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RESEARCH ARTICLE

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Soil water availability shapes species richness in mid-latitude shrub steppe plant communities

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Abstract

Questions: Ecological communities are controlled by multiple, interacting abiotic and biotic factors that influence the distribution, abundance, and diversity of species. These processes jointly determine resource availability, resource competition, and ultimately species richness. For many terrestrial ecosystems in dryland climates, soil water availability is the most frequent limiting resource for plant species. We used field sampling coupled with process-based soil water balance modeling to explore the relative importance of multiple macroclimatic, ecohydrological, and biotic variables on plant species and functional type richness at the landscape scale in dryland plant communities.

Location: Dryland plant communities dominated by big sagebrush (*Artemisia tridentata*) that span climatic and elevational gradients in Wyoming, USA.

Methods: We quantified species richness at 1,000 m^2 and used multiple regression to determine whether mean climatic conditions, multiple metrics of soil moisture from a soil water balance model (SOILWAT2), soil physical and chemical properties, and shrub stand structure (biotic) variables were related to species and functional type richness.

Results: Species richness varied between 16 and 54 across sites. We found that species and functional type richness were related to both macroclimate and ecohydrology, but ecohydrology explained slightly more variation than climate. Biotic variables were always secondary to macroclimate and ecohydrology in our models. Variance partitioning revealed that large portions of variability in species (~54%), forb (~47%), and grass (~40%) richness were explained by ecohydrological variables.

Conclusions: Our results highlight the importance of the spatial and temporal distribution of soil water for dryland plant species richness and suggest that documenting the ways in which climate, vegetation, and soil properties interact to determine soil water availability is critical for understanding biodiversity patterns in dryland plant communities. This work has relevance for other mid-latitude, shrub-dominated dryland plant communities where soil water availability strongly influences ecosystem structure and function.

KEYWORDS

Artemisia tridentata, big sagebrush, climate, dryland, ecohydrology, functional type richness, soil water, SOILWAT2, species richness

1 | INTRODUCTION

Species richness is influenced by interacting ecological processes operating at multiple scales, which shift in relative importance along environmental gradients (Ricklefs, 2004; Shmida and Wilson, 1985), and sampling along these gradients can illuminate the underlying mechanisms that produce these patterns (Whittaker, 1967). For many plant communities, these drivers include abiotic factors, such as climate (large-scale) and soil properties (local-scale), and biotic factors, such as competitive and facilitative interactions (local-scale), which act in concert to determine resource availability and dictate competition for limiting resources (Currie, 1991; Noy-Meir, 1973; Pueyo et al., 2013; Ulrich et al., 2014).

Soil water availability is a key limiting resource in dryland plant communities, which occupy over a third of the terrestrial surface (Reynolds et al., 2007). In these dry places, plant-available soil water is determined not only by precipitation and temperature and their variability, but also by soil properties and vegetation characteristics (Loik, Breshears et al., 2004; Noy-Meir, 1973; Schlaepfer et al., 2012a). While the amount and timing of precipitation are often strongly related to soil water availability (Loik et al., 2004; Schlaepfer et al., 2012a), soil physical properties (e.g., soil texture) and the structure of vegetation (e.g., biomass, leaf area index) modify soil water availability in sites that are climatically similar via their influence on water balance. For example, fine-textured soils can hold water near the surface, making it more vulnerable to evaporative loss and leading to drier surface layers relative to coarse-textured soils (Noy-Meir, 1973). As such, to quantify plant-available soil water and its consequences, an ecohydrological approach that integrates climate, soil properties, and vegetation is required.

The spatial and temporal variability of soil water can influence species and functional type abundance and composition. The coexistence of plant functional types within drylands is a result of competition for soil water both at depth in the soil profile and through time as predictable dry periods occur throughout the year (Epstein et al., 1997; Paruelo and Lauenroth, 1996; Sala et al., 1997). Across common dryland functional type, shrub roots can access deeply-stored water, while many grass and forb species have shallower root systems than shrubs and high root biomass in upper soil layers, resulting in competition between shrubs, grasses, and forbs for shallow soil water resources (Jackson et al., 1996; Sala et al., 1997). Furthermore, the timing and type of precipitation influences plant functional type relative abundance: winter-dominated precipitation regimes characterized by snow can give shrubs a competitive advantage, while summer-dominated regimes often result in increases in grass relative abundance (Gaitán et al., 2014; Paruelo and Lauenroth, 1996). Thus, there is strong evidence that both macroclimate and ecohydrology influence dryland plant communities, but it is unclear to which degree these communities are controlled by climate directly or by specific soil water conditions that result from the interaction of climate, soils, and vegetation.

In contrast to functional type abundance and composition, studies that quantify the influence of macroclimate and spatial and temporal patterns of soil water availability on plant species richness in drylands are scarce (Li et al., 2013). The existing literature on soil water–richness relationships in drylands from around the globe suggests greater soil water availability results in higher plant species richness (western US: Mitchell et al., 2017; Pennington et al., 2017; northwest China: Li et al., 2013; Wang et al., 2017). These findings suggest that greater resource supply provides favorable conditions for plant growth and reproduction, and supports more species on less arid sites. However, all of these studies inferred soil water availability from climate and soil properties and it is unclear which specific aspects of soil water availability are most related to plant species richness in drylands.

