shrub/subshrub | 1.67 ±<br>0.52 | 0        | 0.73 ±<br>0.21   | 1.78 ±<br>1.35   | 149.17 ±<br>69.85  | 5.44 ±<br>10.86  | -28.47 ± 1.25 |
| S3-AZ | shrub/subshrub | 2.00 ±<br>0.82 | 0        | 0.76 ±<br>0.22   | 1.52 ±<br>0.86   | 127.18 ±<br>±48.79 | 17.11 ±<br>37.29 | -27.72 ± 2.36 |
| T1-CO | tree           | 3.00 ±<br>0.00 | 1        | 0.46 ±<br>0.09   | 31.30 ±<br>5.44  | 114.95 ±<br>2.91   | 0.45 ±<br>0.00   | -28.74 ± 2.21 |
| T1-AZ | tree           | 3.00 ±<br>0.00 | 1        | 0.47 ±<br>0.04   | 19.50 ±<br>3.41  | 188.75 ±<br>72.24  | 9.73 ±<br>17.54  | -27.96 ± 0.8  |
| T2-AZ | tree           | 3.00 ±<br>0.00 | 0        | 0.71 ±<br>0.06   | 13.50 ±<br>2.12  | 166.62 ±<br>72.23  | 12.89 ±<br>8.32  | -28.02 ± 0.71 |
| T3-CO | shrub/tree     | 2.00 ±<br>0.00 | 0        | 0.48 ±<br>0.07   | 16.53 ±<br>13.22 | 42.11 ±<br>22.29   | 12.55 ±<br>11.53 | -26.08 ± 0.97 |

Table 4.3 Results of logistic models predicting guild distributions in Arizona and Colorado. Guild codes are listed in Table 4.1. If guild presence was < 10 at a study reach, we used the closest reach as training data and the reach of interest as testing data to determine transferability. AUC= area under the curve, HL = p value for Hosmer and Lemeshow good of fit test, P = probability of occurrence threshold.

| Guild | Region | Reach       | Model                                     | AUC  | Balan. Accuracy (%) | HL     | P    |
|-------|--------|-------------|-------------------------------------------|------|---------------------|--------|------|
| T1    | AZ     | all reaches | T1 ~ GW+ GW <sup>2</sup> + Reach          | 0.89 | 81.4                | <0.001 | 0.59 |
| T1    | AZ     | all reaches | T1 ~ EP + EP <sup>2</sup> + Reach         | 0.79 | 82.7                | <0.001 | 0.57 |
| T1    | AZ     | Beasley U   | T1 ~ GW + GW <sup>2</sup>                 | 1    | 100                 | 0.53   | 0.44 |
| T1    | AZ     | Beasley U   | T1 ~ EP+ EP <sup>2</sup>                  | 1    | 100                 | 0.45   | 0.55 |
| T1    | AZ     | Beasley L   | T1 ~ GW + GW <sup>2</sup> <sup>(BU)</sup> | 0.67 | 70.4                | 0.002  | 0.58 |
| T1    | AZ     | Beasley L   | T1 ~ EP+ EP <sup>2</sup> <sup>(BU)</sup>  | 0.72 | 62.9                | 0.47   | 0.91 |
| T1    | AZ     | Childs      | T1 ~ GW + GW <sup>2</sup>                 | 0.95 | 92.8                | 0.13   | 0.60 |
| T1    | AZ     | Childs      | T1 ~ EP+ EP <sup>2</sup>                  | 0.77 | 85.7                | 0.04   | 0.41 |
| T2    | AZ     | all reaches | T2 ~ GW + GW <sup>2</sup>                 | 0.77 | 75.2                | 0.40   | 0.21 |
| S1    | AZ     | all reaches | S1 ~ GW                                   | 0.79 | 77.6                | 0.76   | 0.15 |
| S1    | AZ     | all reaches | S1 ~ EP                                   | 0.73 | 70.6                | 0.15   | 0.12 |
| S1    | CO     | all reaches | S1 ~ EP*Reach                             | 0.83 | 84.7                | 0.20   | 0.31 |
| S1    | CO     | all reaches | S1 ~ GW*Reach                             | 0.85 | 87.0                | 0.27   | 0.45 |
| S1    | CO     | Uravan      | S1 ~ GW                                   | 0.97 | 95.6                | 0.001  | 0.53 |
| S1    | CO     | Uravan      | S1 ~ EP                                   | 0.88 | 82.6                | 0.75   | 0.27 |
| S1    | CO     | Bedrock     | S1 ~ GW                                   | 0.88 | 79.8                | 0.48   | 0.33 |
| S1    | CO     | Bedrock     | S1 ~ EP                                   | 0.85 | 72.1                | 0.14   | 0.25 |
| S2    | AZ     | all reaches | S2 ~ GW*Reach                             | 0.84 | 77.7                | 0.23   | 0.12 |
| S2    | AZ     | all reaches | S2 ~ EP*Reach                             | 0.83 | 74.0                | 0.99   | 0.14 |
| S2    | AZ     | Beasley U   | S2 ~ GW                                   | 0.90 | 95.0                | 0.80   | 0.58 |
| S2    | AZ     | Beasley U   | S2 ~ EP                                   | 0.90 | 95.0                | 0.51   | 0.64 |
| S2    | AZ     | Beasley L   | S2 ~ GW <sup>(BU)</sup>                   | 0.90 | 80.8                | 0.29   | 0.15 |
| S2    | AZ     | Beasley L   | S2 ~ EP <sup>(BU)</sup>                   | 0.87 | 80.8                | 0.31   | 0.16 |
| S2    | AZ     | Childs      | S2 ~ GW                                   | 0.99 | 96.9                | 0.40   | 0.44 |
| S2    | AZ     | Childs      | S2 ~ EP                                   | 0.99 | 90.6                | <0.01  | 0.36 |
| S2    | CO     | all reaches | S2 ~ EP + Reach                           | 0.82 | 70.3                | 0.99   | 0.27 |
| S3    | AZ/CO  | all reaches | S3 ~ EP + Reach                           | 0.78 | 76.2                | 0.93   | 0.36 |
| S3    | AZ/CO  | all reaches | S3 ~ GW + Reach                           | 0.77 | 72.3                | 0.40   | 0.27 |
| S3    | AZ     | all reaches | S3 ~ EP*Reach                             | 0.70 | 64.4                | 0.31   | 0.22 |
| S3    | AZ     | all reaches | S3 ~ GW                                   | 0.86 | 81.6                | 0.04   | 0.18 |
| S3    | AZ     | Beasley U   | S3 ~ EP <sup>(BL)</sup>                   | 0.70 | 77.5                | 0.67   | 0.71 |
| S3    | AZ     | Beasley L   | S3 ~ EP                                   | 1.0  | 100                 | 0.84   | 0.93 |
| S3    | AZ     | Childs      | S3 ~ EP <sup>(BL)</sup>                   | 0.67 | 67.2                | 0.67   | 0.28 |
| S3    | AZ     | Sheep       | S3 ~ EP                                   | 0.80 | 84.1                | 0.22   | 0.09 |
| S3    | CO     | all reaches | S3 ~ EP + Reach                           | 0.84 | 77.5                | 0.80   | 0.33 |
| S3    | CO     | all reaches | S3 ~ GW*Reach                             | 0.84 | 78.2                | 0.21   | 0.23 |
| S3    | CO     | Uravan      | S3 ~ EP                                   | 0.70 | 74.5                | 0.63   | 0.51 |
| S3    | CO     | Uravan      | S3 ~ GW                                   | 0.79 | 73.9                | 0.09   | 0.19 |

