

Water source niche overlap increases with site moisture availability in woody perennials

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Abstract Classical niche partitioning theory posits increased competition for and partitioning of the most limiting resource among coexisting species. Coexisting plant species may vary in rooting depth, reflecting niche partitioning in water source use. Our goal was to assess the soil water partitioning of woody plant communities across northern Arizona along an elevational moisture gradient using stem and soil water isotopes from two sampling periods to estimate the use of different water sources. We hypothesized that niche overlap of water sources would be higher and monsoon precipitation uptake would be lower at sites with higher moisture availability. Pairwise niche overlap of coexisting species was calculated using mixing model estimates of proportional water use for three sources. Across the moisture gradient, niche overlap increased with site moisture index (precipitation/potential evapotranspiration) across seasons, and site moisture index explained 37% of the variation in niche overlap of intermediate and deeper sources of water. Desert trees

T. E. Kolb School of Forestry, Northern Arizona University, Flagstaff, AZ 86011, USA utilized more winter source water than desert shrubs, suggesting the partitioning of water sources between functional groups. However, seasonal differences in surface water use were primarily found at intermediate levels of site moisture availability. Our findings support classical niche partitioning theory in that plants exhibit higher overlap of water sources when water is not a limiting resource.

Keywords Coexistence \cdot Niche overlap \cdot Water source \cdot Stable isotopes \cdot Plant communities \cdot Moisture gradient

Introduction

The niche diversification hypothesis (Connell 1978) postulates that species coexistence requires specialization along niche axes, which reduces interspecific competition (Armstrong and McGehee 1980; Chesson 2000; Macarthur and Levins 1967). Though Connell did not believe that plants could subdivide their basic resource requirements finely enough to explain their coexistence, subsequent research has found differentiation along niche axes such as light, soil moisture, and available nutrients to explain plant species coexistence (Araya et al. 2011; Levine and HilleRisLambers 2009; Silvertown 2004). In arid environments, pulsed resource availability allows for

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many axes of niche differentiation, particularly with regard to water acquisition strategies (Chesson et al. 2004). Differential use of soil moisture by coexisting plants can be inferred from root stratification (Davis and Mooney 1986; Manning and Barbour 1988), but not all roots actively uptake water. Comparison of water isotopes between stem and soil permits direct estimates of water source use, including temporal variation (Ehleringer et al. 1991).

In the southwestern US ("Southwest"), annual precipitation is bimodal, falling as frontal storms in the winter and as convective storms during the summer monsoon (Lowe 1964; Sheppard et al. 2002). Seasonal isotopic variation in precipitation is primarily caused by differences in the travel distance of air masses and the amount of evaporation, with winter precipitation being more depleted in heavy isotopes than summer precipitation (Dawson et al. 1993; Ehleringer et al. 1991), though variation is also influenced by differences in precipitation event size (Dansgaard 1964) or intensity of upwind convection (Moerman et al. 2013; Risi et al. 2008). Due to lower plant transpiration, lower evaporation, and larger and less intense storms, winter precipitation infiltrates deeply into the soil while summer precipitation often remains near the surface, resulting in a gradient of more isotopically depleted water with depth in the soil profile (Ehleringer and Dawson 1992). Generally, the isotopic composition of water remains unchanged during water transport from the roots to shoots such that the isotopic composition of xylem water reflects the source from which plants extract water (Brunel et al. 1995; Ehleringer and Dawson 1992; Wershaw et al. 1966), though Ellsworth and Williams (2007) demonstrated fractionation of hydrogen isotopes in xerophytic species. Previous studies have used stable isotopes in stem and soil water to investigate differential water sources in coexisting plants communities such as Mediterranean shrublands (Filella and Peñuelas 2003; Moreno-Gutiérrez et al. 2012; Valentini et al. 1992), tropical forests (Drake and Franks 2003; Jackson et al. 1995; Meinzer et al. 1999; Stratton et al. 2000), savannahs (Kulmatiski et al. 2010; Le Roux et al. 1995; Weltzin and McPherson 1997), grasslands (Dodd et al. 1998; Nippert and Knapp 2007; Yang et al. 2011), riparian trees (Busch et al. 1992; Horton et al. 2003), and deserts (Ehleringer et al. 1991). However. differentiation niche across biotic communities has not been tested using stable isotopes of water.

Recent drought, which couples low winter precipitation with high summer vapor pressure deficit (Williams et al. 2013), has exacerbated arid conditions in the Southwest and caused selective mortality of woody plant species, leading to altered species compositions (Allen and Breshears 1998; Bigler et al. 2007; Ganey and Vojta 2011; Koepke et al. 2010). The impact of drought can be observed across many biotic communities, including deserts (McAuliffe and Hamerlynck 2010), pinyon-juniper woodlands (Breshears et al. 2005), mixed-conifer and ponderosa pine forests (Ganey and Vojta 2011; Kane et al. 2014), and subalpine forests (Bigler et al. 2007; Huang and Anderegg 2012). Investigating niche differentiation of water source use can improve understanding of the physiological basis for droughtinduced changes in community composition, given that increased aridity and severe droughts are imminent in the Southwest (Cayan et al. 2010; MacDonald et al. 2008; Prein et al. 2016; Seager et al. 2007; Seager and Vecchi 2010).