We used big sagebrush (*Artemisia tridentata*) plant communities as model dryland ecosystems, as they cover over 42 million hectares in western North America, contain a large number of threatened plants and animals, are undergoing rapid land-use change, and will face increasing management challenges in the coming decades (Knick et al., 2003). Big sagebrush ecosystems span strong climatic and edaphic gradients, and plant species richness can vary significantly across these gradients (Knight, 2014). However, we have a poor understanding of the plant species present, how those species are arranged along climatic and ecohydrological gradients, and how biotic factors modify those relationships (Davies and Bates, 2010; Fowler, 1986; Pennington et al., 2017). Theory broadly predicts different potential outcomes for species richness across large resource gradients associated with latitude and elevation (Currie, 1991; Hawkins et al., 2003), but applying broad-scale theory to make accurate predictions along smaller portions of these gradients is more difficult. In drylands, theories propose that the abundance of species is affected by synergism between competitive and facilitative effects that modulate the direct controls of abiotic conditions (Breshears and Barnes, 1999; Fowler, 1986). Thus, we primarily focus on theoretical frameworks addressing abiotic controls at the plot scale with some treatment of biotic conditions that could influence limiting resources.

We explored the relationships between macroclimatic, ecohydrological, and biotic conditions and plant richness in big sagebrush plant communities at the landscape scale to understand their relative importance. We hypothesized that species and functional type richness would be more strongly related to ecohydrological variables than macroclimate, because ecohydrological variables more accurately capture how much water is available to plants by integrating climate, soil, and vegetation properties. Considering macroclimate alone, we expected species richness to be more closely related to precipitation amount than precipitation variability (Gherardi and Sala, 2015), and we expected there to be higher richness in colder sites relative to warmer sites (Epstein et al., 1997). We also hypothesized that shrub abundance would be negatively related to forb and grass richness, due to competitive interactions rather than facilitation. Our integration of process-based soil water simulation modeling and detailed field measurements offers new insight on how species and functional type richness relate to soil water availability along environmental gradients, compared to a purely climatic approach.

2 | METHODS

2.1 | Study area and site selection

We sampled 48 big sagebrush-dominated plant communities throughout Wyoming, USA (253,340 km^2) across the elevational and climatic extent of these communities within the state. In our study area, these ecosystems typically occupy soils classified as Aridisols and can occur on a variety of soil textures and depths (Appendix S1; Shumar and Anderson, 1986). The elevational range for our sites was 1,310–2,652 m, mean annual temperature (MAT) was 1.6–7.9°C, and mean annual precipitation (MAP) varied between 188 mm and 658 mm (Appendix S1; PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu). Ecohydrologically, winter is the wet season and summer is the dry season for big sagebrush plant communities (Lauenroth et al., 2014; Schlaepfer et al., 2012b).

We located sites using a combination of remotely sensed data on the distribution of big sagebrush land cover types and extensive field scouting. We selected sites for within-plot homogeneity of topography and community composition, minimal evidence of grazing, and no signs of human disturbance. Additionally, we selected sites that had a native understorey of perennial grasses and forbs with little or no presence of exotic plants. While much of the extent of big sagebrush ecosystems has been invaded by exotic grass and forb species, the portion within Wyoming tends to be minimally invaded (Brummer et al., 2016).

2.2 | Sampling design and vegetation data

Between 17 May and 14 July 2016, we sampled a 1,000-m^2 plot at each of 48 sites and recorded the presence of all vascular plant species rooted inside the plot. Each species received a visual estimate of cover by first estimating cover within 100-m^2 subplots to inform our estimates of cover at the 1,000-m^2 spatial scale (Peet, Wentworth, and White, 1998). Additionally, we recorded aspect at the plot origin, elevation, and measured the slope to the nearest degree (Appendix S1). To the extent possible, we sampled plots at peak biomass to follow forb and grass phenology by sampling the driest and warmest big sagebrush communities earlier in the summer and the coolest and wettest sites last.

We measured all shrub individuals, including big sagebrush, to determine density and plant size within a 100-m^2 subplot. We estimated canopy volume of every shrub within the subplot and determined approximate maximum age of the shrub community (Appendix S2).

2.3 | Soil properties and soil water balance modeling

At four locations, we collected soil samples with an auger at 10 cm increments to a depth of 30 cm for a total of 12 soil samples per plot. We used a gravimetric method modified from Bouyoucos (1962) to determine soil texture and averaged soil texture across all samples for each plot for our statistical analysis (Appendix S1).

We used SOILWAT2 to simulate soil water availability with depth and throughout the year for each plot using site-specific inputs. SOILWAT2 is a process-based soil water simulation model that has been parameterized and validated for big sagebrush communities (Bradford et al., 2014a; Schlaepfer et al., 2012a, 2012b). SOILWAT2 uses daily temperature and precipitation data in parallel with vegetation and soil properties to model point-specific daily soil water balance in multiple soil layers. To obtain SOILWAT2 inputs for each site, we used 1/8°-gridded daily temperature and precipitation data for 1980–2010 (Maurer et al., 2002, 2007) and obtained monthly means of relative humidity, wind speed, and cloud cover from the Climate Maps of the United States (NCEI, 2020). We extracted soil depth for each site from SSURGO or STATSGO, depending on data availability (Soil Survey Staff, 1994, 2012), and used site-specific soil texture from our field sampling as input to the model. For any variables used in these analyses, we refer to the upper 30 cm of the soil profile as “top soil layers” and any layers deeper than 30 cm as “bottom soil layers.” In our simulation inputs, soil texture values deeper than 30 centimeters were assumed to be equal to our field-derived values for the 20–30 cm layer. We estimated vegetation parameters (biomass, litter, % live) for shrubs, grasses, and forbs in each site based on site-specific current climatic conditions and the climate–plant functional type abundance relationships from Paruelo and Lauenroth (1996) and applied by Bradford et al. (2014b).