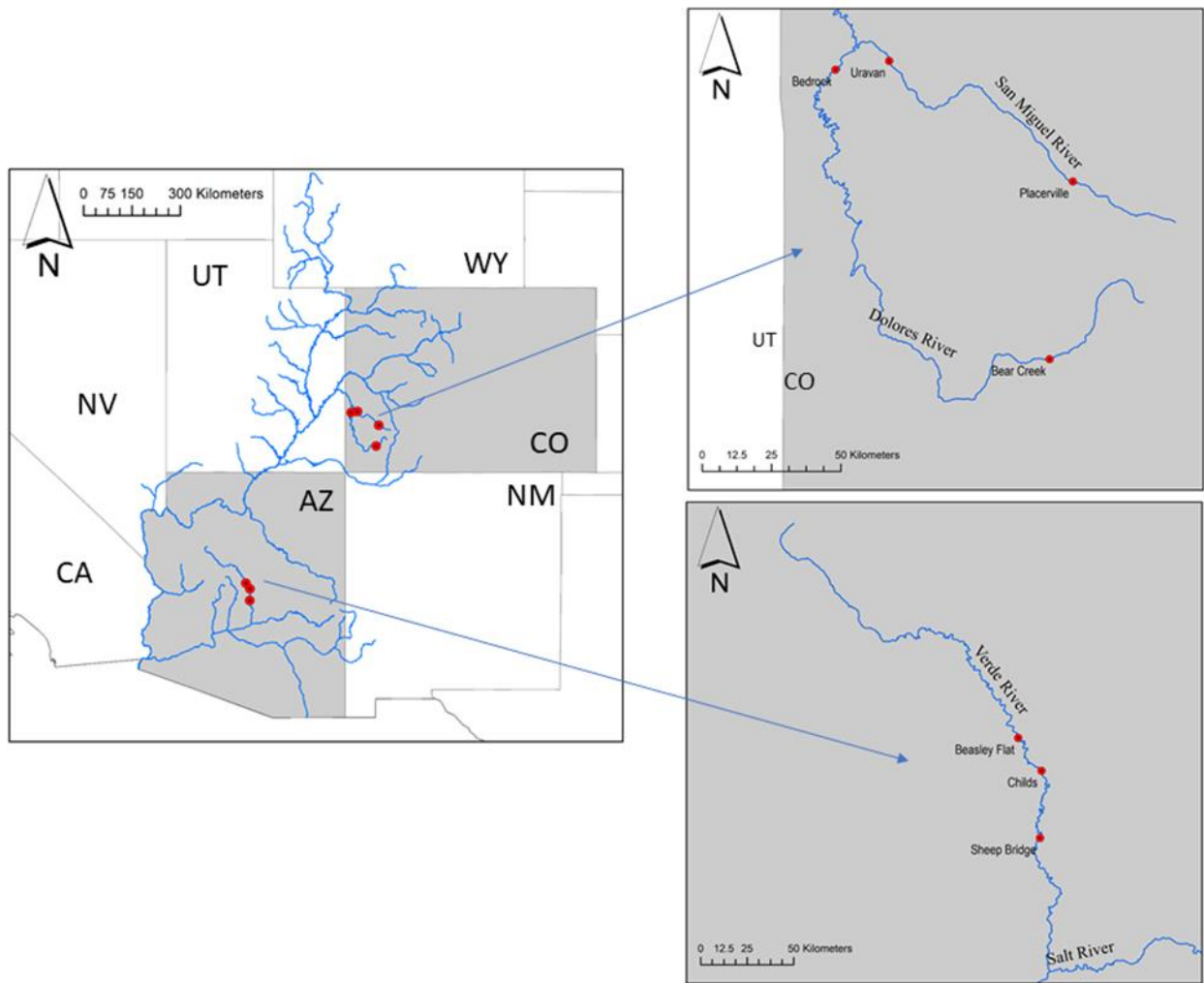


Figure 4.1 Study reaches within the Colorado River Basin (left) on the Verde River in Arizona (bottom right) included Beasley Flat, Childs, and Sheep Bridge. On the Dolores River study reaches were located at Bear Creek and Bedrock and on the San Miguel at Placerville and Uravan (top right). Site specific information can be found in Appendix Table 1.

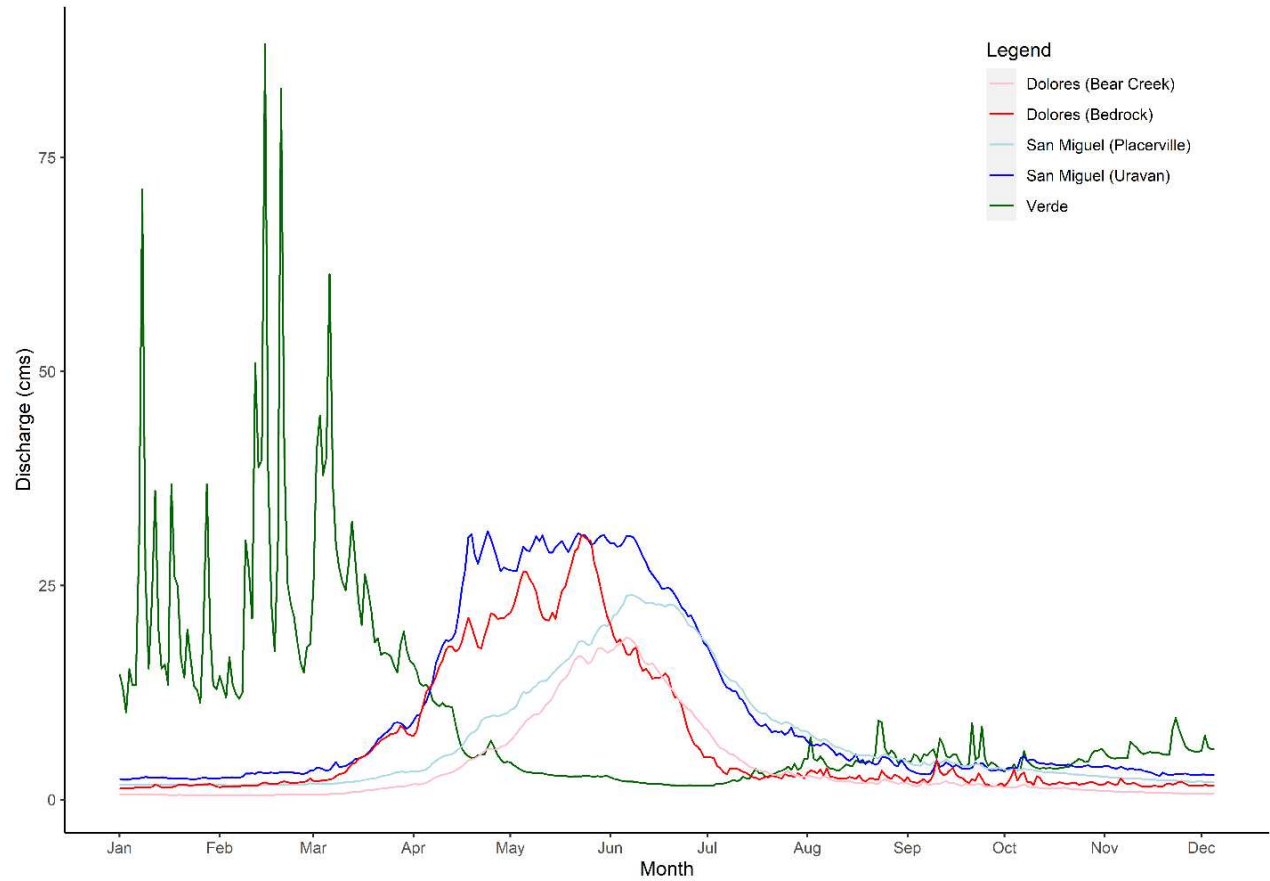


Figure 4.2. Mean daily discharge on the Verde River at Camp Verde (green, USGS gauge #9506000), San Miguel River at Uravan (dark blue, USGS #9177000), San Miguel River at Placerville (lightblue, USGS #9172500), Dolores River at Bedrock (red, USGS #9169500), Dolores River at Rico (pink, USGS #9165000).