Gradients in light (e.g., Kobe 1999), nutrients (e.g., Rebele 2000), and soil moisture (e.g., Dawson 1990) have been used to investigate mechanisms of species coexistence, but studies are often limited to a single biotic community. We utilized an elevational moisture gradient to investigate spatial and temporal variation in water source use across five biotic communities. We compared niche overlap (the inverse of niche partitioning) in water uptake among coexisting species across a moisture gradient and between two times during the growing season, before and after the onset of summer monsoon precipitation. We hypothesized that (1) interspecific niche overlap would increase in plant communities with higher moisture availability and (2) utilization of monsoon precipitation would be higher in plant communities with lower moisture availability.

Materials and methods

Study sites and moisture gradient

Study sites were located along an elevational moisture gradient in Yavapai and Coconino Counties, Arizona, USA, on the edge of the Colorado Plateau. In 2012, five sites were selected based on the observed biotic communities: upland Sonoran Desert, pinyon-juniper woodland, ponderosa pine forest, mixed-conifer forest, and spruce-fir forest (Brown 1994). Latitude ranged from 34.18°N to 35.37°N, site elevation from 799 to 2965 m, mean maximum annual temperature from 26.5 to 13.2 °C, and mean annual precipitation from 376 to 813 mm (Table 1). Precipitation seasonality was similar at all sites; May and June were very dry and the summer monsoon peaked in August (PRISM Climate Group 2013). Amounts of July–September precipitation in 2012 were similar to the 30-year average at all sites (Table 1).

Selected sites were located on hillslope positions with no evidence of riparian, phreatophytic vegetation. Slope, soil texture, and parent material varied among the sites (Table 2). Slopes ranged from 3 to 24.2°. Soils at the pinyon-juniper and ponderosa sites were clay, while soils at all other sites were sandy loam. Texture was determined on soil sampled from depths of 19 to 21 and 34 to 36 cm at five plots per site using the standard hydrometer method adapted from Sheldrick and Wang (1993). Parent material was obtained from SSURGO data accessed through SoilWeb and the Terrestrial Ecosystem Survey of the Coconino National Forest (Miller et al. 1995; Soil Survey Staff). USGS well sites indicate depth to groundwater of > 130 m at nearby sites with similar hillslope positions (USGS 2017), which is beyond the maximum rooting depth of published plant species (Canadell et al. 1996).

Table 1 Location and climate characteristics of study sites

Five 30 m by 30 m plots were established at each site to sample stem water of coexisting woody species. Each plot was divided into four equal quadrants, and woody plants of each species were sampled once per quadrant. A total of 262 individuals of 16 species (Table 3) were sampled prior to the monsoon season in June 2012; resampling occurred during the monsoon season in August 2012, between one and 5 days following a precipitation event. Isotopic fractionation during evaporation through photosynthetic tissues can compromise the fidelity of stem water as an indication of source water. For this reason, desert species with photosynthetic bark were excluded from sampling (e.g., Parkinsonia microphylla and Canotia holacantha). Species composition differed among plots, and depending on natural occurrence, two to four individuals of each species were sampled per plot.

Soil and stem water measurements

Soil samples were collected at the center of each plot to characterize the isotopic signature of the source water for the plant community at each sampling date. Using a 5-cm-diameter soil auger, we sampled three 2-cm-thick soil layers spanning a range of depths: 0–2, 19–21, and 34–36 cm. Depth to bedrock was estimated to be 35 cm at the desert site (Soil Survey Staff) and consistent soil sampling depths were used for all sites. Therefore, IsoMAP was used to infer the isotopic signature of water sources deeper than 35 cm (see "Water source modeling" section). Samples were immediately placed in doubled, plastic zip-top bags,

Sites	Latitude	Longitude	Elevation (m)	MMAT (°C)	MAP (mm)	MSP (mm)	% SP	2012 SP (mm)	Moisture index
Desert	34.18	- 112.16	799	26.5	376	130	34.6	121	0.14
Pinyon- juniper	34.76	- 111.63	1778	19.9	567	179	31.6	231	0.50
Ponderosa	35.02	- 111.66	2140	16.8	719	209	29.1	249	0.79
Mixed- conifer	35.35	- 111.73	2590	14.8	673	250	37.1	248	0.95
Spruce-fir	35.37	- 111.67	2965	13.2	813	287	35.3	262	1.11

Moisture index is the ratio of annual precipitation to potential evapotranspiration, estimated by the Thornthwaite method (1948)

MMAT mean annual maximum temperature, 1981–2010, *MAP* mean annual precipitation, 1981–2010, *MSP* mean summer precipitation, July–September, 1981–2010, % *SP* percent precipitation falling in summer, July–September, 1981–2010, 2012 SP summer precipitation, 2012

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Sites	Slope (°)	% Clay	% Sand	Soil texture	Soil parent material	
Desert	7.1 (1.3)	11.3 (3.1)	76.1 (3.9)	Sandy loam	Alluvium granite ^a	
Pinyon-juniper	3.0 (0.6)	54.9 (1.8)	15.2 (1.5)	Clay	Residuum basalt/cinders ^b	
Ponderosa	5.4 (1.3)	45 (5.2)	26.9 (4.5)	Clay	Residuum basalt/cinders ^b	
Mixed-conifer	5 (1.4)	10.4 (1.9)	63.3 (4.0)	Sandy loam	Residuum andesite ^b	
Spruce-fir	24.4 (1.2)	15.8 (0.8)	66.2 (2.0)	Sandy loam	Residuum andesite/dacite ^b	