2.4 | Analysis

We standardized nomenclature to USDA PLANTS (USDA, NRCS, 2017) and verified identifications using voucher specimens at the Rocky Mountain Herbarium, Laramie, WY, USA. We identified plants that did not possess adequate identifiable characteristics at the species level to genus or functional type, and due to the difficulty associated with proper identification, we treated the grass species *Elymus lanceolatus* and *Pascopyrum smithii* as a species complex. We then assigned each taxon to a functional type: grass, forb, shrub, or succulent. We also assigned each species a native or exotic classification based on USDA PLANTS (USDA, NRCS, 2017). We excluded taxa that were not identifiable to species from our analyses of native and exotic species (n = 210) as well as taxa not identified to the genus level (n = 20). We calculated mean species and functional type richness, including unknown species, but when unknown species were unidentifiable to a functional type, they were omitted (n = 20). To calculate evenness within each of our plots, we used a modified Pielou's index (exp[Shannon Diversity]/richness), using percent cover as our metric for abundance (Jost, 2010).

To explore how climate, soil water availability, and the shrub stand structure were related to species and functional type richness, we grouped predictor variables into three broad categories: macroclimatic, ecohydrological, and biotic variables. We used 30-year averages to characterize macroclimate and to represent the influence of long-term site conditions. Macroclimatic variables included mean annual precipitation (MAP, mm) and temperature (MAT, °C), and additional macroclimatic variables derived from SOILWAT2: mean annual rainfall (mm), mean annual snowfall (mm), correlation between monthly precipitation and temperature, and the UN Aridity Index (MAP/PET; Table 1, Appendices S1, S3). To estimate precipitation variability, we calculated the coefficient of variation of mean annual precipitation over the 30-year period.

For ecohydrological variables, we used field-derived soil texture, salinity, slope, aspect, and elevation as well as output from SOILWAT2 including: actual evapotranspiration (AET, mm), wet degree days in top and bottom soil layers, minimum daily soil water potential (SWP, MPa) in top soil layers, maximum daily SWP in bottom soil layers, dry and wet soil periods for top and bottom layers (days), and soil water availability (SWA, mm) for top and bottom layers for the growing season (April–September) and non-growing season (October–March, Table 1; Appendix S3). We chose to categorize elevation as an ecohydrological variable because of how this variable integrates many soil–climate feedbacks.

In top and bottom soil layers, we used model output to define wet and dry periods in the soil profile. In our variable definitions, wet or dry periods refer to the mean total annual number of days when any top soil layer's water potential >−1.5 MPa (wet periods) or <−3.9 MPa (dry periods) for a site, and wet degree days are mean total annual number of degree days (base 0°C) when any top soil layer's water potential >−1.5 MPa. We used maximum daily SWP in the lower soil layers and minimum daily SWP in the upper soil layers only because the complements of these two metrics (minimum daily SWP in the lower soil layers and maximum daily SWP in the upper soil layers) had extreme outliers for a small number of sites.

We chose these variables a priori from a larger set of macroclimatic and ecohydrological variables available from SOILWAT2. We expected these particular aspects of climate and ecohydrology would be most related to species and functional type richness based on existing theoretical (Sala et al., 1997; Schwinning and Sala, 2004) and empirical studies in drylands (Bates et al., 2006), in addition to previous soil water modeling efforts in big sagebrush ecosystems (Bradford et al., 2014a; Schlaepfer et al., 2012b).

Biotic variables included metrics of the shrub community at each site: density for all shrubs and for big sagebrush (individuals/m^2), mean and median volume for all shrubs and big sagebrush (cm^3), big sagebrush maximum age, and big sagebrush percent canopy cover. We did not include biotic variables for the non-big sagebrush shrub species in plots because of consistent evidence in big sagebrush ecosystems that shrub stand structure influences subordinate species richness while the reverse relationship is not as clear (Davies et al., 2007; Sala et al., 1997).

TABLE 1 Descriptions of macroclimatic, ecohydrological, and biotic predictors that emerged in top models of species and functional type richness. Top layers are <30 cm in depth, while bottom layers are 30–120 cm in depth. A comprehensive list of all variables used in analyses can be found in Appendix S3

Variable name	Variable definition	Variable type
Elevation	Elevation in meters	Ecohydrological
MAT	Mean annual temperature (°C)	Macroclimatic
MAP	Mean annual precipitation (mm)	Macroclimatic
Rainfall	Mean annual rainfall (mm)	Macroclimatic
Snowfall	Mean annual snowfall (mm)	Macroclimatic
UN Aridity Index	Mean yearly aridity index (MAP/PET)	Macroclimatic
AET	Mean annual actual evapotranspiration (mm)	Macroclimatic
CV precipitation	Coefficient of variation of interannual precipitation	Macroclimatic
Slope	Slope of plot to nearest degree	Ecohydrological
Daily max. SWP, bottom layers	Mean maximum daily soil water potential (MPa)	Ecohydrological
Wet degree days, top layers	Degree days with when soil water potential of top layers is >−1.5 MPa	Ecohydrological
Wet degree days, any layer	Degree days with when soil water potential of a layer is >−1.5 MPa	Ecohydrological
SWA, top layers, Oct-Mar	Mean soil water content (mm) of top layers in months 10–3	Ecohydrological
% Clay	Mean % clay in top 30 cm of soil	Ecohydrological
% Sand	Mean % sand in top 30 cm of soil	Ecohydrological
Wet periods, bottom layers	Mean total annual number of days when bottom soil water potential > −1.5 MPa	Ecohydrological
Wet periods, top layers	Mean total annual number of days when top soil water potential >−1.5 MPa	Ecohydrological
Dry periods, top layers	Mean total annual number of days when top soil water potential <−1.5 MPa	Ecohydrological
SWA, top layers, Apr–Sept	Mean soil water content (mm) of top layers in months 4–9	Ecohydrological
ARTR density	Big sagebrush density (individuals/m^2)	Biotic
Max. age	Maximum age of big sagebrush individuals	Biotic

We used multiple regression and model selection using the Akaike Information Criterion (AIC) to explore the relationships between macroclimatic, ecohydrological, and biotic variables, and species richness and functional type richness at 1,000 m^2 (Burnham and Anderson, 2002). We excluded succulents (n = 2 species) from models because of the small range of richness and low cover for this functional type within our dataset (Appendix S4).

