

Ecohydrological niche of sagebrush ecosystems

Daniel R. Schlaepfer,^{1*} William K. Lauenroth¹ and John B. Bradford^{2†}

¹ Department of Botany, University of Wyoming, Laramie, WY 82070, USA

² USDA Forest Service, Northern Research Station, Grand Rapids, MN 55744, USA

ABSTRACT

Spatial and temporal patterns of soil water are major determinants of net primary production and plant functional composition in arid and semiarid ecosystems which cover approximately 30% of global land area. The ‘ecohydrological niche’ defines the components of species’ niche that are described by the relationship between ecohydrological conditions and species occurrence. We modelled the ecohydrological niche of different sagebrush ecosystems types, which are widespread in the semiarid western United States, and identified characteristics, which, if altered, will potentially lead to changes in their geographic distribution. We ran a daily soil water simulation model, SOILWAT, to simulate the water balance in space and time for sites from across the geographic range of sagebrush ecosystems. Additionally, to evaluate the relative importance of weather type, soil texture, soil depth, vegetation biomass, and phenology, we performed a sensitivity analysis using output from SOILWAT. Our results demonstrated that soil water dynamics in sagebrush ecosystems are characterized by spring recharge followed by a dry period (timing dependent on ecosystem type), where top soil layers dry earlier and more completely than the bottom layers. Most response variables were strongly influenced by weather type, followed by phenology of biomass, and soil depth. Reducing the availability of deep soil water during summer dry periods by increasing evaporative demand or reducing spring recharge will potentially lead to shifts in the range of sagebrush ecosystems. Characterizing the ecohydrological niche will be essential for improving our understanding of how semiarid ecosystems will be affected by future climate and biological invasions. Published in 2011. This article is a US Government work and is in the public domain in the USA.



Supporting information may be found in the online version of this article.

KEY WORDS *Artemisia tridentata*; big sagebrush; hydrological processes; semiarid ecosystem; snow accumulation; snow melt; soil moisture; water cycle

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INTRODUCTION

Soil water dynamic is a crucial factor for understanding water-limited, arid to semiarid ecosystems (Porporato *et al.*, 2002; Loik *et al.*, 2004; Lauenroth and Bradford, 2006), which cover approximately 30% of global land area (Peel *et al.*, 2007). The spatial and temporal patterns of available water, i.e. the amount of soil water that is extractable by plants, is a major determinant of aboveground net primary production and plant functional composition (Noy-Meir, 1973; Sala *et al.*, 1988; Sala *et al.*, 1997). Climatic conditions including precipitation, temperature and potential evapotranspiration (PET), which are frequently summarized in climate diagrams (Figure 1(a); Walter and Lieth, 1967), explain general patterns of soil water availability (Rosenzweig, 1968; Thomas, 2010). Climatic conditions can also describe patterns of and impose limits to species occurrence on larger spatial scales (Grinnell, 1917). However, some studies question the strength of the association between

climate and species occurrence (Beale *et al.*, 2008; Chapman, 2010). Hutchinson (1957) formalized the framework of ecological niches and distinguished between fundamental (absence of competition/biotic interactions) and realized niches (including effects of competition/biotic interactions). Species distribution modelling, for instance, is based on relationships between species occurrence and environmental variables, mostly climatic conditions, which are then understood as ‘climatic niches’ (Elith *et al.*, 2006; Broennimann *et al.*, 2007; Franklin and Miller, 2009). It is not obvious, however, whether species distribution models reflect unambiguously the fundamental or realized niches of species (Araújo and Guisan, 2006). Nevertheless, climate niches (for instance, depicted as climate diagrams as in Figure 1(a)) are widely used in species distribution modelling to understand the potential conditions that support particular species or vegetation types across broad spatial scales (Elith *et al.*, 2006), in assessments of climate change effects on species distribution (Thuiller *et al.*, 2005; Hijmans and Graham, 2006), and in predictive modelling of invasive ranges of introduced species (Kriticos and Leriche, 2010). However, at smaller scales other factors than climate can be important to understand species and vegetation type distributions (Elton, 1927; Pearson and Dawson, 2003). For instance, migration and dispersal rates (Engler and

* Correspondence to: Daniel R. Schlaepfer, Department of Botany, University of Wyoming, Laramie, WY 82070, USA.
E-mail: dschlaep@uwyo.edu

† Current Address: US Geological Survey, Southwest Biological Science Center, Flagstaff, AZ 86001, USA.

Guisan, 2009), land cover dynamics (Franklin, 2010), and biotic interactions (Zurell *et al.*, 2009) all influence plant distributions and have been used to improve species distribution modelling predictions. In arid and semiarid areas, perhaps the most informative enhancement of climatic niches is the inclusion of detailed soil water availability patterns. Although proxies of soil water availability have been incorporated into some climatic niche models (Thuiller *et al.*, 2005), these measures often perform poorly and more process-based representations of the water balance have been recommended (Hickler *et al.*, 2009). In this study, we enhance the climate niche approach, i.e. inference of habitat suitability based on a relationship between climatic conditions and species occurrence (Figure 1(a)), by including soil water dynamics and define analogously an 'ecohydrological niche' as the component of species' niches which are described by the relationship between ecohydrological conditions and species occurrence (Figure 1(b)).

Soil water availability is influenced by interactions between abiotic (precipitation, infiltration, bare-soil evaporation, drainage) and biotic processes (plant interception, transpiration). We propose to use the patterns in

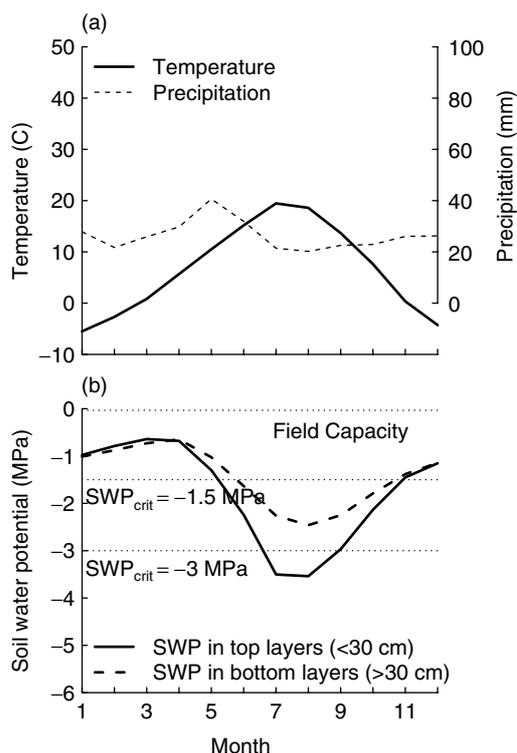


Figure 1. Conceptual representation of the Walter & Lieth-climatic (a) and ecohydrological (b) niche of a site in sagebrush ecosystems. The climatic niche (a) represents a median sagebrush ecosystems site with MAT = 6.9 °C and MAP = 34.2 cm (Table SVI). The ecohydrological niche (b) is characterized by the temporal dynamics of soil water potential (SWP) at different soil depths, which is influenced by climate and weather, soil depth and texture, and vegetation. Soil water is available when water potential is above the critical soil water potential (SWP_{crit}), e.g. -1.5 or -3.0 MPa (dotted lines). Dry periods occur when soil water potential is below SWP_{crit}. Soil profile is represented as top soil layers (<30 cm) and deep soil layers (>30 cm). Soil texture determines the relationship between soil water content and soil water potential, for instance, at field capacity, i.e. -0.033 MPa (dotted line), and at SWP_{crit}.

water availability in space (soil depth) and time (across seasons) to describe the ecohydrological niche of a system (Figure 1(b)). The ecohydrological niche will be quantified by the amount of available soil water, conditions of wet versus dry soils through time, and fluxes of the ecosystem water balance. Wet and dry soils are defined when soil water potential for a soil layer is larger, respectively smaller, than a critical level, SWP_{crit}, chosen as a level of water potential below which plant transpiration rates decrease substantially. These variables summarize the soil water dynamics generated by climatic, edaphic, and vegetation interactions temporally (e.g. daily, monthly, quarterly, yearly) and spatially (soil depth, e.g. top and bottom soil layers, many soil layers). Our concept of the ecohydrological niche combines the abiotic approaches of climatic and hydrological conditions with edaphic and vegetation interactions and allows for a more comprehensive understanding of the water balance and supported vegetation types (Porporato *et al.*, 2002; Loik *et al.*, 2004; Duniway *et al.*, 2010).