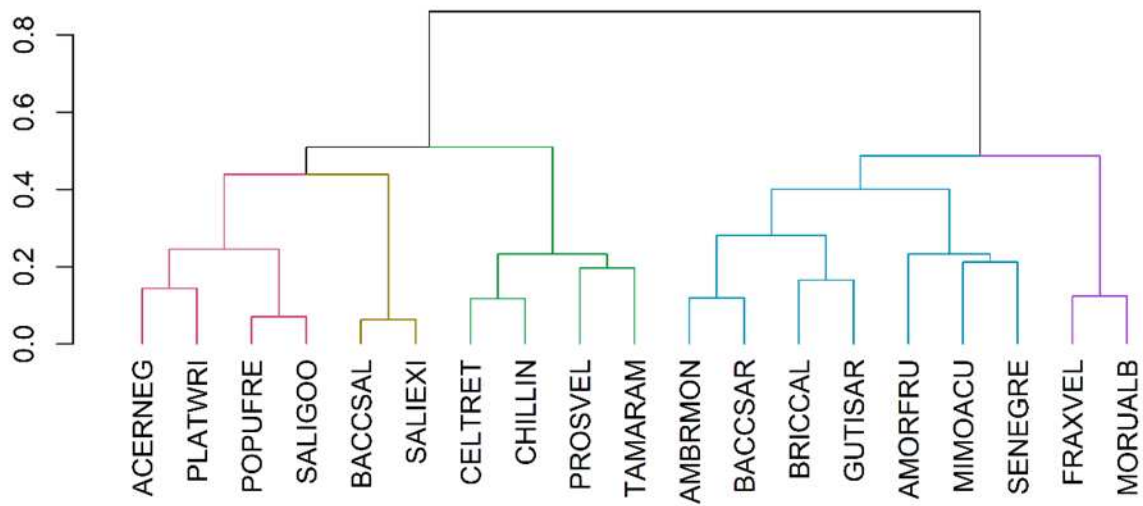
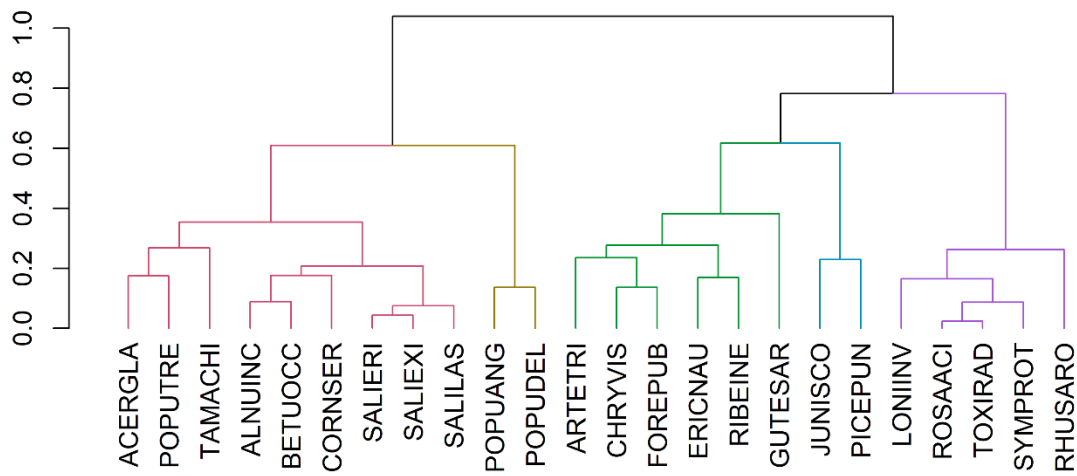


Figure 4.3 Dendrogram from hierarchical cluster analysis to identify woody vegetation guilds on the San Miguel and Dolores Rivers (top) and the Verde River (bottom). Colors represent the distinct vegetaton guilds (Table 4.1). See Appendix Table 6 for the key to species codes.

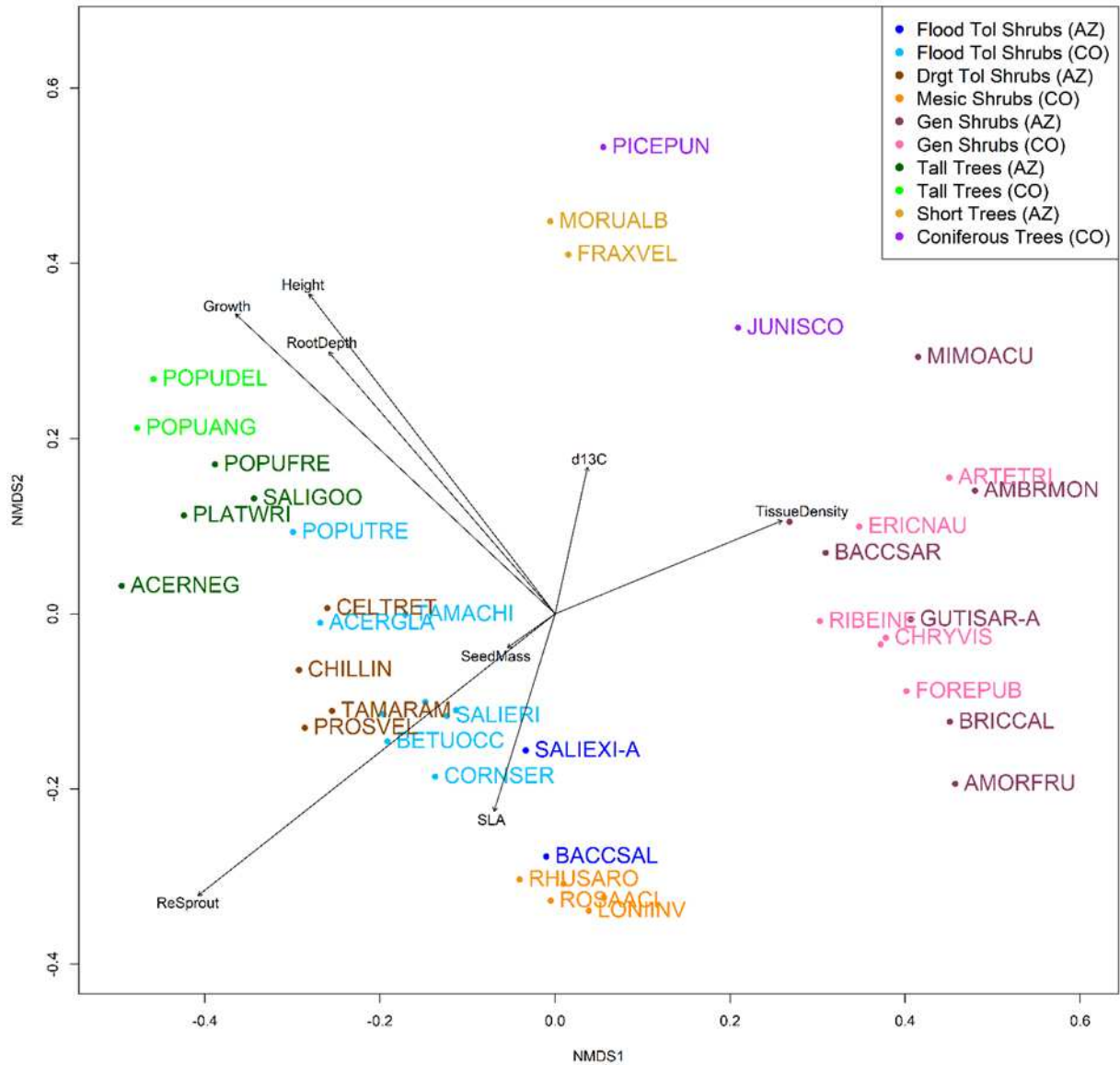


Figure 4.4 NMDS of species trait composition in vegetation guilds delineated in Arizona on the Verde River and in Colorado on the San Miguel and Dolores Rivers. Vectors of functional traits overlaid on top indicate variables that are correlated with guild composition. The length of the vector demonstrates the correlation.