We first built individual linear models for each predictor group (macroclimatic, ecohydrological, biotic) by testing the significance of each predictor against the null hypothesis that the slope was 0, and ranking model suitability using AIC (see Appendix S5 for the top models). Once we had determined the best models from the three predictor groups, we used the terms from the best four models from each predictor group to create composite models containing variables from all three groups (hereafter, "combined models," see Appendix S6).

Our sample size (n = 48) and the predictors we selected (n = 43) could result in model overfitting (Anderson et al., 2001; Burnham and Anderson, 2002); therefore, we limited the number of possible predictors in any model to four. We used the dredge function of the MuMIn package (R Core Team, R Foundation for Statistical Computing, Vienna, Austria) to determine AIC for all possible models and select and interpret models from the all-possible pool. We were judicious in our predictor selection a priori and rejected models containing variable pairs with a Pearson's correlation coefficient >±0.6, including the individual predictor group models and the combined models. Furthermore, we rejected models that exhibited the "reversal paradox": when the direction of the relationship between a predictor and response switches when included in multiple regression (Tu et al., 2008). By constraining the terms in our models in this manner, we were able to achieve two modeling objectives: (a) only use model terms that we could clearly connect to ecological theory; and (b) avoid models with highly correlated terms.

For the top combined model for species richness, forb richness, grass richness, and shrub richness, we used variance partitioning to determine the unique variance in species and functional type richness explained by macroclimatic, ecohydrological, and biotic predictors, along with the shared variance, and the unexplained variance (Legendre, 2008). We used the varpart function of the vegan package for the variance partitioning analysis (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). All analyses were conducted in R version 3.1.3 (R Core Team, 2017).

3 | RESULTS

3.1 | Species richness

We identified 310 unique vascular plant species across our 48 sites. Only big sagebrush occurred in every plot, and four species (*Poa secunda*, the *Elymus lanceolatus* + *Pascopyrum smithii* complex, *Chrysothamnus viscidiflorus*, and *Phlox hoodii*) occurred in more than 40 plots. Of the entire species pool, 49 species had 10 or more occurrences (~16% of species). About 20% of these 49 species were grasses, 10% were shrubs, and the remaining 70% were forbs or the succulent *Opuntia polyacantha*.

Mean species richness on 1,000 m^2 was 35 (coefficient of variation [CV] = 29%), with as few as 16 species and as many as 54 species present (Table 2). We identified more forb species than any other functional type at all sites except one (Appendix S4). For most sites, we observed more grass than shrub species, but four sites had the opposite pattern. Within 1,000 m^2, forb richness varied between 8 and 39 (mean of 22), grass richness ranged between 3 and 16 (mean of 7), and shrub richness ranged between 1 and 7 (mean of 4). Succulents had the lowest species richness (mean of 1) and were absent from 12 sites (Appendix S4). Evenness within plots ranged between 0.09 and 0.55 (mean of 0.24, Appendix S4).

3.2 | Exotic species

All exotic species were forbs or grasses. Exotic species never represented more than 25% of the species within a functional type, and on average represented 6.1% of the total species in sites (Table 2, Appendix S4). We observed exotic species at 36 sites and no exotics at 12 sites. Exotic species were never more numerous than native species (Table 2).

3.3 | Species richness explained by biotic and abiotic variables

The top four models with only ecohydrological variables explained between 43% and 50% of the variability in species richness (Appendix S5). Variables in these models that had positive relationships with richness included: non-growing season soil water availability (SWA) in the top layers, percentage clay, and wet degree days in the top soil layers and in all soil layers, while elevation and mean daily minimum soil water potential (SWP) of the top layers were negatively related to richness (Appendix S5). The top four models with only macroclimatic variables explained between 36% and 43% of the variance in species richness (Appendix S5). These models contained MAP, MAT, the UN Aridity Index, mean

TABLE 2 Mean richness of each plant functional type and native/exotic species for all sites at 1,000 m^2, with ranges shown in parentheses. Site level totals include unknown taxa only identifiable to genus

	Mean species per site	Mean native species per site	Mean exotic species per site
Grasses	7.4 (3–16)	6.4 (2–12)	0.5 (0–2)
Forbs	22.4 (8–39)	17.8 (7–34)	1.3 (0–5)
Shrubs	3.6 (1–7)	–	–
Cacti	0.8 (0–2)	–	–
Total	34.6 (16–54)	28.5 (13–49)	1.8 (0–7)