We applied this ecohydrological niche approach to understand the distribution of semiarid sagebrush ecosystems. Dominated by big sagebrush *Artemisia tridentata* Nutt., the sagebrush ecosystems are of the most widespread ecosystem types in the western United States (McArthur and Plummer, 1978; West and Young, 2000) and play a crucial role in the hydrologic cycle of these water-limited regions. Many vulnerable species, including *Centrocercus urophasianus* (greater sage-grouse), depend on sagebrush ecosystems as crucial habitat (Rowland *et al.*, 2006). Sagebrush ecosystems are also used for livestock grazing and increasingly for recreation. However, sagebrush ecosystems are sensitive to impacts from land use management, climate change, and biological invasions, which have altered them on a large scale (Bradley, 2010). Loss of sagebrush ecosystems is a major conservation concern for vulnerable sagebrush-obligate species and improved models of sagebrush habitat are needed. Sagebrush ecosystems are a particularly apt example for demonstrating the ecohydrological niche concept, because they are influenced by water limitation and by interaction between soil characteristics and seasonal patterns of rain and snow (Sturges, 1979; Burke *et al.*, 1989).

The main objective for this manuscript is to improve our understanding of sagebrush ecosystems by evaluating the ecohydrological niche with a process-based model and by estimating the influence of the temporal and spatial water balance dynamics in the semiarid western United States. We performed two types of analyses with a soil water simulation model, a sampling-based approach to capture natural levels of variation across the range of sagebrush ecosystems and a sensitivity analysis to identify factors and interactions that influence the water balance. We addressed two specific objectives: (i) identify and describe the ecohydrological niche for three big sagebrush ecosystems types across the spatial range of sagebrush ecosystems and (ii) evaluate the

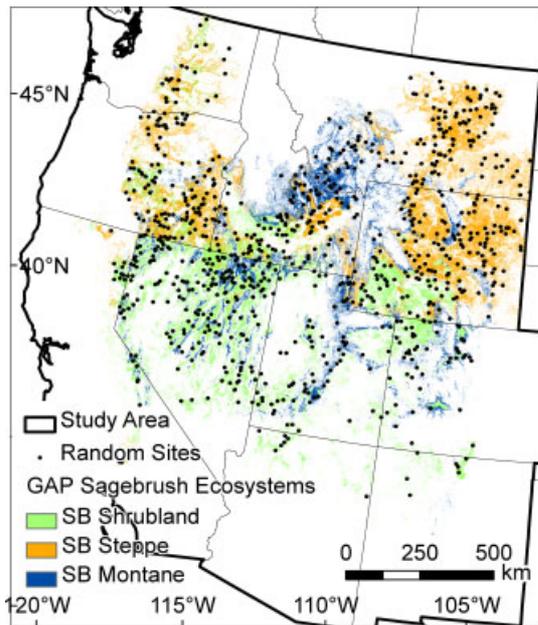


Figure 2. Geographic distribution of three types of sagebrush ecosystems (grid cells $30 \times 30 \text{ m}^2$, regional GAP) in the western United States (study area) and the location of the 898 random sagebrush ecosystems sites. (Please see online version for colour).

relative importance of biotic and abiotic factors that influence the ecohydrological niche.

MATERIALS AND METHODS

Study area and investigated ecosystem types

This study focuses on the $3.1 \times 10^6 \text{ km}^2$ of the 11 western states of the conterminous United States (Figure 2). The main geological features in the study area include the Rocky Mountains, the Great Basin, and the Pacific mountain systems. Climatic conditions cover a wide range, however, overall the study area is semiarid (Table I). Some of the most widespread semiarid ecosystem types of the western United States are dominated by big sagebrush which we used to simulate the ecohydrological niche. We inferred present potential distribution of sagebrush ecosystems from land cover data of regional gap analysis programmes (GAP, grid cells of $30 \times 30 \text{ m}^2$) for the western United States (PNW ReGAP, SW ReGAP, and California, US Geological Survey, 2010). We included those GAP vegetation types for which big sagebrush is a substantial component (Figure 2), i.e. 'Intermountain Basins Big Sagebrush Shrubland' (here, SB-Shrubland), 'Intermountain Basins Big Sagebrush Steppe' (SB-Steppe), and 'Intermountain Basins Montane Sagebrush Steppe' (SB-Montane). Other *Artemisia* species and associated communities form relevant vegetation types as well (Comer *et al.*, 2002) which were, however, excluded from this study. SB-Shrubland covers approximately 6% of the study area that are on average the warmest and driest among the three sagebrush ecosystem types, occurs mostly in broad basins on deep, well-drained soils, and is dominated by *A. tridentata*

ssp tridentata (mostly outside Wyoming and Montana) or by *A. tridentata ssp wyomingensis*. SB-Steppe covers approximately 6% of the study area, occurs on deep soils at lowest average elevation of the three sagebrush ecosystem types and has the lowest snow to mean annual precipitation (MAP) ratio, and is dominated by bunchgrasses and by *A. tridentata ssp tridentata* and *A. tridentata ssp wyomingensis* in a moderately dense shrub layer. SB-Montane covers approximately 3% of the study area at the highest average elevations with more precipitation and a higher snow to MAP ratio than the other types, occurs on deep soils, but also on stony flats and ridges, and is dominated by *A. tridentata ssp vaseyana*, but its composition can be more diverse (Table I, NatureServe, 2009).

Soil water simulation modelling

We used SOILWAT, a daily time step soil water simulation model that was developed and tested in the shortgrass steppe, another water-limited system (Parton, 1978; Sala *et al.*, 1992). SOILWAT uses daily weather, monthly vegetation, and site-specific properties of each soil layer to simulate daily ecosystem water balance, comprised of interception by vegetation and litter, evaporation of intercepted water, infiltration and percolation in the soil profile, bare-soil evaporation and transpiration from each soil layer (Lauenroth and Bradford, 2006). Model outputs are daily, monthly, and annual values of each water balance component (Parton, 1978).