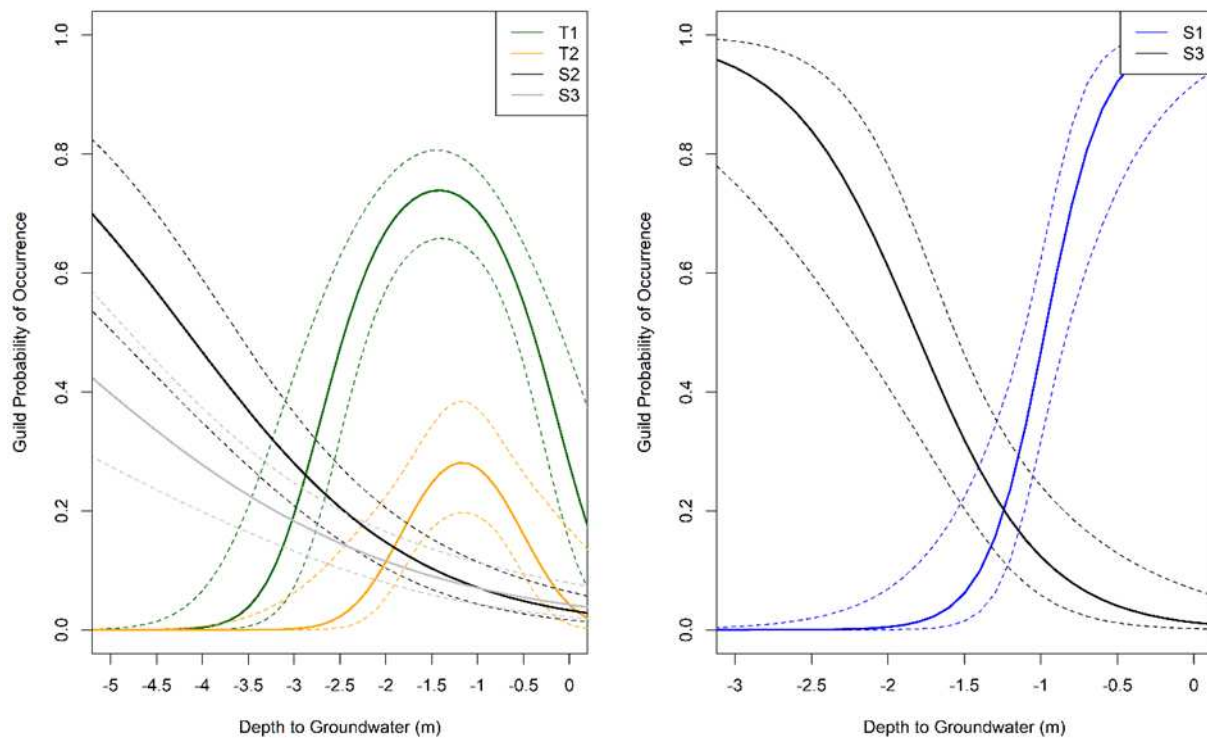


Figure 4.5 Modeled probability of occurrence for guild T1 (green), T2 (yellow), S3 (grey), and S2 (black) in Arizona with 95% confidence intervals (dotted lines). T1 and S2 guilds are co-dominant at groundwater depths between approximately -2.5 and -3.25 m. The T1 guild is more likely to be found where groundwater depth is less than 2.5 m and guild S2 is dominant where groundwater depth is greater than 3.25 m. T2 has a similar response curve to T1 and was more likely in area where groundwater was shallower than 1.5 m. Guild S1 and S3 distributions at Uruan on the lower San Miguel River (right panel) demonstrate that S1 is more likely to be found where groundwater is shallower than 0.9 m and S3 more likely when groundwater is deeper than -1.64 m.

## 5 Synthesis

One of the goals of plant ecology is to predict the assembly of plant communities across environmental gradients. Trait-based approaches test our ability to generalize relationships between plants and environmental attributes to aid in ecosystem management and maintain services and functions. Ranges of morphological, physiological, and life history traits enable plants to establish, grow, and reproduce in response to limited resources and environmental stress. Grouping species with similar traits helps scientists organize complex communities and establish assembly rules based on a mechanistic understanding of a species traits and the environment.

Riparian plant species have traits that allow them to disperse, survive, and reproduce in response to flow and water availability and these gradients are strong predictors of species distributions along rivers. Riparian pioneer species disperse seeds along with peak flows, are fast-growing, and can resprout from root stumps following flood disturbance. Riparian vegetation guilds, or groups of species with similar traits, have been proposed to develop generalized frameworks of riparian plant response. Efforts to understand the assembly of riparian species along hydrologic gradients is important in establishing ecological flows to maintain the complexity of riparian plant communities that provide quality habitat for a diversity of wildlife. The use of riparian vegetation guilds may help predict ecosystem response to changing environmental conditions under future climate and water use scenarios (Lozanovska et al. 2018).

The three preceding chapters investigate the characteristics of riparian vegetation guilds along three rivers in the western US and determine their use in predicting future change in vegetation as well as the provisioning of bird habitat for migratory and resident birds. In the first two chapters our research focused at three study reaches along the Verde River in Arizona while the

third chapter included data from study reaches along the Dolores and San Miguel Rivers in Colorado to assess if riparian guild relationships to hydrologic condition are transferable between river basins.

In the first chapter I defined traits of dominant woody and herbaceous vegetation guilds along the Verde River and questioned the individual and combined influence of guild cover on habitat quality for birds. To quantify bird habitat, I created an index from a combination of vegetation structure and environmental attributes finding that more structurally complex vegetation supported greater bird abundance, richness, and diversity. High quality habitat was explained by percent canopy cover, foliage height diversity, and foliage cover in the understory. I found that pioneer riparian trees best predicted habitat quality followed by drought tolerant riparian shrubs highlighting the need to maintain heterogeneity at both the vertical and horizontal scale. Along the Verde River, the conservation of mosaics of plant communities with contrasting structure is important for overall bird diversity, abundance, and richness. Contraction of riparian forests and species within the tall tree, short tree, and drought tolerant shrub guilds will drastically reduce the proportion of suitable habitat for migrant and resident birds along the Verde River.

In the second chapter I assessed the connection between surface and groundwater along the Verde River and tested if woody and herbaceous vegetation guilds are predicted by groundwater depth during the low flow season and flood exceedance probability compared to individual species models. I questioned how riparian plant communities would change in response to scenarios of lowered groundwater tables and altered flood regimes. Alluvial groundwater at our study reaches was solely maintained by Verde River surface flow and groundwater elevation was strongly driven by variation in river flows. I observed significant groundwater drawdown by riparian vegetation during the growing season, however, nightly recharge from the river maintained elevated groundwater levels throughout the growing season. Shallow alluvial groundwater at our study reaches supported riparian vegetation guilds, especially those that were strong predictors of bird habitat. Along the

Verde River hydrologic condition predicted the presence of tall and short riparian trees, flood tolerant shrubs, drought tolerant, generalist shrubs. I found that guild models for tall trees and short trees had similar prediction accuracies compared to models using individual species suggesting that many species within these guilds occupy similar hydrologic niches due to their functional traits. However, few herbaceous guilds were predicted by hydrologic conditions and occurrences may be driven by other assembly factors. Simulated reductions in floodplain groundwater had the largest impact on riparian plant communities with large decreases in the frequency of tall trees, short trees, and flood tolerant shrubs. Drought tolerant shrubs and generalist shrubs were predicted to encroach on floodplain surfaces with decreases in large winter flood frequency and lowered groundwater tables, but slight reductions were predicted for upland guilds with increased exceedance probability.

In the third chapter I compared riparian vegetation guilds between two study regions and assessed if vegetation-hydrologic relationships were transferable between rivers with varied climate, hydrologic condition, and channel morphology. Our results indicate that although plant species can be grouped based on similar traits, their relationship and predictability on the landscape may be driven by varied hydrologic processes and reach-scale attributes. The use of vegetation guilds may be more transferable between rivers with similar groundwater dynamics, climate, flow regimes, and channel morphology. I found that riparian vegetation zonation was more distinct in Arizona than Colorado due to steeper gradients of groundwater depth and more frequent flooding. Study reaches in Arizona had greater fluvial landform complexity with differences in elevation and depth to groundwater. At higher elevation study reaches on the San Miguel and Dolores Rivers, guilds were more widely distributed along floodplains with less distinct zonation due to shallow groundwater and higher annual rainfall. At the lower elevation reach on the San Miguel, flood tolerant shrubs and generalist shrubs were distributed along similar hydrologic gradients as these guilds along the Verde River. However, at the regulated study reach on the Dolores River generalist shrubs have

encroached lower floodplain surfaces and thresholds for flood tolerant shrubs were different than those along the Uravan. Using our validated bird habitat index from chapter 1, we compared habitat quality across our study reaches in Colorado and Arizona, finding the lowest at the regulated study reach of Bedrock. Across the three study rivers, our results suggest that changes in streamflow and groundwater will have greater magnitude changes in riparian communities where the river is the sole source of alluvial groundwater and higher temperatures and lower rainfall elevate stress on plants.

In this dissertation, I used methodology to objectively group species based on trait similarity. However, some vegetation guilds have large functional trait ranges and species may occupy dissimilar hydrologic niches not predicted by our study. Some of our more speciose guilds, like flood tolerant shrubs, were not predicted at high elevation reaches and information on individual species may be lost in guiding. Additional traits for these regions without steep environmental gradients may improve our understand of vegetation-hydrologic relationships and better distinguish guilds. Additional traits such as seed dispersal timing, aerenchyma tissue, and actual (not potential) re-sprout capability may be more informative along hydrologic gradients with low variation. Furthermore, we used similar traits for herbaceous and woody species, but herbaceous plants may be distributed based on different functional traits that are more crucial to their establishment and survival compared to those for woody plants. However, many herbaceous species are generalists and have wider ecological niches than riparian woody species. In this study we did not assess trait plasticity across study reaches or across age classes of sampled species. Furthermore, we equally weighted traits in the process of guilding, but recognize that some traits may explain more variation in species occurrences than others and be more important for some species, but not others.