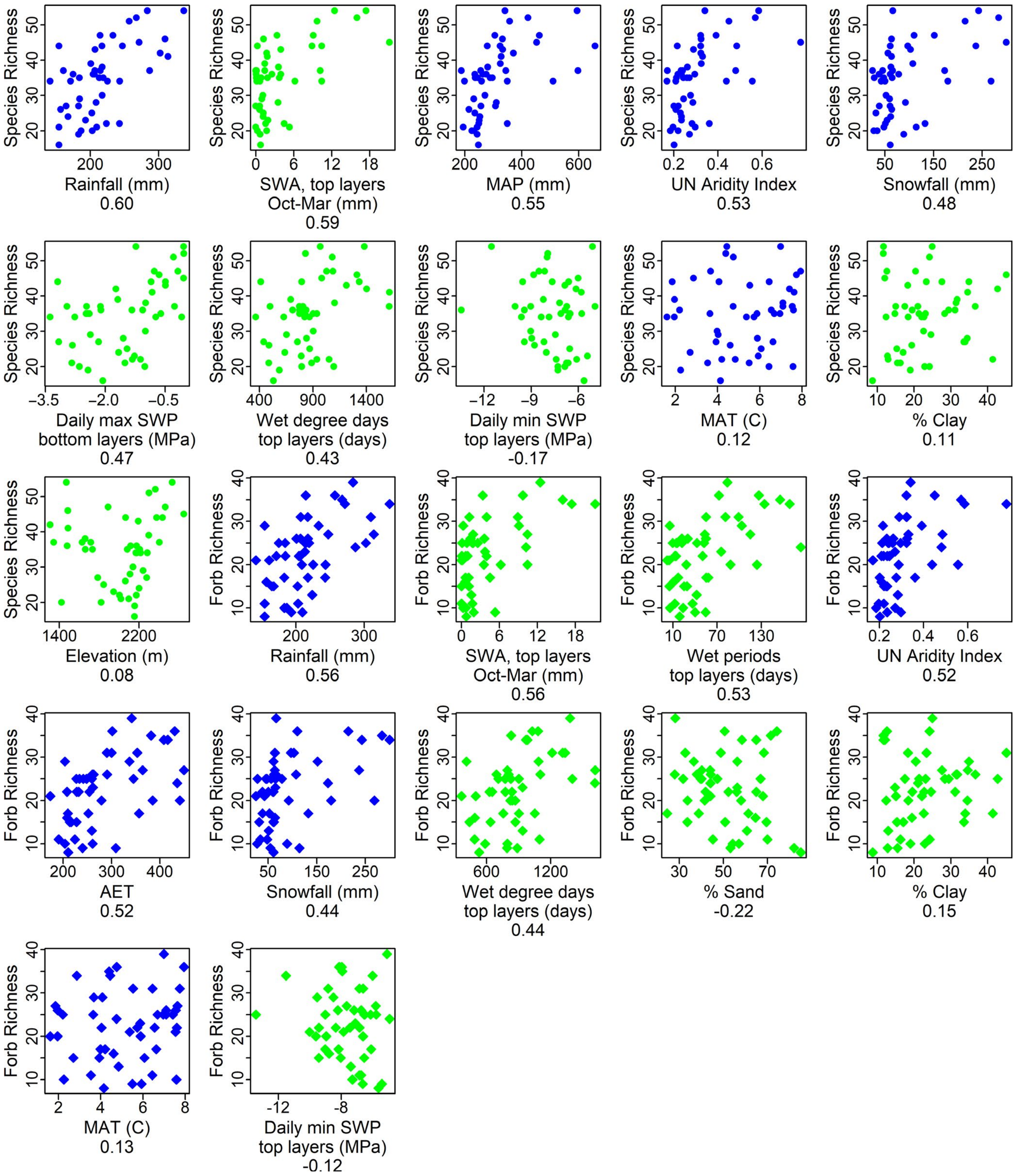

FIGURE 1 Relationships between species (circles) and forb richness (diamonds) and macroclimatic (blue) and ecohydrological variables (green) that emerged in top models. Pearson correlation coefficients are listed for each relationship. Variable definitions are given in Table 1

annual rainfall, and mean annual snowfall, which had positive relationships with richness. No biotic variables were related to species richness (Appendix S7).

In our top four combined models, species richness was strongly positively related to non-growing season SWA in top layers, weakly positively related to MAT and percentage clay, and weakly negatively related to mean daily minimum SWP in the top layers (Figure 1, Appendix S6). Variance partitioning for species richness revealed that the majority of the explanatory power in any given model was attributable to ecohydrological variables (Figure 3, Appendix S6).

In our top model of species richness, 38% of the variation in richness was uniquely attributable to a single ecohydrological variable: non-growing season SWA in top layers (Appendix S6). Mean annual temperature (MAT), mean daily minimum SWP in the top layers, and percentage clay uniquely explained an additional 7%, 4%, and 4% of variability, respectively (Figure 3, Appendix S6).

3.4 | Functional type richness explained by biotic and abiotic variables

A similar pattern emerged for functional type richness: ecohydrological variables were most related to functional type richness in both top and combined models (Figure 3, Appendices S5, S6). Ecohydrological models explained up to 41% of the total variability in forb richness, and several ecohydrological predictors had positive relationships with forb richness: non-growing season SWA in top layers, number of days with all top soil layers wet, wet degree days in the top soil layers, and percentage clay (Figure 1, Appendix S5). Variables with negative relationships to richness included mean daily minimum SWP in the top layers and percentage sand. Macroclimatic models explained up to 38% of the total variability in forb richness and included mean annual rainfall, UN Aridity Index, AET, mean annual snowfall, and MAT (Figure 1, Appendix S5). No biotic variables were related to forb richness (Appendix S5).

The top four combined models explained up to 46% of the total variability in forb richness (Appendix S6). Non-growing season SWA in top layers was strongly positively related to species richness, while MAT and percentage clay were weakly positively related to forb richness (Figure 1). Minimum daily SWP in the top layers and percentage sand were weakly negatively related to forb richness (Figure 1). In the top model of forb richness, most of the explained variability was again attributable uniquely to non-growing season SWA in top layers (35%, Figure 3). The unique variance that percentage clay and MAT explained in that model was 6% and 5%, respectively (Figure 3, Appendix S5).

In the ecohydrological models, grass richness had negative relationships with daily minimum SWP in the upper soil layers, elevation, and slope, but had positive relationships with growing season and non-growing season SWA in top layers as well as wet degree days (Figure 2). Ecohydrology alone explained up to 50% of the total variance in grass richness (Appendix S5). Three macroclimatic predictors had positive relationships with grass richness: mean annual rainfall, AET, and MAP, while two had negative relationships with grass richness: precipitation variability (CV) and correlation between monthly temperature and precipitation (Figure 2). The top macroclimatic models explained as much as 43% of the total variability in grass richness (Appendix S5). Grasses were the only functional type in which richness was related to shrub stand structure. Grass richness was weakly positively related to big sagebrush density and weakly negatively related to big sagebrush maximum age (Figure 2). The top biotic models explained as much as 16% of the total variability in grass richness (Appendix S5).