Table 2 Comparison of soil characteristics across five study sties

Soils were sampled from 19 to 21 and 34 to 36 cm depths at five plots per site. Slope, clay content, and sand content are reported as site-level means with ± 1 SE in parentheses

^aSSURGO data accessed from Web Soil Survey (Soil Survey Staff)

^bTerrestrial Ecosystem Survey of the Coconino National Forest (Miller et al. 1995)

Table 3Species identity,sample size, and plant sizeof 262 individuals acrossfive study sites

	n	Mean size (SE)	Range of sizes
Desert			
Acacia greggii (ACGR)	17	1.2^{a} (0.1)	0.4–1.8
Dodonaea viscosa (DOVI)	6	1.2^{a} (0.1)	1.0-1.7
Prosopis velutina (PRVE)	7	1.8^{a} (0.1)	1.4-2.2
Simmondsia chinensis (SICH)	15	$1.1^{a} (0.1)$	0.6-1.8
Ziziphus obtusifolia (ZIOB)	7	$1.5^{a}(0.1)$	0.8-1.9
Total	52		
Pinyon-juniper			
Arctostaphylos pungens (ARPU)	7	0.9^{a} (0.1)	0.6-1.3
Juniperus osteosperma (JUOS)	18	39.5 ^b (3.7)	12.3-70.5
Mahonia fremontii (MAFR)	14	$1.3^{a}(0.1)$	0.5-2.0
Pinus edulis (PIED)	20	$12.5^{\rm c}$ (2.1)	3.9-39.7
Total	59		
Ponderosa			
Pinus ponderosa (PIPO)	20	$31.4^{\rm c}$ (1.8)	22.1-53.1
Quercus gambelii (QUGA)	16	26.6 ^c (3.2)	3.3-47.5
Total	36		
Mixed-conifer			
Pinus ponderosa (PIPO)	5	57.3 ^c (13.3)	19.8–94.4
Pinus strobiformis (PIST)	17	35.8 ^c (5.4)	7.5–92.6
Populus tremuloides (POTR)	20	26.4° (1.5)	15.8-41.2
Pseudotsuga menziesii (PSME)	6	34.4 ^c (5.1)	22.1-53.0
Total	48		
Spruce-fir			
Abies lasiocarpa (ABLA)	20	27.6 ^c (3.3)	11.6-56.8
Picea engelmannii (PIEN)	20	32.5 ^c (2.0)	19.5–53
Pinus strobiformis (PIST)	7	31.1 ^c (8.6)	7.2–65.3
Populus tremuloides (POTR)	20	21.9 ^c (1.1)	13.3-30.6
Total	67		

Species codes are shown in parentheses. Size was measured as ^aheight (m) for shrubs, ^bbasal diameter (cm) for *Juniperus osteosperma*, and ^cdiameter at breast height (cm) for trees stored in a cooler, and transported to a - 18 °C freezer within 8 h of collection (Ehleringer and Osmond 1989). Water from each soil sample was extracted using a cryogenic vacuum line. Each soil sample was placed in a 25 × 150 mm glass tube and packed with glass wool to prevent movement of soil particles into the vacuum line; the glass tubes were placed on the extraction line, and samples were extracted for 1 h (West et al. 2006). Extracted water was transferred to 12 × 32 mm screw-top vials that were sealed and stored at 4 °C until isotopic analysis (West et al. 2006). Each extracted soil sample was paired with a soil subsample that was weighed, dried for 24 h at 105 °C, and reweighed to calculate gravimetric soil water content.

At each sampling period, a well-suberized branch segment or a 6-cm-deep trunk core, depending on accessibility, was taken from each individual plant. Water isotopic composition does not vary between branch and trunk (Busch et al. 1992). Each plant sample was quickly removed and placed into a 21×70 mm glass vial, sealed with a screw-top lid and Parafilm, placed in a plastic zip-top bag, and transported in a cooler to a - 18 °C freezer for storage until cryogenic water extraction following procedures described above, but without the glass wool. Immediately following extraction, we placed two small pieces of granular activated carbon in the extracted water, which was then filtered through a 0.2-µm membrane syringe filter to remove the charcoal and any organic compounds that may interfere with accurate isotopic measurements.

Isotopic measurements

Isotopic analyses of all water samples were conducted via isotope ratio infrared spectroscopy (IRIS) using either the Picarro G1102-i wavelength-scanned cavity ring down spectrometer (Picarro, Inc., Santa Clara, CA, USA) or the Los Gatos Research DLT-100 offaxis cavity output spectrometer (LGR, Mountain View, CA, USA) interfaced with a liquid autosampler. Samples were hand-injected into the Picarro until three acceptable measurements were made. Twelve injections per sample were measured using the LGR, and the means of the last five injections were used in actual calculations. Normalization and drift calculations were applied to all runs based on known, inhouse standards created from Vienna Standard Mean Ocean Water (VSMOW, 0‰), Standard Light Antarctic Precipitation (δ^2 H – 428‰, δ^{18} O – 55‰), and Greenland Ice Sheet Precipitation (δ^2 H – 190‰, δ^{18} O – 24.8‰). For some species, organic compounds have been found to interfere with accurate IRIS measurements, although use of activated charcoal moderately reduced deviations from values measured with isotope ratio mass spectrometry (IRMS), and low deviation was detected in pines (West et al. 2010). All δ^2 H and δ^{18} O values are reported in delta (δ) notation, in which δ expresses the isotopic ratio of the sample relative to VSMOW on a per mil basis

$$\delta = \left(R_{\text{sample}} / R_{\text{standard}} - 1 \right) \times 1000, \tag{1}$$

where *R* is the molar ratio of the heavy to light isotopes (e.g., ${}^{2}\text{H}:{}^{1}\text{H}, {}^{18}\text{O}:{}^{16}\text{O}$).