We assessed riparian guild occurrences across two environmental gradients; depth to alluvial groundwater and flood exceedance probability. Recent studies argue for the inclusion of multiple assembly processes and the accounting of differences across ecoregions. Spasojevic and Suding

(2012) examined trait patterns along stress-resource gradients in the alpine tundra and found evidence for at least three assembly processes along an environmental gradient. Another study questioned whether the theory of limiting similarity (segregation of species resource uses based on traits) or assembly rules using abiotic filters will restrict viable strategies between environments characterized by either low productivity/high disturbance or high productivity/low disturbance (Fraser et al. 2016). On large alluvial rivers, abiotic gradients of groundwater depth and flood frequency have been shown to drive plant community composition, but other results suggest the interaction of other multiple processes including climate, channel and floodplain morphology, and competition.

#### *Final remarks*

Historic water planning throughout the west assumed that climate will be stationary. However, we are entering an era of uncertainty, with patterns of precipitation and temperature that fall outside of the historic record (Acreman et al. 2014). This work contributes to predicting how riparian plant communities could change in response to climate-driven changes in streamflow and how these effects will cascade to other ecosystem components including habitat for diverse species of birds. Alterations to keystone riparian plants will also shift connections between the aquatic and terrestrial environment along rivers, changing patterns of nutrient uptake, invertebrate communities, and abundances of terrestrial predators like bats, birds, and spiders. Our research suggests that vegetation guilds are more transferable within regions of similar flow, climate, and valley morphology, but practitioners should be wary of using guilds to understand river reaches between regions of disparate climate where elevation and valley form will have large influences on reach-scale hydrology.

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## Appendix

Appendix Table 1. Groundwater and exceedance probability thresholds for vegetation guilds and individual species along the Verde River in Arizona.

| <b>Guild</b>             | <b>Groundwater Threshold</b> | <b>EP Threshold</b> |
|--------------------------|------------------------------|---------------------|
| Tall Trees               | -0.38 to -2.5 m              | 1.00 to 75.0 %      |
| <i>Salix gooddingii</i>  | -0.6 to -2.18 m              | <i>na</i>           |
| <i>Populus fremontii</i> | -0.7 to -1.95 m              | <i>na</i>           |
| Short Trees              | < -1.44 m                    | <i>na</i>           |
| Flood Tolerant Shrubs    | < -0.90 m                    | <i>na</i>           |
| Drought Tolerant Shrubs  | > -1.84 m                    | < 3.0%              |
| Generalist Shrubs        | > -2.18 m                    | < 2.0%              |
| Short wetland herbs      | < -1.11 m                    | <i>na</i>           |
| Tall wetland herbs       | < -1.32 m                    | > 5%                |

Appendix Table 2. Information for each study reach in Arizona and Colorado. Temperature and precipitation data are average annual values.

| Site         | River      | USGS Gage # | Flow Record | Elev (m) | Temp °C | Precip (cm) | Watershed Area (km <sup>2</sup> ) |
|--------------|------------|-------------|-------------|----------|---------|-------------|-----------------------------------|
| Beasley Flat | Verde      | 9506000     | 1989-2019   | 909      | 17.28   | 32.28       | 11999.42                          |
| Childs       | Verde      | 9506000     | 1989-2019   | 807      | 18.05   | 36.50       | 12277.67                          |
| Sheep Bridge | Verde      | 9508500     | 1989-2019   | 626      | 19.90   | 36.62       | 14239.77                          |
| Bear Creek   | Dolores    | 9165000     | 1952-2017   | 2416     | 3.78    | 63.37       | 442.89                            |
| Bedrock      | Dolores    | 9171100     | 1986-2017   | 1509     | 10.33   | 33.83       | 5257.68                           |
| Placerville  | San Miguel | 9172500     | 1951-2017   | 2171     | 7.61    | 41.37       | 764.05                            |
| Uravan       | San Miguel | 9177000     | 1954-2017   | 1539     | 12.06   | 33.17       | 3470.59                           |

Appendix Table 3. RMSE for 1-D hydraulic models at study reaches using known and predicted water surfaces. At Arizona study reaches, we validated models using upstream pressure transducer measurements across a range of flows. At Colorado reaches without in-stream pressure transducers, models were validated using surveyed water surface elevations at low flow in 2018. We calculated RMSE using the two surveyed water surface elevations at lower flows (bold) as we were unable to attain water surface elevations at high flows.

| Study Region | River      | Reach        | Modeled Flows (cms)                        | Mean RMSE |
|--------------|------------|--------------|--------------------------------------------|-----------|
| Arizona      | Verde      | Beasley Flat | 5.09, 70.22, 288.84, 1410.23               | 0.05      |
| Arizona      | Verde      | Childs       | 5.09, 70.22, 288.84, 1410.23               | 0.08      |
| Arizona      | Verde      | Sheep        | 6.05, 70.50, 212.09, 1436.00               | 0.08      |
| Colorado     | San Miguel | Placerville  | <b>4.24, 10.19</b> , 43.33, 58.05, 77.59   | 0.05      |
| Colorado     | San Miguel | Uravan       | <b>1.87, 10.38</b> , 38.23, 130.00, 154.04 | 0.01      |
| Colorado     | Dolores    | Bear Creek   | <b>0.49, 3.89</b> , 30.89, 46.156, 61.44   | 0.04      |
| Colorado     | Dolores    | Bedrock      | <b>0.14, 2.39</b> , 77.02, 119.78, 143.28  | 0.03      |

Appendix Table 4. Proportional percent of vegetation guilds in plots at the seven study reaches. Short trees (T2) were not present in Colorado and coniferous trees (T3) were not found in plots in Arizona and are represented by NA.

| <b>Reach</b> | <b>T1</b> | <b>S1</b> | <b>S2</b> | <b>S3</b> | <b>T2</b> | <b>T3</b> |
|--------------|-----------|-----------|-----------|-----------|-----------|-----------|
| Beasley Flat | 44        | 13        | 24        | 29        | 17        | NA        |
| Childs       | 51        | 23        | 24        | 6         | 20        | NA        |
| Sheep Bridge | 60        | 17        | 14        | 12        | 15        | NA        |
| Bedrock      | 33        | 41        | 0         | 31        | NA        | 0         |
| Bear Creek   | 36        | 68        | 34        | 3         | NA        | 13        |
| Uravan       | 39        | 38        | 24        | 28        | NA        | 0         |
| Placerville  | 10        | 81        | 35        | 0         | NA        | 27        |

Appendix Table 5. Predicted percent of vegetation guild presence at each study reach (% Study Reach Area), at groundwater level declines of 0.50 m and 1.00 m, and daily flows reduced by 5%, 10%, and 20%. Guild presence was predicted using logistic models with exceedance probability and depth to groundwater (Table 4.3). Probability of Occurrence Threshold (Prob) represents the probability value that optimizes model sensitivity (proportion of observed positives that are predicted to be positive) or specificity (proportion of observed negatives predicted to be negative).