The top four combined models for grasses explained up to 51% of the variability in richness (Appendix S6). Grass richness had a strong positive relationship to growing season SWA in the top soil layers and mean annual rainfall and a weaker positive relationship to big sagebrush density (Figure 2). Grass richness was also weakly negatively related to elevation, minimum daily SWP in the top soil layers, and variability of precipitation (Figure 2, Appendix S6). In the top combined model, growing season SWA explained 33% of the variability in grass richness, while elevation, minimum SWP of top layers, and big sagebrush density uniquely explained an additional 12%, 2%, and 3.8%, respectively (Figure 3).

Our top models of shrub richness contained only ecohydrological variables and explained a smaller fraction of variance in richness than for other functional types (up to 21%, Figure 3). Shrub richness had weak positive relationships with all ecohydrological predictors, including: slope, elevation, number of days with all dry bottom soil layers, and number of days with all top soil layers wet (Figure 2, Appendix S5). In the top combined model, slope and number of days with all dry bottom soil layers uniquely explained 10% and 11% of the variation in shrub richness, respectively (Figure 3).

4 | DISCUSSION

We investigated the landscape-level patterns of species and functional type richness in dryland plant communities in relation to macroclimatic, ecohydrological, and biotic variables. Richness varied among our sites and this variability was not uniform across functional types. We found that simulated indices of SWA, particularly the amount of non-growing season SWA and wet days in top soil layers, were closely related to species richness. Mean annual rainfall also had a clear, positive relationship with species richness (Figure 1), but our best models of species and functional type richness primarily included ecohydrological variables over climatic variables. This is because climate is only one of several factors that influence SWA. However, climate significantly influences ecohydrology in big sagebrush ecosystems (Schlaepfer et al., 2012b), which is reflected in the relatively large fraction of variance in richness explained by precipitation when it was included in top models. Combining soil water variables with other variable types led to only slight increases in the explanatory power of models of species, forb, and grass richness (<10%), while shrub richness was only related to ecohydrology.

Species richness was strongly and positively related to non-growing season SWA in top layers (Figure 1). Soil water dynamics in big sagebrush ecosystems is characterized by predictable intra-annual surplus and deficits of water throughout the soil profile, characterized as the ecohydrological niche (Schlaepfer et al., 2012b). Precipitation that occurs during the summer months is usually quickly lost back to the atmosphere due to high potential evapotranspiration. This leads to dry soil conditions during the growing season, especially for top soil layers (Schlaepfer et al., 2012a). Most water that enters the soil profile does so during the cold months when plants are less active, leading to percolation of water into deeper soil layers and storage of