Moisture index

To quantify site moisture availability, we calculate site-level moisture index as the ratio of precipitation to potential evapotranspiration (PET). Average monthly temperature and precipitation from 1981 to 2010 were obtained as 2.5 min resolution grids from PRISM (2013). PET was calculated following Thornthwaite (1948):

$$\operatorname{PET}_{i} = 1.6 \left(\frac{10t_{i}}{I}\right)^{(6.75 * 10^{-7})I^{3} - (7.71 * 10^{-5})I^{2} + (1.792 * 10^{-2})I + 0.49239},$$
(2)

where t_i is the mean maximum monthly temperature, and *I* is the heat index. The heat index is calculated as a sum across all months of $(t_i/5)^{1.514}$. Annual PET and the climate moisture index were summed from monthly values and characterized for each site. Lower climate moisture indices indicate higher aridity.

Water source modeling

Isotope values were analyzed in a Bayesian mixing model framework using the 'simmr' package (Parnell et al. 2013). The mixing model compares source water isotopic signatures to those of stem water samples to estimate the proportional contribution (posterior distribution) of different water sources. One constraint of mixing model is that mixtures (e.g., stem water isotopes) have to lie within the span of the sources (e.g., soil and precipitation isotopes) in isotopic space (see Fig. 2). However, due to erroneously depleted surface soil water isotopes in the desert in June (Fig. 2a), we were unable to estimate the source proportions for desert plants in June.

We ran mixing models for co-occurring species at each site in each month except the desert in June. Three water sources were used: (1) surface (0-2 cm), (2) intermediate (plot-level averages of 19-21 and 34-36 cm weighted by soil water content), and (3) winter (modeled winter precipitation). Due to significant overlap in isotopic composition of soil water from 19 to 21 and 34 to 35 cm, the isotopic composition of the two depths was aggregated a priori weighted by soil water content to form the intermediate source (Phillips et al. 2005). Furthermore, the stem water isotopic mixtures at some sites were composed of more depleted sources than the soil water isotopes. Therefore, we estimated the isotopic composition winter precipitation (November-April) for each site to include as the "deep" end member in the mixing models. The isotopic composition of winter precipitation was estimated from IsoMAP by modeling mean and standard deviations of δ^{18} O and δ^{2} H based on GNIP data from 1960 to 2010 (IAEA/WMO 2011; Welker 2000). Predictor variables in the model included maximum and minimum temperature, precipitation, elevation, latitude, and longitude (Center 1998; PRISM Climate Group 2013); model performance was relatively high for both $\delta^{18}O$ and $\delta^{2}H$ $(R^2 = 0.83 \text{ and } 0.84, \text{ respectively}).$

Niche overlap index

To quantify site-level niche overlap, we compared the 95% credible interval (CI) of the proportional contribution of each source between species pairs. Niche overlap (O) was calculated by:

$$O_{AB,s} = 2 \cdot \left(\frac{W_{AB,s}}{W_{A,s} + W_{B,s}}\right),\tag{3}$$

where $W_{A,s}$ and $W_{B,s}$ are the widths of the 95% CI of proportional water use of source *s* for species A and B, respectively, and $W_{AB,s}$ is the width of the intersection of the 95% CI of $W_{A,s}$ and $W_{B,s}$ (adapted from Sepulveda et al. 2012). Niche overlap can take on values between 0 and 1, where 0 indicates no overlap and 1 indicates complete overlap. Because sites had variable numbers of woody species (Table 3), the number of species pairs ranged from 1 at the ponderosa site to 10 at the desert site.

Statistical analysis

Statistical analysis was performed in R version 3.3.2 (R Core Team 2016). Soil water content was naturallog transformed to improve normality and analyzed with a two-way ANOVA to test for differences between month, depth, and their interaction. Posthoc comparisons were made using Tukey's HSD. Mixing model estimates are reported as posterior means and 95% CIs. In a Bayesian framework, comparisons between estimates are significant at the 0.05 level if the mean of one estimate is excluded from the CI of the other. To test species differences in water source utilization, we compared means and CIs between co-occurring species for each month and source. To understand seasonal differences in water source use, a second set of comparisons were made between months for each species and source. The relationship between niche overlap (O) and the moisture index was explored with beta regression models using the 'betareg' package (Cribari-Neto and Zeileis 2010), which allow for separate models of mean and precision to account for heteroscedasticity in O. Initial data visualization indicated that surface O varied non-linearly with site moisture index, so only intermediate and winter O(n = 96) were modeled. Exploratory data analysis indicated that month was not a significant covariate for intermediate and winter sources, so June and August values were combined by source in subsequent analyses. Model selection was performed with likelihood ratio tests. Significance was defined as P < 0.05.