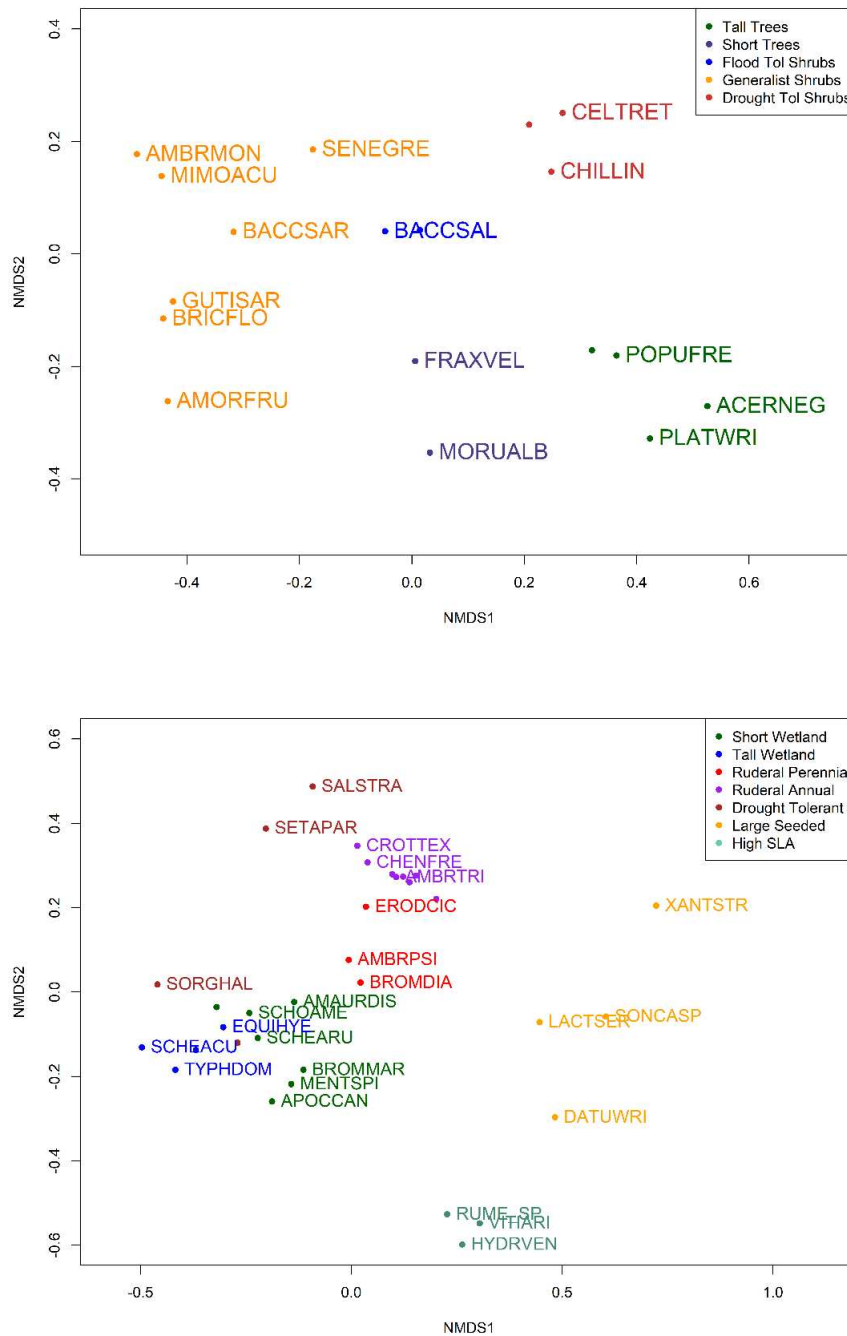
| <b>Groundwater Models</b>            |                         |                      |                     |                     |               |
|--------------------------------------|-------------------------|----------------------|---------------------|---------------------|---------------|
| <b>Guild</b>                         | <b>Study Reach</b>      | <b>% Study Reach</b> | <b>0.50 GW Drop</b> | <b>1.00 GW Drop</b> | <b>Prob</b>   |
| T1                                   | Upper Beasley Flat (AZ) | 57.3                 | 46.8                | 30.3                | 0.44          |
| T1                                   | Lower Beasley Flat (AZ) | 68.0                 | 67.0                | 62.7                | 0.58          |
| T1                                   | Childs (AZ)             | 76.7                 | 74.2                | 58.9                | 0.60          |
| T2                                   | Upper Beasley Flat (AZ) | 44.8                 | 20.1                | 2.9                 | 0.21          |
| T2                                   | Lower Beasley Flat (AZ) | 23.8                 | 13.3                | 4.7                 | 0.21          |
| T2                                   | Childs (AZ)             | 68.9                 | 60.3                | 22.6                | 0.21          |
| T2                                   | Sheep (AZ)              | 36.1                 | 19.3                | 12.5                | 0.21          |
| S1                                   | Upper Beasley (AZ)      | 32.3                 | 6.0                 | 1.0                 | 0.15          |
| S1                                   | Lower Beasley (AZ)      | 16.7                 | 7.0                 | 2.5                 | 0.15          |
| S1                                   | Childs (AZ)             | 66.3                 | 30.4                | .57                 | 0.15          |
| S1                                   | Sheep (AZ)              | 28.3                 | 15.3                | 7.1                 | 0.15          |
| S1                                   | Uravan (CO)             | 32.1                 | 7.3                 | 0.02                | 0.53          |
| S2                                   | Upper Beasley Flat (AZ) | 15.8                 | 18.7                | 22.7                | 0.58          |
| S2                                   | Lower Beasley Flat (AZ) | 74.3                 | 86.4                | 95.6                | 0.97          |
| S2                                   | Childs (AZ)             | 28.4                 | 32.6                | 37.0                | 0.44          |
| S3                                   | Upper Beasley Flat (AZ) | 34.6                 | 39.8                | 54.0                | 0.18          |
| S3                                   | Lower Beasley Flat (AZ) | 23.3                 | 46.0                | 64.6                | 0.18          |
| S3                                   | Childs (AZ)             | 30.4                 | 34.6                | 39.6                | 0.18          |
| S3                                   | Sheep Bridge (AZ)       | 1.7                  | 10.0                | 45.4                | 0.18          |
| <b>Exceedance Probability Models</b> |                         |                      |                     |                     |               |
| <b>Guild</b>                         | <b>Study Reach</b>      | <b>% Study Reach</b> | <b>EP 5%</b>        | <b>EP 10%</b>       | <b>EP 20%</b> |
| T1                                   | Upper Beasley Flat (AZ) | 54.9                 | 54.8                | 54.9                | 54.5          |
| T1                                   | Lower Beasley Flat (AZ) | 35.1                 | 33.2                | 30.9                | 25.8          |
| T1                                   | Childs (AZ)             | 75.0                 | 74.8                | 74.6                | 74.3          |
| S1                                   | Upper Beasley Flat (AZ) | 25.1                 | 21.2                | 18.4                | 13.9          |
| S1                                   | Lower Beasley Flat (AZ) | 24.6                 | 22.0                | 18.2                | 11.2          |
| S1                                   | Childs (AZ)             | 56.7                 | 59.2                | 61.1                | 57.6          |
| S1                                   | Sheep Bridge (AZ)       | 70.9                 | 71.2                | 71.9                | 73.3          |
| S1                                   | Bedrock (CO)            | 83.4                 | 81.6                | 79.7                | 78.7          |
| S1                                   | Uravan (CO)             | 52.1                 | 50.3                | 47.1                | 40.1          |
| S2                                   | Upper Beasley Flat (AZ) | 18.9                 | 19.6                | 20.0                | 20.8          |
| S2                                   | Lower Beasley Flat (AZ) | 51.4                 | 57.2                | 63.6                | 70.2          |
| S2                                   | Childs (AZ)             | 45.0                 | 46.4                | 47.8                | 48.7          |
| S3                                   | Upper Beasley Flat (AZ) | 24.3                 | 24.6                | 25.1                | 26.1          |
| S3                                   | Lower Beasley Flat (AZ) | 10.7                 | 11.0                | 11.3                | 11.8          |

|    |             |      |      |      |      |
|----|-------------|------|------|------|------|
| S3 | Childs (AZ) | 55.6 | 56.7 | 59.3 | 67.0 |
| S3 | Sheep (AZ)  | 73.4 | 74.2 | 74.5 | 75.6 |
| S3 | Uravan (CO) | 25.1 | 27.5 | 31.1 | 39.0 |