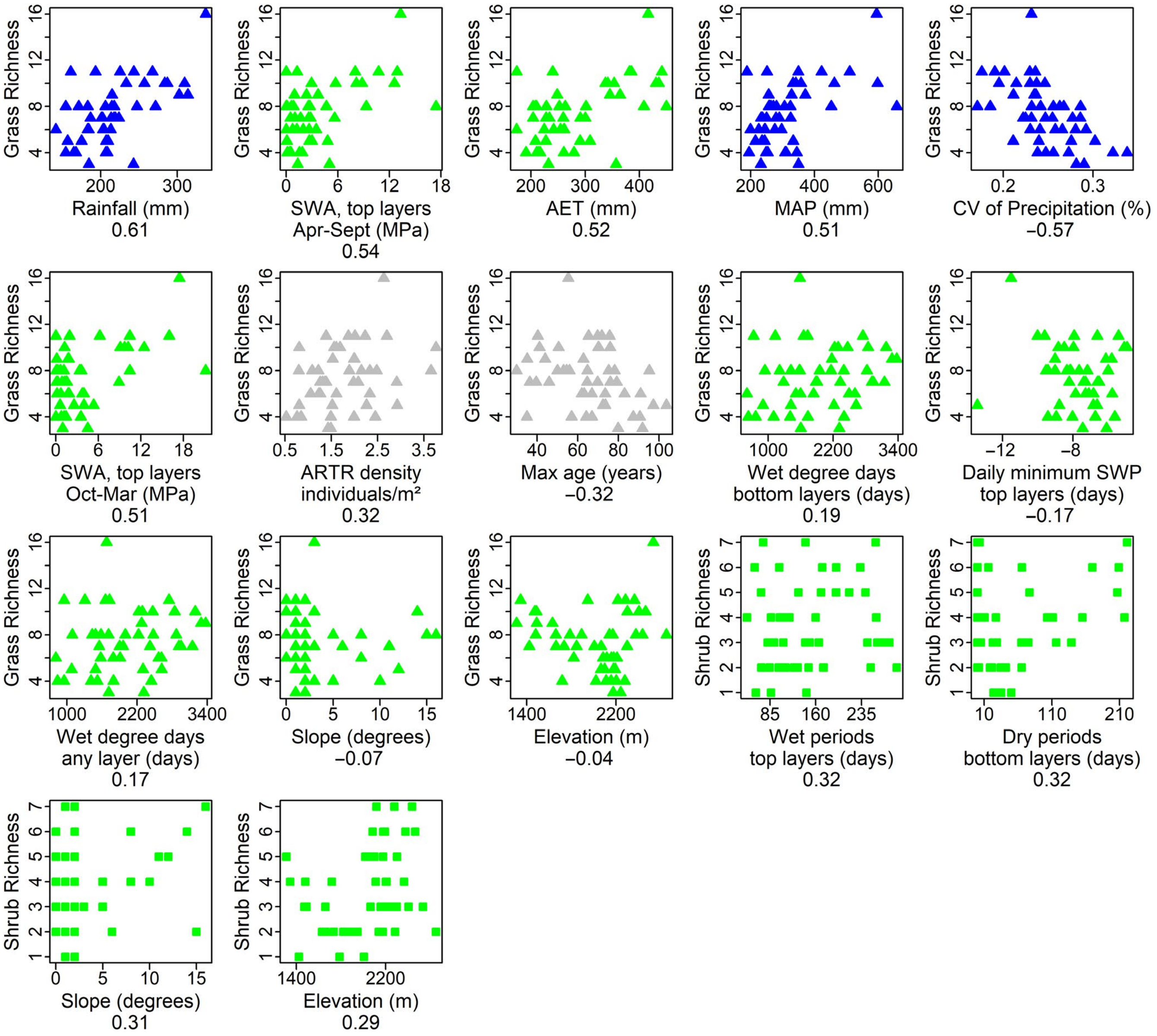

FIGURE 2 Relationships between grass (triangles) and shrub richness (squares) and macroclimatic (blue), ecohydrological (green), and biotic (gray) variables that emerged in top models. Pearson correlation coefficients are listed for each relationship. Variable definitions are given in Table 1

water at depth. Thus, we think that the emergence of non-growing season SWA in the top soil layers in our richness models supports evidence of the importance of non-growing season precipitation events (Milchunas, Forwood, and Lauenroth, 1994). In addition, higher non-growing season (October–March) SWA likely provides resources for cool-season species at the onset of their growth each year, with potential implications for richness. Furthermore, we found mean annual snowfall to be an important predictor of forb and species richness, a macroclimatic variable that is strongly positively related (r = 0.88) to non-growing season SWA (Appendices S5, S8). Together, the explanatory power of mean annual snowfall and non-growing season SWA in our models compliments existing evidence on the importance of precipitation type and precipitation timing for the storage of soil water in this ecosystem (Schlaepfer et al., 2012b). Though the seasonal patterns of SWA vary across dryland ecosystem types, our findings are consistent with other studies that found richness is linked to soil water dynamics in Mediterranean shrublands (de la Riva et al., 2018), Patagonian steppe (Gaitán et al., 2014), and drylands globally (Ulrich et al., 2014).

Variability in precipitation was negatively related to grass richness, and emerged in all of our top macroclimate models for this functional type (Appendix S5). This may reflect this functional type's dependence on shallow soil water, which is most rapidly depleted during the summer months, and thus negatively affected by precipitation variability (Sala, Lauenroth, and Parton, 1992; Schwinning and Sala, 2004). Other studies have shown that precipitation variability can shift plant community composition and control maximum plant height in drylands (Gherardi and Sala, 2015;

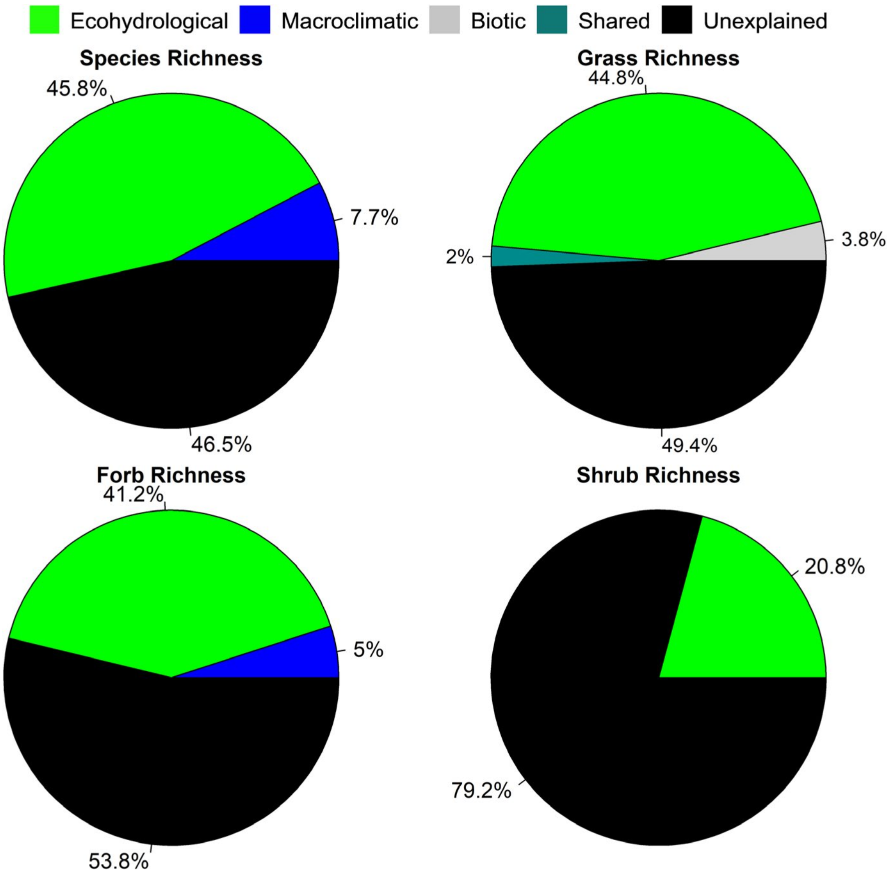

FIGURE 3 Variance partitioning of the top combined model for species richness and functional type richness. Model terms have been grouped by category (ecohydrological, climatic, biotic) for simplicity, and variables included in each top model can be found in Appendices S5 and S6

Le Bagousse-Pinguet et al., 2017), but we did not explore those relationships here.