Results

Soil moisture

Soil moisture generally increased with elevation and from June to August (Fig. 1; Table 4), but the depth at which soil water content was highest also shifted with elevation and month. At lower elevations (desert, pinyon-juniper, and ponderosa sites), soil water content was greatest at lower depths in both months, while at the two high-elevation forests soil moisture was Fig. 1 Gravimetric soil water content (mean \pm SE) at the 0–2, 19–21, and 34–36 cm depths for June and August. Letters indicate significant differences between depths and seasons within each site



either distributed more evenly across the soil profile (June) or highest in the surface layer (August). Universally, soil moisture did not differ significantly between the 19–21 and 34–36 cm depths. Except for the desert site, overall soil moisture was significantly higher in August than June (Table 4). At the ponderosa, mixed-conifer, and spruce-fir sites, the depth by month interaction was significant, indicating that the monsoon rains altered the depth profile of soil moisture. Surface soil moisture was exceptionally high at the mixed-conifer and spruce-fir sites in August, as our sampling day coincided with monsoon precipitation ($\sim 3 \text{ mm } 1$ day prior to sampling in mixed-conifer, $\sim 8.5 \text{ mm}$ day of sampling in spruce-fir).

Isotopic composition of stem and source water

The δ^2 H and δ^{18} O of stem water fell along or below the global meteoric water line (GMWL, Craig 1961) across all sites and in both months (Fig. 2). Slopes of stem water isotopic composition (not shown) were lower than that of the GMWL in both months and increased between June (1.91–2.66, Fig. 2a–e) and August (2.90–6.87, Fig. 2f–j), with higher increases evident with higher site elevation. Generally, source water composition was also linear with slopes lower than the GMWL. However, water from the desert surface was more depleted in δ^2 H than the intermediate source water in June and was thus excluded from mixing model analyses. Slopes of source water isotopic composition (not shown) increased from June (2.07–3.56, excluding the desert site) to August (3.11–7.06), with higher increases with higher elevation.

Mixing model estimates

Proportion of water uptake of at least one source varied by species or month at all sites except for the mixed-conifer (Fig. 3). Seasonal differences were only detected in the surface source. In the desert, \sim 75% of water used in August by Acacia greggii and Prosopis velutina came from the winter source, while the remaining species utilized a significantly lower proportion of this source (Fig. 3a). No significant species differences were found in either surface or intermediate sources. But at the pinyon-juniper site, both surface and winter sources of water were utilized differentially by co-occurring species in June (Fig. 3b); these differences disappeared in August. In June, Pinus edulis utilized a higher proportion of surface water than Juniperus osteosperma and Mahonia fremontii and a lower proportion of winter water than M. fremontii. J. osteosperma, M. fremontii, and P. edulis increased the use of surface water in August. At the ponderosa site, species and seasonal differences were only found in the surface source (Fig. 3c), with

	df	F	Р
Desert			
Month	1	0.84	0.370
Depth	2	11.51	< 0.001
Month * depth	2	0.41	0.670
Resid	24		
Pinyon-juniper			
Month	1	13.42	0.001
Depth	2	47.57	< 0.001
Month * depth	2	0.73	0.490
Resid	24		
Ponderosa			
Month	1	20.36	< 0.001
Depth	2	13.17	< 0.001
Month * depth	2	3.92	0.034
Resid	23		
Mixed-conifer			
Month	1	67.32	< 0.001
Depth	2	9.80	0.001
Month * depth	2	7.26	0.003
Resid	24		
Spruce-fir			
Month	1	36.38	< 0.001
Depth	2	27.09	< 0.001
Month * depth	2	18.46	< 0.001
Resid	24		

 Table 4
 Two-way
 ANOVA tables for each site testing the significance of month and depth on soil water content

Bolded P values are significant

Pinus ponderosa using significantly more surface water than *Quercus gambelii* in both months. Only *P. ponderosa* had a significant increase in surface water use between June and August. No species differences were found at the two highest-elevation forests (Fig. 3d, e). The co-occurring species at the mixed-conifer sites used similar proportions of water for all sources in both months. At the spruce-fir site, estimates of source water proportions were more constrained in June than August, rendering it more difficult to identify significant differences. Only *Picea engelmannii* increased utilization of surface water between June and August.

Niche overlap

Pairwise niche overlap was lower at sites and within sources with significant species differences in water use proportions (Fig. 4). Across pinyon-juniper, mixed-conifer, and spruce-fir sites, surface niche overlap was compared between sites and months (desert was excluded due to only August values, ponderosa due to low sample size). Notably, surface niche overlap increased significantly from June to August only in the pinyon-juniper woodland; surface niche overlap did not increase across seasons at either high-elevation forest ($F_{5,30} = 2.391$, P = 0.06). The highest and lowest niche overlap values occurred at the ponderosa site, where only two species coexisted. P. ponderosa and Q. gambelii used non-overlapping proportions of surface water in both months, but nearly completely overlapping proportions of winter water in August due to wide CIs. Across sites, niche overlap generally increased with site elevation.

To test our hypotheses that niche overlap would increase with site moisture availability, we modeled pairwise niche overlap as a function of moisture index, with source and month as additional covariates. Only intermediate and winter overlap were considered, because surface overlap did not vary linearly across sites (due to 0 values at the ponderosa site). A reduced mean model excluding month as a predictor variable explained as much variation in niche overlap as the full model (likelihood ratio test, $\gamma^2 = 0.160$, P = 0.689), indicating that niche overlap did not vary significantly between months when the moisture index and water source were accounted for. The final mean and precision model pooled niche overlap for both months and included moisture index, water source, and their interaction (Table 5); the covariates explained 37% of the variation in intermediate and winter niche overlap. Mean niche overlap increased faster with moisture index for winter versus intermediate water sources, while variance in niche overlap was higher at low moisture index only for winter water sources (Fig. 5).