We adapted SOILWAT for sagebrush ecosystems in four steps. First, we incorporated improved estimates of snowfall, accumulation, melt, loss (sublimation and wind redistribution), and snowpack temperature based on the snow module of SWAT2K (Neitsch *et al.*, 2005) that performed well in a model comparison study (Debele *et al.*, 2010). We calibrated the snow module using daily snow water equivalent data for 29 years from ten random SNOTEL station from across the study area (root mean square error (RMSE) = 15.9, coefficient of determination (R^2) = 0.69), and validated model output with data from another ten random stations (RMSE = 30.5, R^2 = 0.33; Appendix S1, Supporting Information). Second, we added a module simulating hydraulic redistribution, i.e. the movement of water in the soil by roots from wetter to drier soil areas, based on the model developed for big sagebrush by Ryel *et al.* (2002). The simulated soil water potential with hydraulic redistribution compared well with a dataset of 100 days measured in Rush Valley, UT, in a big sagebrush stand (RMSE = 0.26, R^2 = 0.80; Appendix S1; Ryel *et al.*, 2002). Third, we estimated sagebrush ecosystem and vegetation-specific parameters of SOILWAT, e.g. SWP_{crit} , aboveground biomass components, seasonal distribution of biomass (phenology), and rooting profile, based on available field data and a literature overview (Appendix S1). Unfortunately, literature data could not provide enough details to distinguish between different vegetation types except for SWP_{crit} ; however, we tested importance of amount of biomass

Table I. Summary of geographic and edaphic input parameters and climatic input variables (mean and SD) for the random points compared among the three sagebrush (SB) ecosystems types.

	SB-Shrubland		SB-Steppe		SB-Montane		ANOVA	
	Mean	SD	Mean	SD	Mean	SD	<i>F</i>	<i>p</i>
Area of extent (10 ⁶ km ²)	0.18		0.19		0.10			
Number of random points	357		348		193			
<i>Geographic parameters</i>								
Longitude (WGS84)	-114.74	4.12a	-111.06	5.31c	-112.63	3.45b	59	<0.001
Latitude (WGS84)	40.80	2.20a	44.51	1.87c	42.41	2.38b	272	<0.001
Elevation (m, a.s.l.)	1683	398b	1312	453a	2157	346c	267	<0.001
<i>Edaphic parameters</i>								
Soil depth (cm)	112	39b	97	35a	103	30ab	15	<0.001
Average sand in soil profile (%)	44	14b	37	13a	41	9b	31	<0.001
Average clay in soil profile (%)	20	9a	26	11b	22	7a	29	<0.001
<i>Climatic variables</i>								
Mean annual temperature (C)	7.4	2.1c	6.9	1.6b	3.8	2.0a	251	<0.001
Mean annual precipitation (mm)	295	68a	324	58b	479	118c	365	<0.001
Snow-MAP ratio	0.25	0.08b	0.21	0.08a	0.41	0.11c	344	<0.001
Correlation coefficient between monthly temperature and precipitation	-0.16	0.26a	0.13	0.36b	-0.11	0.29a	83	<0.001
Annual potential evapotranspiration (mm)	870	66c	832	58b	766	67a	171	<0.001

Overall differences in input parameters and variables among ecosystem types tested with one-way ANOVA (*F*-statistics, Holm-adjusted *p*-values). Different letters per row indicate significant differences among ecosystem types ($\alpha = 0.001$, Tukey HSD).

and phenology in the sensitivity analysis. For instance, mean annual aboveground total biomass was estimated to 284 g/m². SWP_{crit} was estimated based on critical levels of xylem pressure, which is a proxy of soil water potential (Kolb and Sperry, 1999b), causing 50% decrease in hydraulic conductivity due to cavitation at -4.9 MPa for *A. tridentata* ssp *wyomingensis*, -3.9 MPa for ssp *tridentata*, and -3.0 MPa for ssp *vaseyana* (Kolb and Sperry, 1999a). On the basis of the GAP sagebrush ecosystem type description, we assigned the SWP_{crit} of ssp *vaseyana* to SB-Montane and SWP_{crit} of ssp. *tridentata* (which is higher than the one of ssp *wyomingensis*) to both SB-Shrubland and SB-Steppe. Additionally, we included SWP_{crit} = -1.5 MPa as a base line; this is supported by a decrease in transpiration and leaf area of big sagebrush by 50% when water potential decreased from -1 to -2.5 MPa (Kolb and Sperry, 1999b). Fourth, we compared simulation results against field data (Appendix S2). Unfortunately, only Reynolds Creek Experimental Watershed in southwestern Utah (Wight *et al.*, 1986) provided enough data for a model-data comparison. SOILWAT simulated inter- and intra-annual dynamics of actual evapotranspiration (AET) and transpiration well, and any differences were within the published spread (Appendix S2). We concluded that SOILWAT describes sagebrush ecosystems realistically.

The model did not include runoff-runon because it plays a minor role of the water balance in semiarid

ecosystems, in particular, averaged across moderate to larger spatial scales (Wilcox, 2003; Loik *et al.*, 2004), and is therefore ecologically of smaller importance. For instance, measurements in a sagebrush ecosystem at the Reynolds Creek Experimental Watershed in Utah indicate that runoff is mostly very infrequent and occurs consistently only at the watershed highest in elevation, although runoff was still less than 2% of the water balance (Wilcox *et al.*, 1989). We also ignored an explicit representation of snow redistribution by wind and snow sublimation because complex snow models often show similar performance as the simple models used here (Debele *et al.*, 2010) and because more complex models need high-resolution data of wind, landscape vegetation, and topography that are not available here (Hiemstra *et al.*, 2006; MacDonald *et al.*, 2009). Precipitation reached either bare soil or was intercepted by vegetation and litter, thereby implicitly accounting for throughfall and ignoring stemflow which is close to zero in semiarid systems (Owens *et al.*, 2006) where most of the precipitation events are small (Lauenroth and Bradford, 2009).

Response variables describing an ecohydrological niche

We described the ecohydrological niche as three groups of response variables that differ in their combination of spatial and temporal resolution: 'snapshot' group, low spatial and high temporal resolution; 'zoom' group, high spatial and medium temporal resolution; and 'overview'

group, low spatial and low temporal resolution. Monthly soil water potentials (24 values) for a median top and bottom soil layer represented the 'snapshot' response variables. Relative frequencies (36 values) of days with wet soil (i.e. soil water potential is larger than SWP_{crit} , Figure 1(b)) of each layer normalized for the soil profile for each quarter of the year (January–March, April–June, July–September, and October–December) were used as the 'zoom' response variables. Annual fluxes (13 values) of the water balance and 8 values describing annual dry periods were selected as 'overview' response variables. The fluxes of the water balance were snowfall, snowmelt, sublimation, canopy and litter interception, rainfall, intercepted evaporation, top soil infiltration, top soil evaporation, transpiration from top soil, percolation to bottom soil, hydraulic redistribution between soil layers, transpiration from bottom soil, and deep soil drainage. The other variables were start and end of annual dry periods, i.e. >10 days with at least one soil layer with soil water potential $\leq SWP_{crit}$ after 1 April in the top four soil layers (<30 cm) and in the bottom soil layers (>30 cm), and total and maximum continuous number of days all layers in the top or bottom soil are dry.