Studies in dryland plant communities have found that richness is affected by elevation (Stohlgren, Schell, and Vanden Heuvel, 1999), precipitation (Davies and Bates, 2010; Mitchell et al., 2017), and soil properties (Pennington et al., 2017; Stohlgren et al., 1999), all of which influence SWA. Soil texture has repeatedly emerged as an important predictor of species richness in big sagebrush ecosystems, with silt explaining the most variation in richness in some studies (Pennington et al., 2017; Stohlgren et al., 1999), and clay in others (Shumar and Anderson, 1986). We found that species richness had a negative relationship with minimum daily SWP, along with weak positive relationships with percentage clay, MAT, and wet degree days. This suggests that fine-textured soils often support greater species richness than coarse-textured soils, despite higher bare soil evaporation rates (Noy-Meir, 1973). Collectively, this suggests that species richness is greatest in wet, warm sites with fine-textured soils that have high water- and nutrient-holding capacity, particularly in top soil layers. We hypothesize that higher richness in these settings may result from a greater number of individuals and hence species due to abundant resource supply (the more-individuals hypothesis, Srivastava and Lawton, 1998), specifically the "soft" formulation of the more-individuals hypothesis (sensu Storch, Bohdalková, and Okie, 2018). We found richness to have a weak positive relationship with total cover (Appendix S9), suggesting a potential relationship between more individuals (i.e., cover) and higher richness. However, we did not measure density, so we cannot be sure if we recorded greater cover because there were more individuals, or if the individuals present were simply larger. Thus, our results only offer weak support of the more-individuals hypothesis.

Contrary to our expectations, none of our biotic variables (shrub size, density, or age) were significant predictors of species richness. This suggests that the majority of species in our sites (forbs) may not be strongly influenced by shrub stand structure. Contrasting relationships have been shown in Mediterranean shrublands: richness increased as the size of individual shrubs increased (Maestre and Cortina, 2005), while others have found functional type richness to be more closely related to aridity than biotic interactions (de la Riva et al., 2018). In our study, grasses were the only functional type for which richness was related to shrub stand structure characteristics. Grass species richness was weakly positively related to big sagebrush density and weakly negatively related to the maximum age of big sagebrush, indicating grass richness was lowest in shrub communities composed of few, large, old individuals. This supports our hypothesis of a negative relationship between shrub abundance and richness, at least for grasses. Importantly, other aspects of the plant community that we did not measure may have been more sensitive to shrub stand structure, such as species relative abundance (Breshears and Barnes, 1999) and productivity (Gaitán et al., 2014).

There is a growing body of literature that provides evidence that positive biotic interactions (i.e., facilitation) have equal or more explanatory power as abiotic conditions for the structure and composition of dryland plant communities (Poulos et al., 2014), or at least that ecohydrological patterns are modulated by biotic factors (Pueyo et al., 2013). We did not test for the direct effects of facilitation or competition. Our results suggest that, except for a few relationships, the biotic variables we measured were mostly unrelated to richness. However, competitive and facilitative interactions may have influenced richness at our sites and contributed to the unexplained variance in our models of richness.

Shrub richness was weakly positively related to the number of dry days in bottom soil layers, which may be the result of reduced competitive dominance of big sagebrush, allowing for other shrub species to persist. However, this should be interpreted with caution, as shrub richness was the lowest among our functional types and our models explained less variability in shrub richness (Figure 3). Instead, this suggests that shrub richness may be controlled by factors not considered in our analysis, such as disturbance or management history (Mitchell et al., 2017; Stohlgren et al., 1999). In drylands in Northwest China, Wang et al. (2017) also found that biotic factors explained less variation in shrub richness than other functional types and macroclimatic variables were not related to shrub richness. Our work and that of Wang et al. (2017) suggest that macroclimate is not strongly related to shrub richness, and instead local environment factors, such as soil properties or disturbance history, influence the number of shrub species present.

The low abundance and richness of exotic species in our sites is a reflection of both our site selection criteria and the relatively minimally invaded status of big sagebrush communities in Wyoming. Large areas dominated by big sagebrush in the Great Basin, Snake River Plain, and Columbia Plateau are severely invaded by cheatgrass (*Bromus tectorum*), despite having similar land-use history to our study area. Key differences in climate and/or lower cover of native perennial herbaceous vegetation in the invaded areas may explain why cheatgrass is less abundant in our study area (Brummer et al., 2016). While we sampled sites with *Bromus tectorum* present, it was always present at lower abundances than native grass species (Appendix S4).

5 | CONCLUSIONS

The dryland plant communities we studied exhibited considerable variability in species and functional type richness across sites. Although species richness was related to both macroclimatic and ecological variables, richness most closely tracked soil water availability, particularly in the top soil layers. The importance of ecohydrological variables underscores the value of including direct estimates of soil water availability in addition to climate and vegetation structure (Piedallu et al., 2013). This work contributes to the larger body of knowledge documenting the ecological processes that influence richness in dryland plant communities (Li et al., 2013; Ulrich et al., 2014; Wang et al., 2017) in an ecosystem type that is likely to experience substantial conservation challenges in the coming decades (Knick et al., 2003; Knight, 2014).

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AUTHOR CONTRIBUTIONS

KP and WL developed the concepts and methods of this study; SJ, KP, JB, and WL refined methods and contributed to both estimating parameters for SOILWAT2 and data analysis. SJ wrote the first draft of the manuscript and all authors contributed substantially to subsequent drafts.

DATA AVAILABILITY STATEMENT

All data used in analyses are available either in the appendices or are archived at https://zenodo.org/badge/latestdoi/245242595.

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SUPPORTING INFORMATION

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

Appendix S1. Locations and site-level descriptions of study

Appendix S2. Descriptions of macroclimatic, ecohydrological, and biotic predictors

Appendix S3. Description of shrub sampling protocol

Appendix S4. Richness by functional type and native/exotic status for each plot

Appendix S5. Model summaries for the top three or four models for species and functional type richness grouped by model type

Appendix S6. Combined model summaries for the top four models for species and functional type richness

Appendix S7. Relationships between species richness and biotic variables

Appendix S8. Pearson's correlation between all predictor variables used in analyses

Appendix S9. Relationships between species and functional type richness and cover

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