Discussion

Plant communities in more arid environments have lower interspecific niche overlap, as quantified by their dissimilarity in use of intermediate and winter sources, а

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Fig. 2 Isotopic composition of stem and source water in June (a-e) and August (f-j). Error bars on source points represent \pm SD, as used in the Bayesian mixing models (see text for

explanation of pooling soil and modeling winter precipitation isotopic compositions). The global meteoric water line (GMWL) is plotted in each panel for reference



Fig. 3 Proportional uptake of water (mean \pm CI) by plant species in June and August from three sources at **a** desert, **b** pinyon-juniper, **c** ponderosa, **d** mixed-conifer, and **e** spruce-fir sites. Water uptake proportion could not be estimated for the desert in June due to insufficient range of source isotopic compositions. Significant differences between species in June

than communities in more mesic environments (Fig. 5). While month was not a significant factor in the final regression model, 5 out of 16 species increased their surface water use between June and August (Fig. 3b, c, e). In the pinyon-juniper woodland, most species utilized a higher proportion of surface water in response to monsoon precipitation, which increased site-level niche overlap from June to August (Fig. 4). Variation in niche overlap is primarily driven by site moisture availability in the intermediate and winter sources and by seasonal shifts in the surface source, highlighting the importance of both spatial and temporal partitioning for coexisting woody species.

and August are indicated by lower and uppercase letters, respectively. Asterisks symbolize significant differences between the months of the same species. Panels without letters or asterisks had no significant differences among species or months

Moisture availability and evaporative demand

Soil moisture availability increased with elevation as expected by the adiabatic rate of cooling, which increases precipitation and decreases evaporation. Soil moisture was expected to increase following the arrival of the summer monsoon, but this shift was only apparent at the ponderosa, mixed-conifer, and spruce-fir sites (Fig. 1; Table 4). We believe this could be due to three non-exclusive factors. First, because the timing and magnitude of monsoon precipitation is difficult to predict (Loik et al. 2004), our sampling dates occurred between 1 and 5 days following monsoon storms, which may partially account for variable patterns in surface soil moisture. The two high-elevation sites were sampled only 1 day after substantial rain events. Second, soil evaporation remains high during the monsoon season at lower Fig. 4 Pairwise niche overlap (mean \pm SE) of each source in June and August across sites. Niche overlap could not be determined for the desert site in June; niche overlap at the ponderosa site lacks error bars because only one species pair is present



 Table 5 Beta regression of niche overlap with a logit link function for the mean model and a log link function for the precision model

	Z values	Р
Mean models		
Intercept: intermediate	1.780	0.075
Intercept: winter	- 3.296	< 0.001
Slope: intermediate	4.854	< 0.001
Slope: winter	2.700	0.007
Precision model		
Intercept: intermediate	4.797	< 0.001
Intercept: winter	- 4.725	< 0.001
Slope: intermediate	1.304	0.192
Slope: winter	2.793	0.005
Pseudo $R^2 = 0.3736$		

Mean and precision were both modeled with source, moisture index, and their interaction to account for heteroscedasticity in niche overlap

elevations, such that periodic sampling may not capture transient soil moisture pulses. Finally, arid plant communities are well adapted to pulsed monsoon precipitation (Schwinning and Ehleringer 2001), including extensive lateral roots that efficiently utilize and further reduce surface moisture (Gibbens and Lenz 2001). Taken together, these factors could explain why soil moisture, particularly in the surface layer, did not increase after the onset of monsoon storms at the desert and pinyon-juniper sites.

The evaporative environment experienced by the plant communities can be inferred from the isotopic composition of stem and source water. The degree to which the stem and source water isotopes fall below the GMWL indicates the evaporative enrichment of the water sources available to the plants (Craig 1961; Ehleringer and Dawson 1992). Slopes of both stem and source isotopic composition were more similar across sites in June than August (Fig. 2), indicating that monsoon precipitation provided a greater release from evaporative demand at high elevations. We detected erroneous values for surface soil isotopes in the desert in June based on the non-linear relationship of $\delta^2 H$ and $\delta^{18} O$ across source isotopes. Because surface soil samples were extremely dry (< 1% soil water content), there was likely a high proportion of bound water (Walker et al. 1994) and incomplete extraction could account for the erroneously depleted values (West et al. 2006).

Spatial partitioning across the moisture gradient

We found source water differentiation by coexisting species and low niche overlap at the three lowestelevation sites (Fig. 3). All desert species utilized a high proportion of winter source water compared to plants at other sites. Because winter precipitation **Fig. 5** Niche overlap of intermediate and winter sources as a function of moisture index. Lines indicate beta regression model fits