Effects of abiotic parameters on the ecohydrological niche of sagebrush ecosystems

We simulated the water balance for sites over the entire geographic range of sagebrush ecosystems. We kept biotic parameters constant while we varied abiotic determinants of the water balance (here, precipitation, temperature, soils, and PET through influence of latitude on incoming solar radiation). We randomly sampled a total 898 sites from the three GAP sagebrush ecosystem types (Figure 2, Appendix S3), which were represented proportionally to their spatial extent (Table I). The random sample was constrained to one site per cell of the coarsest grid in the data, i.e. the 1/8-degree weather data, to prevent 'pseudo-replication' of data based on coarser grids. For each site of our random sample, we extracted data on daily weather and site-specific properties of each soil layer (Table I). Weather input was 1/8-degree gridded, daily weather data from 1949 to 1999 (Maurer *et al.*, 2002). We obtained monthly data on relative humidity, cloud cover, and wind speed from the 'Climate Maps of the United States' (<http://cdo.ncdc.noaa.gov/cgi-bin/climaps/climaps.pl>). Elevation for each site was obtained from the 30 × 30 m² National Elevation Dataset (<http://ned.usgs.gov>). Soil information on depth, bulk density, sand content, and clay content was retrieved from a 1-km gridded STATSGO dataset (CONUS-SOIL, Miller and White, 1998) for up to nine soil layers (lower limits: 5, 10, 20, 30, 40, 60, 80, 100, and 150 cm). The CONUS-SOIL data are based on gridded and recategorized STATSGO data, which aggregate phases of soil series to a minimum linear dimension of 1.25 km per 1 × 2 quadrangle at a 1 : 250 000 scale (Soil Survey Staff, 1994). We estimated soil water contents at field capacity and permanent wilting point for each soil layer based on sand and clay content (Cosby *et al.*, 1984).

We ran SOILWAT for each of the 898 sites for 50 years from 1950 to 1999 (using data from 1949 as a startup). The 81 response variables of groups 'snapshot', 'zoom', and 'overview' were calculated for each of the 898 sites. Additionally, we calculated associations between response variables from these three groups and input variables and parameters. We calculated Pearson product-moment correlation coefficients between monthly soil water potentials for a median top and bottom soil layer and monthly PET values. Spatial distributions of these correlation coefficients were generated using ordinary kriging with the Geospatial Wizard in ArcGIS 9.3.1 (ESRI, California, USA). We partitioned variance for each response variable with a random effects model of sites and years with no interaction using the 'lmer' function in the package 'lme 4' (Bates *et al.*, 2011) in the R version 2.12.2 (R Development Core Team, 2011).

Sensitivity of the ecohydrological niche of sagebrush ecosystems to varying biotic and abiotic model parameters

We ran SOILWAT for 50 years for 3125 scenarios. These scenarios were defined by the combinations of five levels each (based on the 5th, 25th, 50th, 75th, and 95th percentiles of the distributions found among the 898 sites) of the factors weather type (warm/dry to colder/moister, Appendix S4), soil texture [clay loam (20% sand–33% clay), loam (33%–27%), loam (40%–23%), loam (48%–19%), and sandy loam (62%–12%)], soil depth (50, 72, 104, 142, and 152 cm), biomass (142, 213, 284, 355, and 427 annual average total aboveground biomass, g/m²), and biomass phenology (peak biomass in April, May, June, July, and August). We conducted an analysis of variance (ANOVA) with fixed main effects weather type, soil texture, soil depth, biomass, and biomass phenology and their second order interactions to assess sensitivity of the water balance to changes in the factors using R version 2.12.2 (R Development Core Team, 2011). Response variables were the 81 variables from the three groups 'snapshot', 'zoom', and 'overview'. Because SOILWAT contains no true random processes (Parton, 1978), we used the ranking of the mean squares from the ANOVA to estimate relative importance of the factors and do not report *F*-statistics and *p*-values, since *F*-statistics assume that the data include an error term with a non-zero standard deviation (Simpson *et al.*, 1997).

RESULTS

Abiotic conditions associated with the ecohydrological niche of the sagebrush ecosystems

Sagebrush ecosystems occurred over a large portion of the US Intermountain West with SB-Shrubland being predominantly present at lower latitudes, SB-Steppe being at higher latitudes both in the western and eastern part of the study area, and SB-Montane being in central areas and in mountain ranges (Figure 2). A broad range of

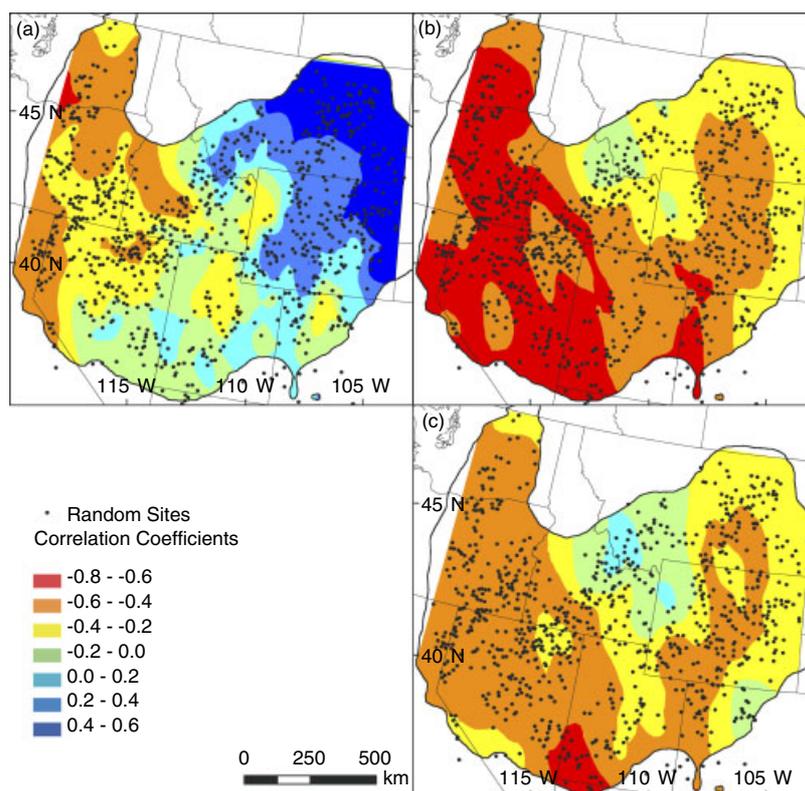


Figure 3. Geographic distribution of the correlation between precipitation and temperature (a) and between potential evapotranspiration (PET) and soil water potential in the top soil layers (<30 cm) (b), and soil water potential in the bottom soil layers (>30 cm) (c) predicted by ordinary kriging. (Please see online version for colour).

edaphic and climatic conditions was found supporting sagebrush ecosystems with small differences among sagebrush ecosystem types (Table I). The soil of a median sagebrush ecosystem site had a depth of 1 m with a loamy texture. MAP and mean annual temperature (MAT) differed among types with SB-Montane being the coldest, wettest type with the largest snow-MAP ratio of 41% (Table I). SB-Shrubland was on average the warmest with 7.4 C, and SB-Steppe was the one with the highest MAP of 324 mm/year (Table I). The semiarid climate was illustrated with a 2.9-fold larger annual PET than MAP for SB-Shrubland that decreases to 2.6 for SB-Steppe and was smallest for SB-Montane with a ratio of 1.6 (Table I). The snow-MAP ratio of 21–25% for SB-Shrubland and SB-Steppe suggested that snow accumulation and spring snowmelt is an important component of water balance of sagebrush ecosystems even for the warmer and drier sagebrush types (Table I). The correlation between monthly temperature and precipitation was negative along the western margin of sagebrush ecosystems, and became zero and positive towards the northeastern corner of the distribution (Figure 3(a)). Variance partitioning of the climatic input variables was the same among sagebrush types and suggested that on average $88 \pm 7\%$ (mean \pm SD) of the variance was found among the spatial distribution of the 898 sites and only $12 \pm 7\%$ of the variance occurred as temporal variability over the 50 years of the weather within sites (Table SV).