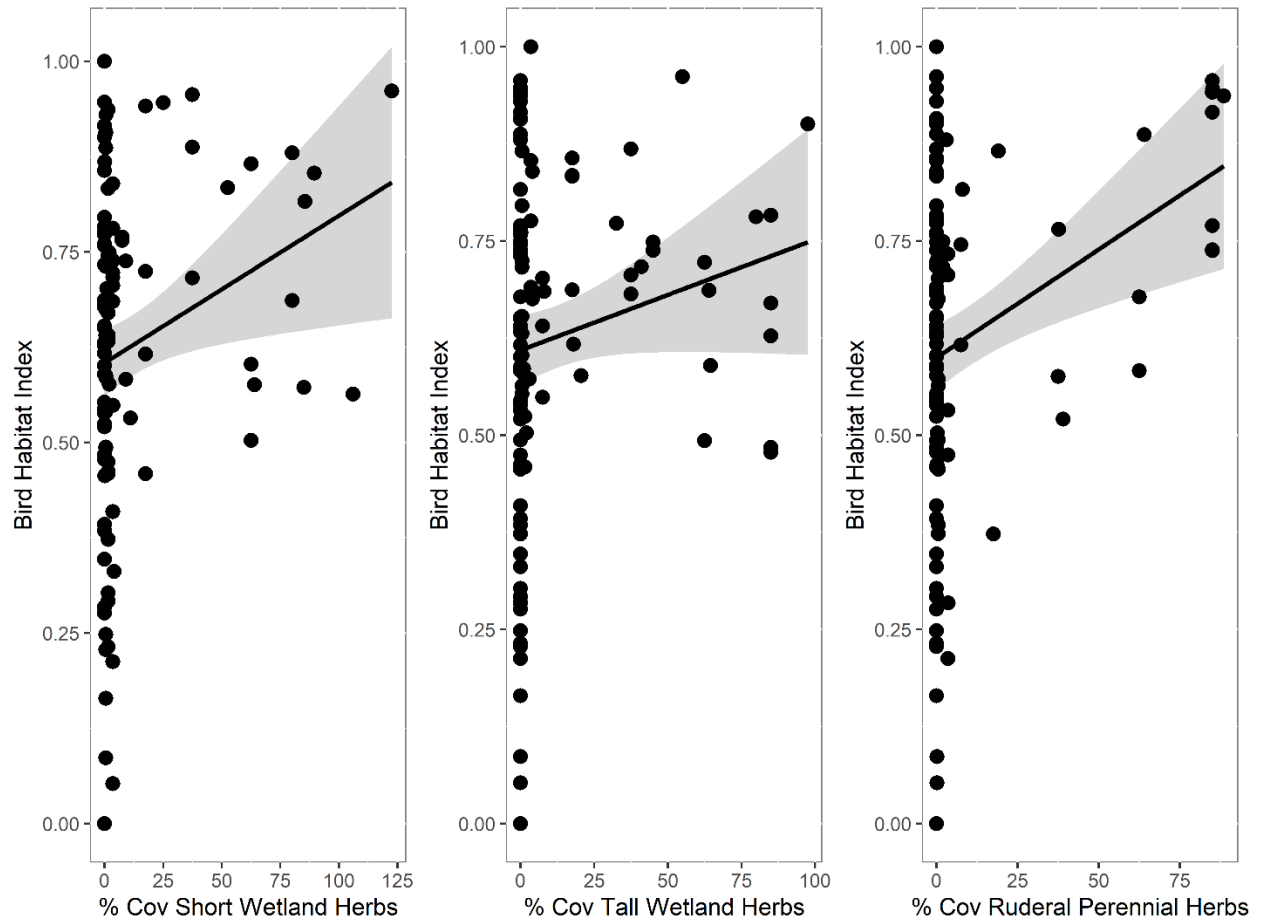
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Appendix Table 6. Woody species and codes used in Figure 4.3 and Figure 4.4.

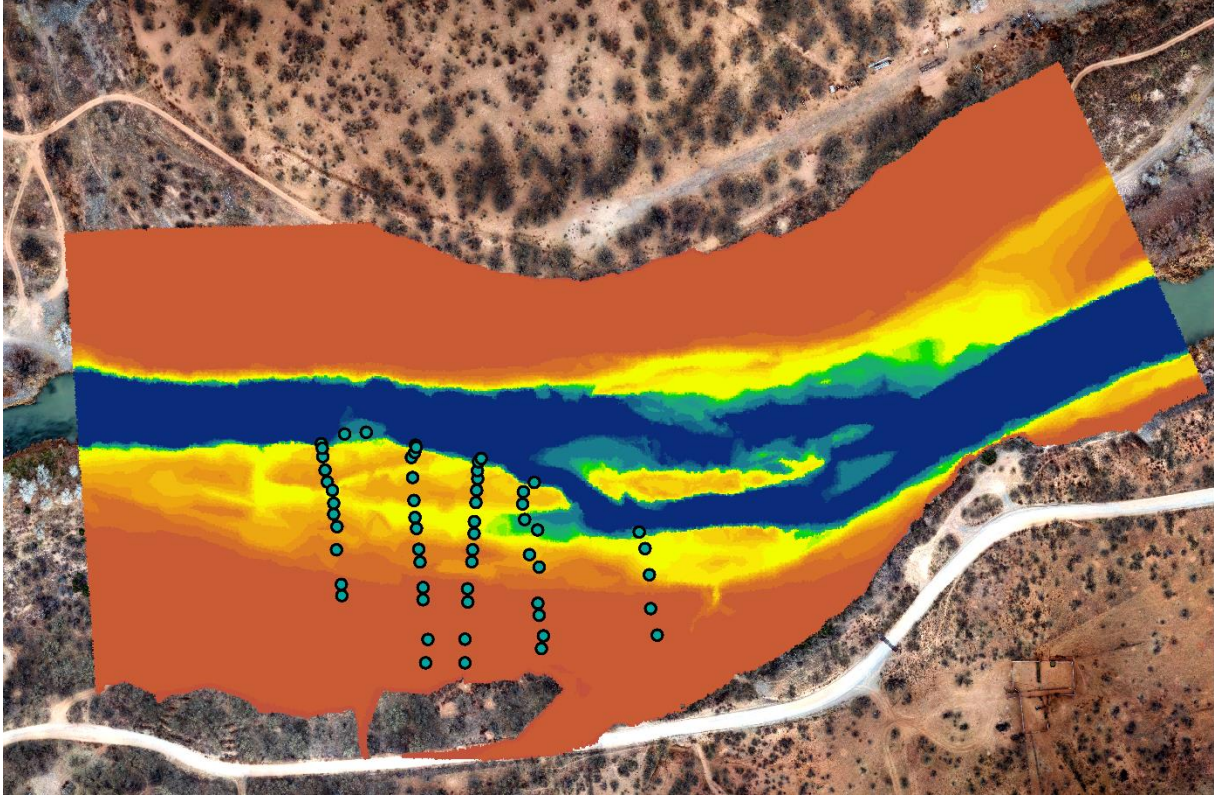
| Code     | Species                             |
|----------|-------------------------------------|
| POPUFRE  | <i>Populus fremontii</i>            |
| SALIGOO  | <i>Salix gooddingii</i>             |
| PLATWRI  | <i>Platanus wrightii</i>            |
| ACERNEG  | <i>Acer negundo</i>                 |
| FRAXVEL  | <i>Fraxinus velutina</i>            |
| MORUALB  | <i>Morus alba</i>                   |
| SALIEXI  | <i>Salix exigua</i>                 |
| BACCSAL  | <i>Baccharis salicifolia</i>        |
| CELTRET  | <i>Celtis reticulata</i>            |
| PROSVEL  | <i>Prosopis velutina</i>            |
| CHILLIN  | <i>Chilopsis linearis</i>           |
| TAMAAM   | <i>Tamarix ramosissima</i>          |
| GUTISAR  | <i>Gutierrezia sarothrae</i>        |
| BRICFLO  | <i>Brickellia floribunda</i>        |
| AMORFRU  | <i>Amorpha fruticosa</i>            |
| SENEGREG | <i>Senegalia greggii</i>            |
| MIMOACU  | <i>Mimosa aculeaticarpa</i>         |
| AMBRMON  | <i>Ambrosia monogyra</i>            |
| BACCSAR  | <i>Baccharis sarothroides</i>       |
| POPUDEL  | <i>Populus deltoides</i>            |
| POPUANG  | <i>Populus angustifolia</i>         |
| JUNISCO  | <i>Juniperus scopulorum</i>         |
| PICEPUN  | <i>Picea pungens</i>                |
| ALNUINC  | <i>Alnus incana</i>                 |
| BETUOCC  | <i>Betula occidentalis</i>          |
| CORNSER  | <i>Cornus sericea</i>               |
| SALIERI  | <i>Salix eriocephala</i>            |
| SALILAS  | <i>Salix lasiandra</i>              |
| TAMACHI  | <i>Tamarix chilensis</i>            |
| ACERGLA  | <i>Acer glabrum</i>                 |
| POPUTRE  | <i>Populus tremuloides</i>          |
| LONIINV  | <i>Lonicera involucrata</i>         |
| SYMPROT  | <i>Symphoricarpos rotundifolius</i> |
| TOXIRAD  | <i>Toxicodendron radicans</i>       |
| ROSAACI  | <i>Rosa acicularis</i>              |
| RHUSARO  | <i>Rhus aromatica</i>               |
| ARTETRI  | <i>Artemisia tridentata</i>         |
| CHRYVIS  | <i>Chrysothamnus viscidiflorus</i>  |
| FORESPUB | <i>Forestiera pubescens</i>         |
| ERICNAU  | <i>Ericameria nauseosa</i>          |
| RIBEINE  | <i>Ribes inermis</i>                |