generally infiltrates deeper in the soil profile (Ehleringer and Dawson 1992), this finding is consistent with a meta-analysis that also found the greatest rooting depths in arid environments (Canadell et al. 1996). In particular, desert trees (A. greggii, P. velutina) used even higher proportions of winter water than desert shrubs (Dodonaea viscosa, Simmondsia chinensis, Ziziphus obtusifolia), consistent with other studies of rooting patterns across functional groups (Canadell et al. 1996; Schenk and Jackson 2002). On sandy-loam soils, the rooting system of P. velutina is characterized by a deep taproot and extensive lateral roots (Fravolini et al. 2005), which could be used to access winter precipitation where groundwater is not available. Similar differentiation in stem $\delta^2 H$ was observed in cold deserts among different functional groups (Ehleringer et al. 1991) and among shrubs with different rooting patterns (Chimner and Cooper 2004; Donovan and Ehleringer 1994; Gebauer et al. 2002; Schwinning et al. 2005). In the Patagonian desert, 50% of total root biomass was located in the upper 10 cm of the soil and maximum rooting depth was almost 270 cm, suggesting that desert plants access water from a wide range of depths (Schulze et al. 1996). Desert niche overlap was low for the winter water source because of differential utilization by trees and shrubs, but not low for surface or intermediate sources. Woody desert perennials tend to have extensive lateral roots above the calcic and petrocalcic horizons (Gibbens and Lenz 2001), thus limiting niche partitioning above these soil horizons. Though we found strong evidence of niche partitioning at low site moisture availability, soil horizon development in arid systems could limit niche partitioning, as strong horizons could be impenetrable to plant roots and impede plant performance (McAuliffe 1994; McAuliffe and Hamerlynck 2010).

In the pinyon-juniper woodland, both surface and winter water use in June notably differed between coexisting species (Fig. 3b). Prior to the arrival of monsoon precipitation, P. edulis utilized a larger proportion of surface water than M. fremontii and J. osteosperma and a smaller proportion of winter water than M. fremontii. P. edulis may have more shallow roots near the soil surface (Flanagan et al. 1992; West et al. 2007a) and a greater ability to recover root hydraulic conductivity (West et al. 2007b) than J. osteosperma, which supports the greater use surface water by P. edulis. One study found that P. edulis and J. osteosperma utilize more shallow water than cooccurring shrub species (Flanagan et al. 1992), but our data do not suggest Arctostaphylos pungens or M. fremontii are very deeply rooted. Because of the strong species differentiation surface and winter water use, June niche overlap was relatively low, particularly in the surface source (~ 0.5).

Only surface water utilization differed between coexisting *P. ponderosa* and *Q. gambelii*, and this

difference was maintained following the arrival of monsoon precipitation (Fig. 3c). P. ponderosa utilized a higher proportion of surface water than Q. gambelii in both months, which is supported by its rooting distribution. Though P. ponderosa usually forms a deep taproot and a wide network of lateral roots that extend beyond the crown, the majority of roots are concentrated in the top 45 cm (Hermann and Petersen 1969). Furthermore, fine-textured soils can restrict the downward development of P. ponderosa roots (Berndt and Gibbons 1958), and our ponderosa site was located on clay soils (Table 2). We did not find significantly increased use of winter water by Q. gambelii due to wide CIs of the posterior estimates. However, since surface water use was significantly lower in Q. gambelii than P. ponderosa, it follows that Q. gambelii must access a higher portion of deeper water sources, which is consistent with its identity as a clonal species with an extensive rooting system and low ratio of aboveground to belowground biomass (Clary and Tiedemann 1986). Williams and Ehleringer (2000) also found that Q. gambelii generally relies upon deep water with a winter isotopic signature. Niche overlap was low in the surface source due to the presence of only two coexisting species, but high otherwise because of poorly resolved posterior estimates.

In the high-elevation forests, we found no species differences in source water use by coexisting species (Fig. 3d, e). Winter water use was relatively low in the mixed-conifer and spruce-fir sites relative to the lower elevation sites, possibly reflecting higher availability of moisture at the soil surface (Fig. 1). Interestingly, P. ponderosa was a member of both the ponderosa and mixed-conifer forests, and Pinus strobiformis and Populus tremuloides were both members of the mixedconifer and spruce-fir forests. Though they coexisted as part of distinct plant communities, P. ponderosa, P. tremuloides, and P. strobiformis generally utilized similar proportions of all three water sources regardless of site. P. tremuloides was the only exception, as it utilized significantly more surface water in June at the mixed-conifer than the spruce-fir site, despite similar soil water contents. P. tremuloides was also the only deciduous member of the high-elevation forest communities, and spring leaf out in this species is influenced by both temperature and genetic controls (Cottam 1954). We infer that the higher elevation population (spruce-fir) was not yet fully leafed out by June, resulting in reduced transpirational demand and lower surface water use relative to its lower elevation counterpart. Nonetheless, niche overlap was relatively high across all sources (> 0.5) and similar between mixed-conifer and spruce-fir forests, likely because the moisture index is around one (Table 1), indicating that precipitation is sufficient to meet evaporative demand and the coexisting species are not waterlimited.

Utilization of monsoon precipitation

We were unable to quantify June water use and therefore the seasonal shift in water sources for the desert site. However, due to the consistently low soil moisture in both June and August, we infer that monsoon precipitation either failed to infiltrate or did not persist in the soil profile. A rainfall addition experiment (Lin et al. 1996) using labeled water found that two of the five cold desert shrubs showed little uptake of monsoon rains in July or September due to two possible explanations: either woody perennials allocate carbon for deep roots to access a more steady water source (Ehleringer and Dawson 1992), or shallow root mortality induced by high soil temperatures (Hendrick and Pregitzer 1993). In addition, fine root growth may require a steady supply of new C provided by photosynthesis (Pregitzer et al. 2000), which remains low during the pre-monsoon dry period (Szarek and Woodhouse 1978). Regardless of season, desert plants, particularly trees, primarily utilize winter sources of water (Fig. 3a).