Dynamics of the ecohydrological niche of sagebrush ecosystems

Variance partitioning among the response variables were almost the same among sagebrush types and was comparable to the climatic input variables; most of the variance ($76 \pm 10\%$, mean \pm SD, in the 'snapshot' group, $92 \pm 6\%$ in the 'zoom' group, $80 \pm 11\%$ in the 'overview' group) occurred among sites (Table SV). However, soil water potential showed a strong seasonal dynamic in the top soil layers for all sagebrush ecosystem types ('snapshot' variables, Figure 4(a)); the top soil layers had a high potential during winter and spring, followed by a steep decline in late spring and early summer that increased again by winter. The bottom soil layers had more stable soil water potentials (Figure 4(b)); nevertheless, they also experienced a marked reduction in the summer months, which was recharged slowly during winter and spring months. SB-Shrubland and SB-Steppe were more similar in seasonal soil water potential dynamics than SB-Montane with SB-Steppe experiencing the least spring recharge and SB-Shrubland the driest summer periods (Figure 4). The most pronounced and latest spring recharge of both top and bottom soils that led to on average the least driest conditions occurred in SB-Montane (Figure 4) that are reflected in a later start and shorter duration of dry periods when compared with a fixed SWP_{crit} (Table II). Dry periods, based on ecosystem type specific SWP_{crit} , started in the top soil layers earlier (mid-summer for SB-Shrubland and SB-Steppe, late summer

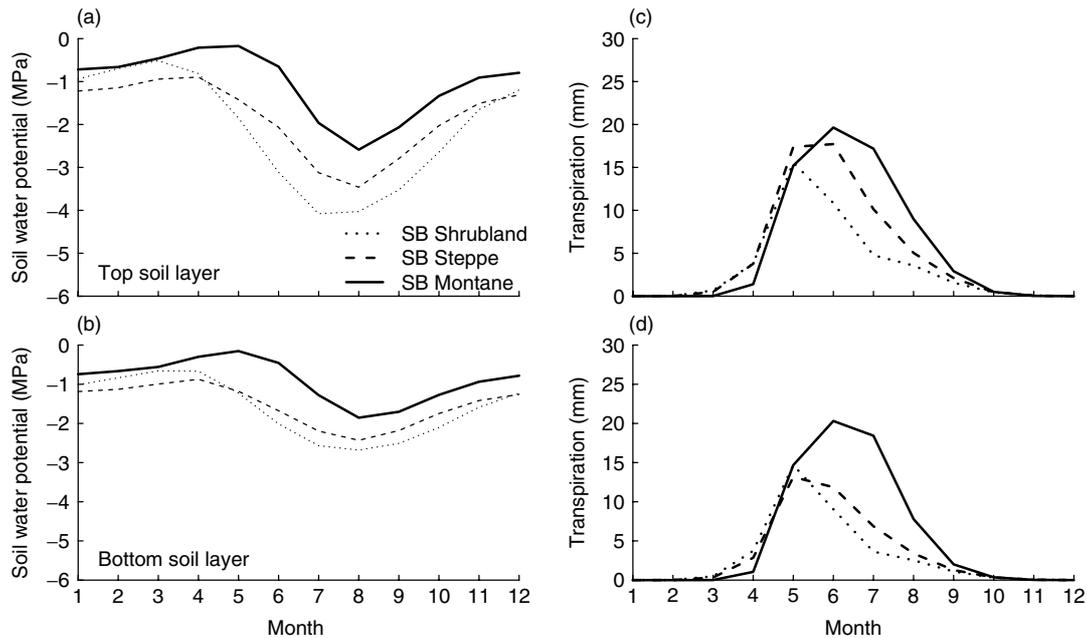


Figure 4. Monthly dynamics of median soil water potential ('snapshot' response variables) in the top soil layers (a, <30 cm) and bottom soil layers (b, >30 cm) and of transpiration in the top soil layers (c) and bottom soil layers (d) for the three sagebrush (SB) ecosystem types.

Table II. Differences in length of annual dry periods among the three sagebrush (SB) ecosystem types (>10 days with at least one soil layer with soil water potential < SWP_{crit}, after 1 April corresponding to a day of year of 90) in the top four soil layers (<30 cm) and in the bottom soil layers (>30 cm), and total and maximum continuous number of days all layers in the top or bottom soil are dry (mean and SD) under two cases: (i) the same SWP_{crit} value for all ecosystem types and (ii) ecosystem type depending values of SWP_{crit} (see Materials and Methods section).

	SB-Shrubland		SB-Steppe		SB-Montane	
	Mean	SD	Mean	SD	Mean	SD
(i) Constant SWP _{crit} = -1.5 MPa						
<i>Top soil layers</i>						
Start of dry periods (day of year)	123	32	118	35	190	44
End of dry periods (day of year)	320	13	317	13	302	15
Total number of days all soil layers are dry	183	38	174	42	96	46
Longest period all soil layers are dry (days)	106	37	89	35	56	30
<i>Bottom soil layers</i>						
Start of dry periods (day of year)	129	43	120	37	195	49
End of dry periods (day of year)	308	32	302	24	302	14
Total number of days all soil layers are dry	141	50	146	44	65	55
Longest period all soil layers are dry (days)	133	51	124	41	55	46
(ii) Ecosystem type depending SWP _{crit} (MPa)						
	-3.9		-3.9		-3.0	
<i>Top soil layers</i>						
Start of dry periods (day of year)	172	45	185	41	241	66
End of dry periods (day of year)	292	16	281	17	304	27
Total number of days all soil layers are dry	38	19	24	18	27	24
Longest period all soil layers are dry (days)	33	16	20	15	20	18
<i>Bottom soil layers</i>						
Start of dry periods (day of year)	281	70	317	58	300	58
End of dry periods (day of year)	317	38	335	34	325	33
Total number of days all soil layers are dry	0	0	0	0	1	9
Longest period all soil layers are dry (days)	0	0	0	0	1	7

for SB-Montane) than in the bottom soil layers (October/November), and ended earlier (October/November) compared with the dry periods in the bottom soil layers which typically lasted to November/December (Table II). Additionally, the top soil layers experienced approximately 30 days when all layers were dry, whereas the bottom soil layers were hardly ever completely dry with

very little differences among ecosystem types (Table II). These patterns of soil water dynamics over soil depth and season were confirmed when looking at a higher spatial resolution of soil depth ('zoom' variables, Figure S4).