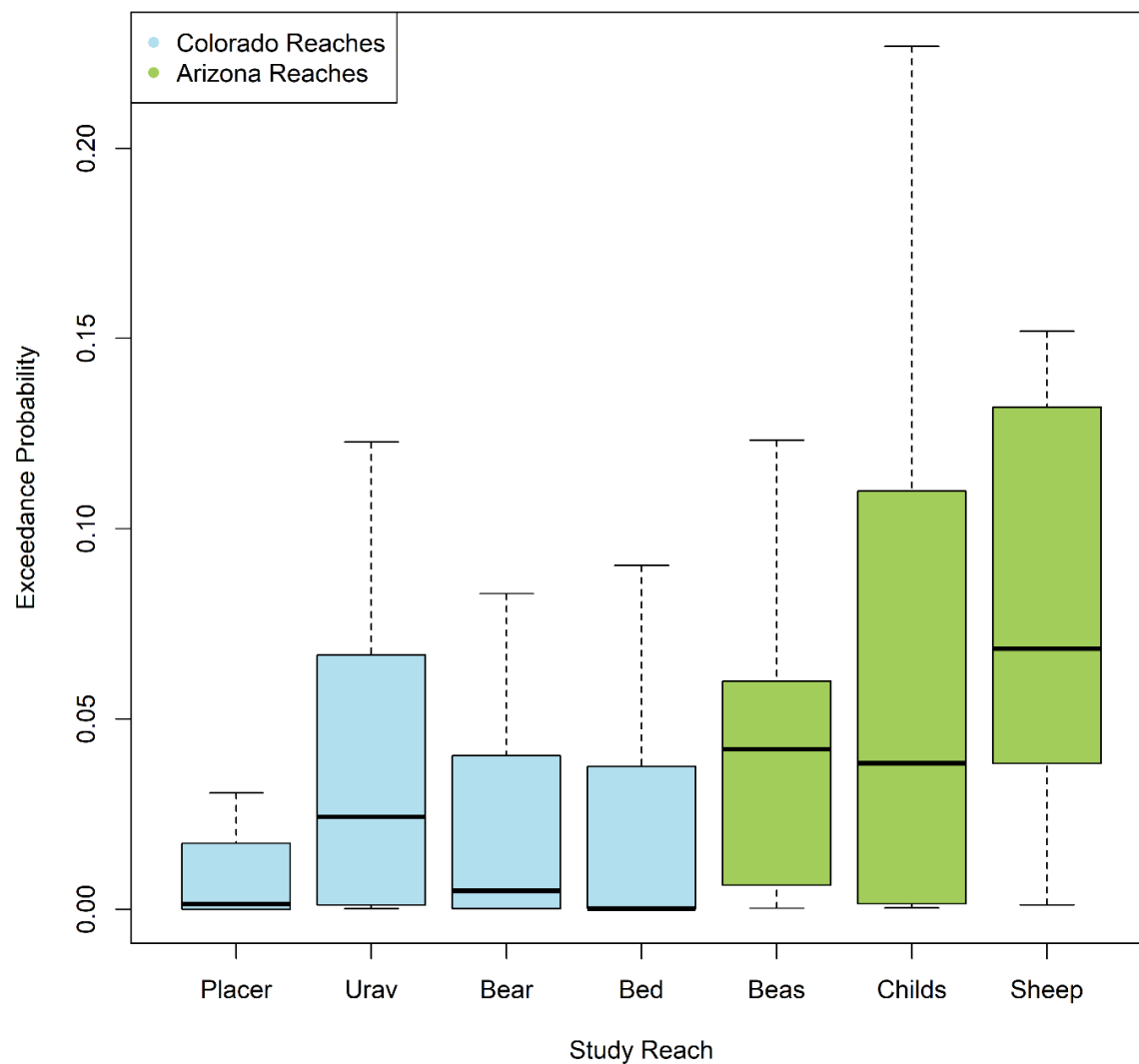
Appendix Figure 1. Variation in species trait composition for woody (top) and herbaceous and graminoid species (bottom). Species have been grouped based on the results of the cluster analysis with differences in composition supported with post-hoc PERMANOVA. In herbaceous grouping, E (drought tolerant herbs) and F (large seeded herbs) were not statistically different, but we chose to keep them as separate guilds based on the results of the cluster analysis. All other flow response guilds had distinct trait compositions. Due to the similarity of some species, not all are displayed on the ordination to avoid text overlap.



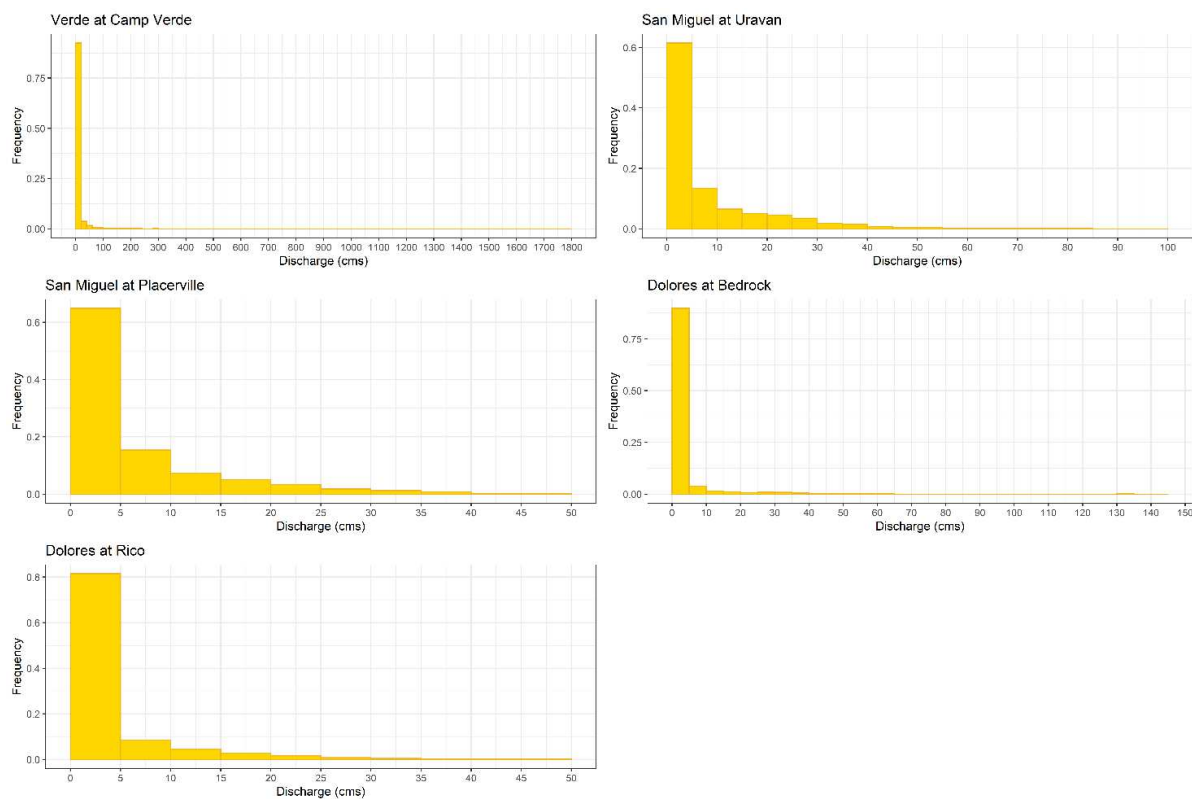
Appendix Figure 2. Relationship between herbaceous/grass flow response guilds on the Verde River, AZ. Guild A consists of disturbance and inundation tolerant herbs and grasses (e.g. *Schoenoplectus americanus*, *Apocynum canabium*). Guild B consists of disturbance intolerant inundation tolerant sedges and reeds (e.g. *Phragmites australis*, *Typha dominigensis*). Guild C consists inundation and disturbance intolerant herbs and grasses (e.g. *Bromus diandrus*, *Ambrosia psilostachya*).



Appendix Figure 3. Map of flood exceedance probability at Upper Beasley Flat. Circles indicate vegetation plots and exceedance probability decreases across the floodplain from blue to orange. Exceedance probabilities ranged from 0.0002 (dark orange) on upper terraces surfaces to 1 (dark blue) in the channel.



Appendix Figure 4. Inundation exceedance probability for study plots at reaches along the Verde, San Miguel, and Dolores Rivers.



Appendix Figure 5. Flow frequency distributions for each study river and reach using the last 30 years of the daily flow record. At Colorado study reaches, bin width is 5 cms, while Verde River binwidth is 20 cms due to the larger range in flows in the flow record.