Among the species for which we had 2 months of water utilization data, seasonal increase in surface water utilization only occurred in five species, primarily those at intermediate elevations (Fig. 3b, c). In the pinyon-juniper woodland, niche overlap was higher in August than June, which indicates that coexisting plants converged upon similar sources of water during the monsoon rains. We found that both P. edulis and J. osteosperma responded to monsoon precipitation, a result that has been inconsistently reported in the literature. Generally, higher use of monsoon precipitation has been found for P. edulis than J. osteosperma (Flanagan et al. 1992; West et al. 2007a), although J. osteosperma utilized monsoon precipitation in a normal year following a dry year (Flanagan et al. 1992). Williams and Ehleringer (2000) found that across a gradient of strong to weak monsoon precipitation, both species used surface moisture, with surface moisture utilization peaking in August or September (Williams and Ehleringer 2000). Furthermore, the effect of the monsoon gradient was mediated by an El-Niño year in 1993, which resulted in higher winter and spring precipitation. In 1993, the sites south of the average monsoon boundary had high usage of monsoon precipitation by both species, but usage markedly declined by both species north of the boundary (Williams and Ehleringer 2000). This trend suggests that uptake of monsoon precipitation depends upon the interaction between antecedent soil moisture conditions and the relative contribution of monsoon precipitation as well as physiological differences between P. edulis and J. osteosperma (West et al. 2007b). Our study took place in 2012 following a dry La-Niña winter, when subsequent summer precipitation was above normal (Overpeck 2013). Similar utilization of summer precipitation by both P. edulis and J. osteosperma in 2012 could reflect the strong constraint of a dry winter overcoming species differences in physiology.

In the ponderosa forest, we found monsoon precipitation utilization by *P. ponderosa* but not by *Q.* gambelii. However, Kerhoulas et al. (2013) reported that P. ponderosa predominantly uses winter precipitation regardless of season, stand density, or tree size. One reason for this discrepancy could be differences in rooting depth due to soil texture. Because fine-textured soils limit the downward growth of *P. ponderosa* roots (Berndt and Gibbons 1958; Hermann and Petersen 1969) and our soils had 45% clay content on average, it is likely that rooting depth was severely restricted at our sites such that the lateral roots of P. ponderosa intercepted monsoon precipitation. Additionally, in contrast to the P. ponderosa dominated site used by Kerhoulas et al. (2013), we deliberately selected plots where additional woody plants coexisted with P. ponderosa. Therefore, species differences between the P. ponderosa and more deeply rooted Q. gambelii could also explain why only P. ponderosa utilized monsoon precipitation at this site. We did not find evidence of monsoon water uptake by Q. gambelii. Williams and Ehleringer (2000) found that Q. gambelii only utilized monsoon precipitation at the two southern-most sites (33.6 N and 34.3 N). Consistent with their findings, Q. gambelii at our site (35.02 N) maintained similar proportions of surface water use even after the onset of monsoon precipitation. In the case of dominant *P. ponderosa* co-occurring with the subdominant *Q. gambelii*, the substantial differences in rooting strategy (Berndt and Gibbons 1958; Clary and Tiedemann 1986) could account for differential responses to monsoon precipitation.

At the two high-elevation forest sites, most species did not shift utilization of any water source between June and August, even though August sampling occurred only 1 day following a monsoon storm. Only P. engelmannii responded to monsoon precipitation by increasing surface water uptake. The vertical rooting distribution of *P. engelmannii* is related to soil texture and horizon development. In soils rich with organic matter, P. engelmannii roots are abundant near the surface but decline sharply with depth (Wardle 1968), often limited to the top 45 cm when soils are underlain by bedrock or clay hardpans (Alexander and Shepperd 1984). Our spruce-fir site was located on steep slope (Table 2) with shallow soils, such that *P. engelmannii* likely had a shallow rooting distribution and thus greater access to monsoon precipitation. Most mature tree species at high elevations do not use monsoon precipitation, likely because soil water content is sufficient to meet transpirational demands even during the pre-monsoon dry period.

Conclusion

Across the elevational moisture gradient, coexisting plants utilized different proportions of intermediate and winter water sources (e.g., low niche overlap) when site moisture availability is limiting (e.g., when the moisture index is low), which supports our hypothesis of spatial niche partitioning along a moisture gradient. Contrary to our expectations, we did not find a consistent trend in monsoon precipitation usage with the moisture gradient. Rather, plants growing at both low moisture and high moisture sites generally eschew monsoon precipitation, though for different reasons. Utilization of monsoon precipitation was highest at intermediate moisture sites such as the pinyon-juniper and the ponderosa, where the monsoon provides sufficient additional moisture for growth and transpiration to offset costs in root growth and maintenance. Importantly, we found evidence of higher niche partitioning in water sources in more arid ecosystems, which is consistent with classical niche partitioning theory. With soil moisture predicted to decrease because of increased aridity in the Southwest, our results suggest that woody plant coexistence may be limited by the ability to partition belowground water resources.

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Author contributions JG, TK, BH, and GK conceived and designed the study; JG conducted fieldwork and lab analyses; JG and BH analyzed data; JG wrote the manuscript; and BH, TK, and GK provided editorial advice.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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