The annual water balance of sagebrush ecosystems ('overview' variables) was driven by an AET that satisfied in the median case 32% of PET for SB-Shrubland,

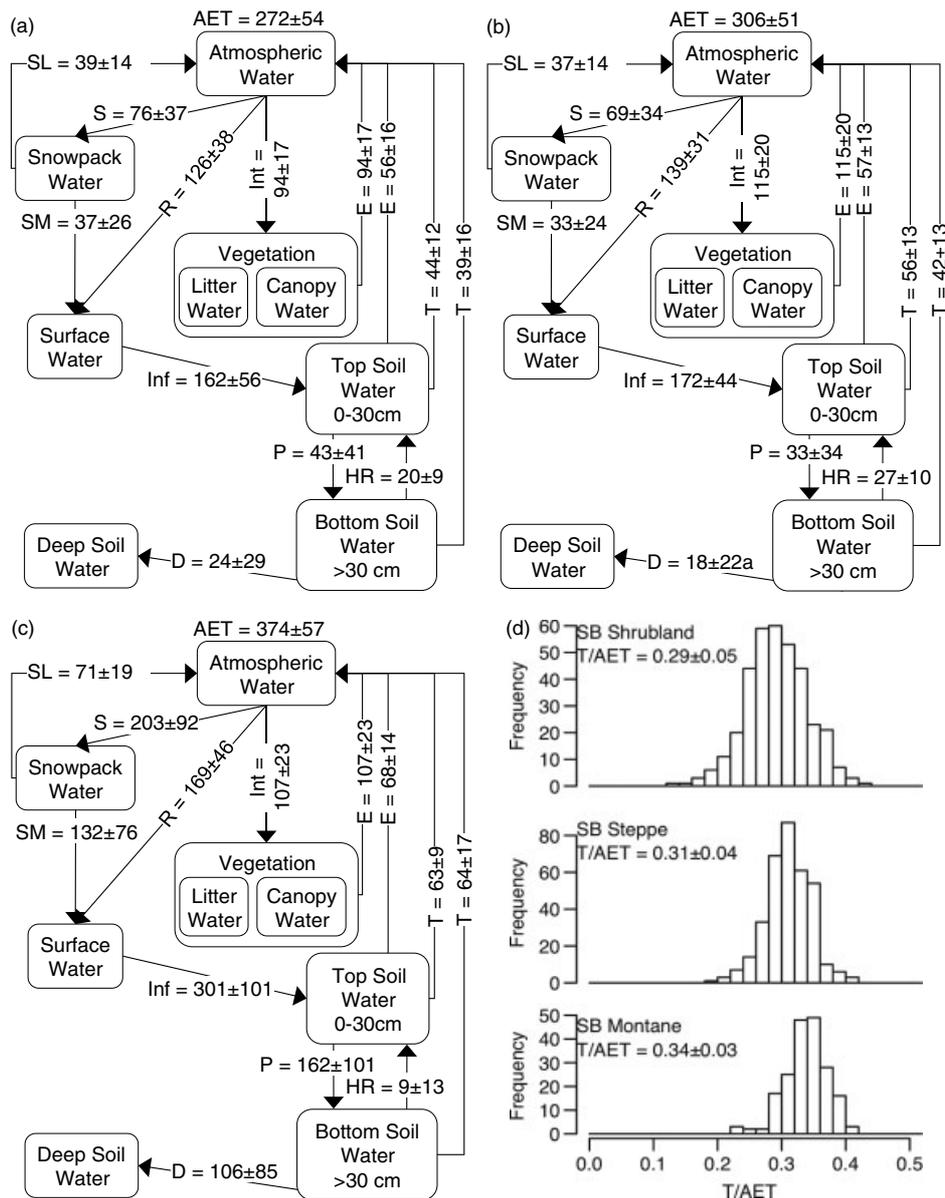


Figure 5. Annual water fluxes ('overview' response variables) for the three sagebrush (SB) ecosystems types (a) SB-Shrubland, (b) SB-Steppe, and (c) SB-Montane. Median values and SD are shown for each component of the water balance (mm/year). Fluxes included are *R*, rainfall; *S*, snowfall; *SL*, snow loss (sublimation and wind redistribution); *SM*, snow melt; *Int*, interception by vegetation and litter; *Inf*, infiltration; *P*, percolation into bottom soil layers; *HR*, hydraulic redistribution; *D*, deep soil drainage; *T*, transpiration; *E*, evaporation; and *AET*, actual evapotranspiration (sum of transpiration, evaporation, and snow loss). Frequency distribution of *T/AET* shown in panel (d).

37% for SB-Steppe and reached 49% for SB-Montane (Figure 5). The largest component of AET was vegetation-intercepted evaporation for SB-Shrubland and SB-Steppe followed by transpiration, bare-soil evaporation, and snow loss; for SB-Montane, transpiration was the largest component of AET (Figure 5). Total transpiration was larger in SB-Montane than in SB-Shrubland or SB-Steppe. Differences in transpiration for both soil layers among ecosystem types, but more pronounced for the bottom soil layers, occurred mostly during summer because peak transpiration in SB-Montane was later than for the other types (Figure 4(c,d)). Top and bottom soil layers contributed about equal parts of the water transpired by plants in SB-Montane, whereas transpiration was stronger influenced by top soil layers in

SB-Shrubland and SB-Steppe (Figures 4 and 5). About 50% of MAP (63% for SB-Montane) reached the soil as rain or snowmelt, 11–15% was lost from the snowpack as sublimation and redistribution, and the rest was intercepted and evaporated. Of the water that infiltrated the soil, about a third was evaporated back from the top soil layers (23% for SB-Montane), 10–15% recharged the deep soil water (35% for SB-Montane), and the remainder (51% for SB-Shrubland, 57% for SB-Steppe, and 42% for SB-Montane) was available for transpiration. Hydraulic redistribution lifted about half as much water from the bottom soil layers to the top layers in SB-Shrubland and SB-Steppe as percolation moved water from top to bottom layers, but hydraulic redistribution amounted to less than 10% in SB-Montane (Figure 5).

Table III. Ranks of the mean ranks of mean squares based on ANOVA table of the main factors and their two-way interactions for the three groups (see Appendix S4 for full list, *df*, MS and SS).

	Rank among 24 variables of soil water potential in top and bottom soil layers ('snapshot' group)	Rank among 36 variables of quarterly nine soil layer normalized frequency of days with wet soils ('zoom' group)	Rank among 22 variables describing dry periods and the water balance ('overview' group)
Weather type	1	2	1
Soil texture	7	4	7
Soil depth	3	1	4
Amount of biomass	4	6	3
Phenology of biomass	2	3	2
Weather × Texture	12	8	11
Weather × Depth	5	5	6
Weather × Amount	9	10	8
Weather × Phenology	6	7	5
Texture × Depth	13	13	14
Texture × Amount	15	15	15
Texture × Phenology	14	11	12
Depth × Amount	11	12	13
Depth × Phenology	10	9	9
Amount × Phenology	8	14	9

Correlations between climatic and ecohydrological variables emphasized the large influence of climate, but also indicated spatial and temporal dynamics in the ecohydrological niche. The variability in the frequency of wet days among soil layers decreased slightly in wet years, resulting in a more homogenous contribution of soil layers to yearly wet days (Figure S5(e–g)). Additionally, the correlation between top soil water potential and PET was negative across the entire range, i.e. top soil water potential is high (wet) when PET is small, with a gradient from stronger negative values in the south-west to north-east (Figure 3(b)). The correlation between bottom soil water potential and PET followed a similar gradient as for top soils, was overall less negative, and reached positive values only in the central-northern part of the sagebrush ecosystems distribution (Figure 3(c)). SB-Shrubland had the smallest correlation values for both top and bottom soil layers and SB-Montane the least negative ones. Both correlations were associated with the correlations between temperature and precipitation and also with the ratio of snow to MAP.

Sensitivity of the ecohydrological niche of sagebrush ecosystems to varying biotic and abiotic conditions

'Snapshot' response variables (monthly soil water potentials) were most influenced by weather type (Table III); an increase in MAT reduced soil water potentials (Figure 6(a)). Phenology of biomass, i.e. the timing of peak biomass, was the second strongest influence with medium peaks causing the smallest soil water potentials (Figure 6(q)) followed by soil depth (Tables III, SVII and SVIII). 'Zoom' response variables (quarterly frequencies of wet soil days in each layer) were most influenced by soil depth with increasing depth causing a lower frequency of wet soils (Tables III, SIX–SXII, and Figure 6(j)). Weather type was the second most important factor for 'zoom' variables with an increase in MAT

reducing the frequency of wet soils (Figure 6(b)) followed by phenology of biomass (Table III). 'Overview' response variables (dry periods, water balance) were mostly affected by weather type, phenology of biomass, and amount of biomass (Tables III, SXIII and SXIV). Increasing MAT extended the dry periods in the top soil (Figure 6(d)) and increased *T/AET* overall (Figure 6(c)). Medium timing of peak biomass and increases in biomass resulted in an increase of *T/AET* (Figure 6(o,s)).

DISCUSSION

Our soil water simulations provide a detailed description of the ecohydrological conditions under which different sagebrush ecosystems types occur in the semiarid western United States. These results enhance our understanding of the ecological niche of sagebrush ecosystems with information on the spatial and temporal dynamics of soil water availability, duration and intensity of dry periods, and fluxes of the water balance. They also demonstrate how biotic factors modulate associations between soil water dynamics and the climatic niche, and edaphic and geographic factors.

The climatic niche of sagebrush ecosystems

Seasonality of precipitation showed a pronounced gradient across the range of sagebrush ecosystems (Figure 3(a)). The western part of the range and the areas close to the mountains receive most precipitation during the cold season, whereas in the northeastern part precipitation falls also during the warm season. However, even in the northeastern part, the majority of sagebrush ecosystems sites receive a relevant part of MAP as winter precipitation. Snowfall accumulates during the cold season and snowmelt releases a pulse of water that modulates the temporal and spatial dynamic of the water balance (Tabler, 1975; Burke *et al.*, 1989). Snowmelt

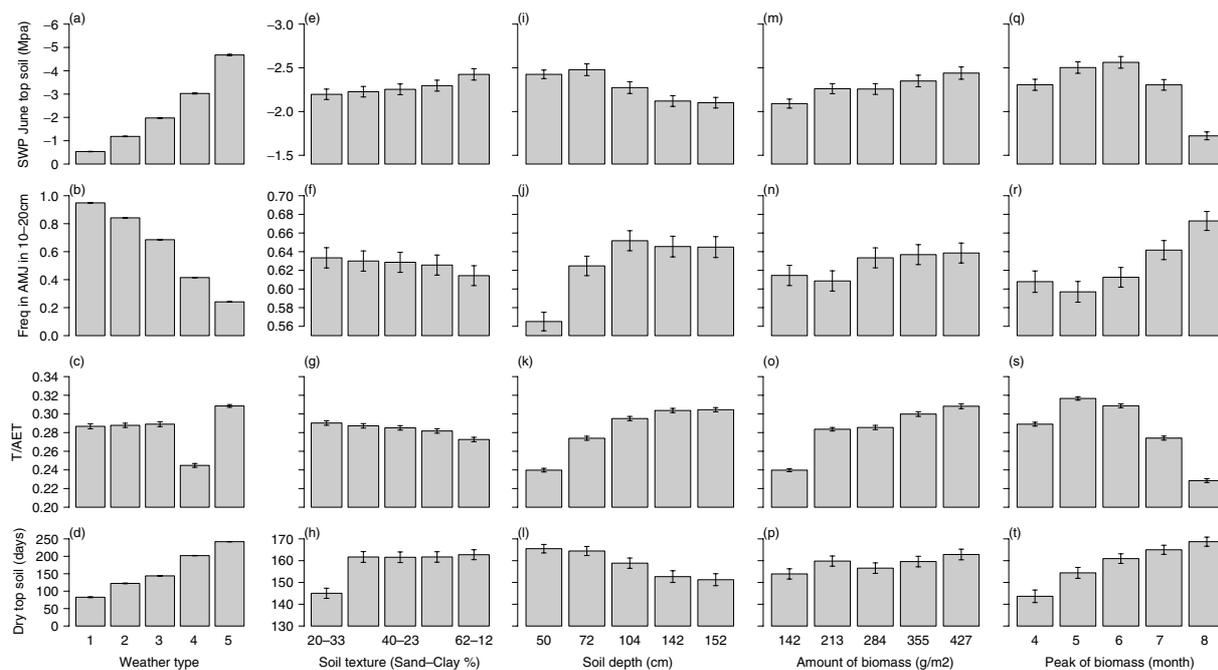


Figure 6. Effects of weather type (a–d), soil texture (e–h), soil depth (i–l), amount of biomass (m–p), and phenology of peak biomass (o–t) on selected response variables from groups ‘snapshot’, ‘zoom’, and ‘overview’, soil water potential in the top soil in June (representing ‘snapshot’ variables), normalized frequency of days with wet soils during the second quarter (April–June) in soil layer 10–20 cm (representing ‘zoom’ variables), T/AET (representing ‘overview’ variables, water balance), and the total number of dry days in the top soil (representing ‘overview’ variables, dry periods), [means and standard errors (SE); see text for details of factor levels]. Note y-axes show different ranges between weather type and others factors.

and winter precipitation when evaporative demand is small can recharge the soil profile (Loik *et al.*, 2004; Williams *et al.*, 2009). Paruelo and Lauenroth (1996) found that a large portion of the variability of western North American shrub abundance can be explained by MAP and winter precipitation. Besides seasonality and snow, the precipitation regime of sagebrush ecosystems is dominated by small events (<5 mm) and short intervals between events (1–10 days, Lauenroth and Bradford, 2009). Small events provide insufficient water to penetrate soil layers below a depth accessed by bare-soil evaporation (Lauenroth and Bradford, 2009). In an environment with a high evaporative demand and average periods without precipitation of around 10 days, the top soil layers are regularly dry (Lauenroth and Bradford, 2009). Consequently, interactions between precipitation regime and soil depth and texture influence species composition and productivity in cold desert systems (Paruelo and Lauenroth, 1996; Schwinning *et al.*, 2005) and in particular in sagebrush ecosystems (Evans *et al.*, 1991; Bates *et al.*, 2006; Ivans *et al.*, 2006; Loik, 2007).

The ecohydrological niche of sagebrush ecosystems

We incorporated relevant fluxes of the water balance of sagebrush ecosystems (Figure 5) as recognized by other soil water simulation studies in semiarid ecosystems (Bradford and Lauenroth, 2006; Lauenroth and Bradford, 2006; Manfreda *et al.*, 2010). However, models are skillful generalizations of nature (Shugart, 1984; Oreskes, 2003) and we omitted certain aspects from the model that

were considered of low importance (see Materials and Methods section).

We found that soil water dynamics in sagebrush ecosystems are characterized by a temporal pattern of spring recharge followed by a dry period that develops in late spring and lasts until early winter, associated with a spatial pattern where top soil layers dry earlier and more completely than the bottom layers. This recharge is consistent across different sagebrush ecosystem types, but was most pronounced and also later in spring for SB-Montane. Recharged bottom soil layers are contributing a relevant portion of annual transpiration which is important for occurrence of sagebrush ecosystems (Sturges, 1977, 1993). For instance, a year with missing spring recharge leads to decreased biological activity and carbon uptake during the growing season (Kwon *et al.*, 2008). Soil water dynamics in sagebrush ecosystems can therefore be best described as storage dominated.

In semiarid ecosystems, plant interactions are dominated by belowground competition (Burke *et al.*, 1998). Plant functional groups occupy different rooting zones and access different pools of water (Sala *et al.*, 1992, 1997). Previous studies have indicated that big sagebrush plants have a root system that can extend up to 2 m deep (Sturges, 1977; Seyfried and Wilcox, 2006; Cleary *et al.*, 2010). Soil water dynamics in sagebrush ecosystems contrast to temporal patterns in another semiarid system, the shortgrass steppe, where the majority of precipitation falls during the warm season and snow tends not to accumulate (Sala *et al.*, 1997; Lauenroth and Bradford, 2006). Thus, in shortgrass steppe, the soil layers are normally

dry, i.e. 60–80% of days, and are wet only infrequently for short spells (Lauenroth and Bradford, 2006); still, the top layers are the ones that are most often wet (Sala *et al.*, 1992). Our result that a large part of water used for transpiration in sagebrush ecosystems comes from the deeper soil layers provides further support for the importance of utilization of stored water from deep soil layers in sagebrush ecosystems.

The water balance of semiarid ecosystems, including sagebrush ecosystems, is characterized by a large evaporative demand (Noy-Meir, 1973; Lauenroth and Bradford, 2006). Our results suggest that sagebrush ecosystems have a small ratio of AET/PET and transpiration from the top soil layers are restricted during the summer because they are dry during much of the growing season, which limits the ratio of T/AET . However, transpiration in SB-Montane that has a higher MAP and more pronounced and later spring recharge than other sagebrush ecosystems is larger and less attenuated mid-summer resulting in a larger T/AET . In comparison, shortgrass steppe has also a small AET/PET of about 25%, whereas T/AET is much larger with a mean of 51% (Lauenroth and Bradford, 2006). Because the top soils in shortgrass steppe are the most likely layers to be wet, transpiration from these layers is high, equaling bare-soil evaporation, and contributing to a high T/AET (Lauenroth and Bradford, 2006). In contrast, a temperate oak-hickory forest in North Carolina (MAP = 109 cm) can satisfy on average 61% of PET through AET and T/AET still reaches 54% (Oishi *et al.*, 2010).

Sensitivity analysis response variables of the 'snapshot' and 'overview' groups were most influenced by weather type and phenology of biomass. The most influential input factors for the 'zoom' response variable group were soil depth and weather type. The weather types were selected by increasing MAT from sites from across the entire geographic region of sagebrush ecosystems, but because of correlations with MAP, also with decreasing MAP. This combination, while necessary to maintain realistic relationships between weather variables, exacerbated the inferred influence of weather, causing even drier soil conditions than would have resulted from increased MAT alone. Nevertheless, the sensitivity analysis demonstrated the importance of both vegetation and soil characteristics in describing the ecohydrological niche. The analysis also showed that the amount of biomass is not one of the most influential factors suggesting that the simplification of using the same set of vegetation parameters for all sites is justified.

Previous studies have characterized differences among the sagebrush ecosystem types in terms of climate, and, to a lesser extent, vegetation conditions (Davies and Bates, 2010). Our results suggest that variation in climatic conditions among the sagebrush ecosystem types translated into subtle differences in water balance dynamics. SB-Shrubland and SB-Steppe are more similar to each other than to SB-Montane. They showed similar patterns and partitioning of water fluxes, except that

SB-Steppe intercepted and evaporated a larger component of precipitation than SB-Shrubland due to the fact that more precipitation falls during the warm season. SB-Montane is distinct both in the large amount of winter precipitation and the larger total amount of MAP. This results in later peak spring soil water potential, moister conditions throughout the soil profile, less hydraulic redistribution, and also increased percolation into deep soil layers. Consequently, transpiration of SB-Montane is increased despite a shorter growing season.

Despite these subtle differences in soil water dynamics, when viewed across the entire distribution of sagebrush ecosystems in the western United States (McArthur and Plummer, 1978; West and Young, 2000), we found that sagebrush ecosystems show a set of consistent patterns in the ecohydrological niche. First, spring recharge in all or most soil layers occurred across the entire geographic range of sagebrush ecosystems. Second, AET and T/AET were relatively constrained despite large variation in the amount of water infiltrating to the top soil. Third, soil water potential in the top soil layers was negatively correlated to PET across the entire range, i.e. top soil layers are dominated by a dry period during the warm season, whereas deeper soil layers are to a smaller degree. The largest part of the variance in water balance variables was consistently found among sites and not between years. These consistent patterns define characteristics of the ecohydrological niche of sagebrush ecosystems in general and suggest specific conditions that may indicate sensitivity to changing conditions, e.g. through climate change or disturbances.

Justification for the concept of an ecohydrological niche

Our results suggested that the climate niche is a reasonable first approximation for understanding temporal soil water dynamics and the distribution of species and plant functional groups (Thuiller *et al.*, 2005; Elith *et al.*, 2006; Hijmans and Graham, 2006). However, introducing the concept of an ecohydrological niche improved our previous understanding of sagebrush ecosystems compared to the climate niche alone. We illustrated how ecosystem water balance and distribution of species and plant functional groups can be influenced by interactions between rooting profiles, phenology and amount of biomass, and the spatio-temporal distribution of soil water.

The concept of using an ecohydrological niche as a framework to integrate climate and soil controls over plant distribution can be applied to a diversity of ecosystems. However, ecohydrological processes are likely to be most important in water-limited arid and semiarid ecosystems (Porporato *et al.*, 2002; Lauenroth and Bradford, 2006; Tietjen *et al.*, 2010). Using an ecohydrological niche shifts the focus from climatic variables to a more comprehensive water balance perspective in which the amount and timing of available water to

plants is most important (Loik *et al.*, 2004). Additionally, any type of niche measure and definition needs to be explicit about the temporal and spatial scales, at which the niche operates (Soberón, 2007; Holt, 2009). In particular, the scale of modelling an ecohydrological niche needs to account for the high spatial heterogeneity of soil characteristics and the temporal dynamic of soil water fluxes.

The link between climate, phenology, and water availability will have a large influence on the ecohydrological niche of sagebrush ecosystems under future climates. Regionally averaged annual temperatures in areas of sagebrush ecosystems are predicted to rise by 1.5 to 7 °C by 2100 depending on emission scenario (Karl *et al.*, 2009). Associated with rising temperatures will be an increase in potential evaporation and a decline in snowpack (Seager *et al.*, 2007). Increasing temperature causes less snow accumulation, a smaller portion of precipitation that falls as snow, and earlier snowmelt (Adam *et al.*, 2009; Stewart, 2009). This could cause a reduced amount of water to rewet soil in spring and supply water to deeper soil layers. Another important factor influenced by climate change is precipitation regime. Fewer but larger precipitation events are predicted for the future (Karl *et al.*, 2009). The importance of the timing and size of growing season rainfall events will increase and determine occurrence of sagebrush ecosystems (Loik, 2007), especially in areas with reduced snowpack and spring recharge. Reducing the storage characteristic of the system and the availability of deep soil water will likely lead to shifts in the range of sagebrush ecosystems (Paruelo and Lauenroth, 1996; Shafer *et al.*, 2001). This work illustrates that ecohydrological niche provides a process-based understanding of semiarid ecosystems by assessing the spatial and temporal pattern of available soil water through explicit incorporation of feedbacks and interactions of soil and vegetation with climatic and weather conditions. This approach will be essential for improving our understanding of how these systems will be affected by future conditions.

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