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FOCUS ARTICLE

Subsurface plant-accessible water in mountain ecosystems with a Mediterranean climate

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Enhanced understanding of subsurface water storage will improve prediction of future impacts of climate change, including drought, forest mortality, wildland fire, and strained water security. Previous research has examined the importance of plant-accessible water in soil, but in upland landscapes within Mediterranean climates, soil often accounts for only a fraction of subsurface water storage. We draw insights from previous research and a case study of the Southern Sierra Critical Zone Observatory to define attributes of subsurface storage; review observed patterns in their distribution; highlight nested methods for estimating them across scales; and showcase the fundamental processes controlling their formation. We review observations that highlight how forest ecosystems subsist on lasting plant-accessible stores of subsurface water during the summer dry period and during multiyear droughts. The data suggest that trees in these forest ecosystems are rooted deeply in the weathered, highly porous saprolite or saprock, which reaches up to 10–20 m beneath the surface. This review confirms that the system harbors large volumes of subsurface water and shows that they are vital to supporting the ecosystem through the summer dry season and extended droughts. This research enhances understanding of deep subsurface water storage across landscapes and identifies key remaining challenges in predicting and managing response to climate and land use change in mountain ecosystems of the Sierra Nevada and in other Mediterranean climates worldwide.

This article is categorized under:
Science of Water > Hydrological Processes
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KEYWORDS
critical zone, regolith, vegetation

1 | INTRODUCTION

In Mediterranean climates, the bulk of precipitation arrives in winter and thus is temporally offset from the peak in solar energy (i.e., temperature and sunlight) in the summer. As a result, plant water use and primary production depend not only on total annual precipitation, but also on how much wet-season moisture can be stored in the ecosystem, both above and below ground, and then used by plants during subsequent summer dry periods (Arkley, 1981; Graham, Rossi, & Hubbert, 2010). In many areas, seasonal snowpack can temporarily store much of the incoming winter precipitation and release it in late spring and early summer (Bales et al., 2011; Barnett, Adam, & Lettenmaier, 2005). However, this snowmelt pulse is

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generally too brief to sustain transpiration throughout the summer dry period. Continued photosynthesis during this favorable growing season may require that roots tap additional water stores in deep soil and weathered bedrock (Arkley, 1981; Fellows & Goulden, 2015; Graham et al., 2010; Kelly & Goulden, 2016).

Studies of plant water use have historically focused on water stored in the near-surface soil. However, observations across a range of mountain ecosystems in Mediterranean climates have shown that active roots reach well below the soil, into weathered bedrock and fractures, and that plant available water storage in deep regolith greatly exceeds the moisture stores in soil (Arkley, 1981; Graham et al., 2010; Schenk & Jackson, 2002; Schwinning, 2010). This deep moisture allows higher levels of vegetation density and primary production than soil alone can support (Graham et al., 2010). Interdisciplinary study of the deep profile is showcasing the growing field of critical zone science (Brantley et al., 2017; Riebe, Hahm, & Brantley, 2016). Critical zone research is providing an innovative, interdisciplinary framework that integrates pedogenic, geomorphic, hydrologic, biologic, and chemical processes to predict how drought, wildland fire, climate warming, land management and other perturbations combine to impact ecosystems and hydrology (Anderson, von Blanckenburg, & White, 2007; Brantley, Goldhaber, & Vala Ragnarsdottir, 2007).

Critical zone observatories (CZOs), combine the cross-disciplinary measurements and perspectives that are needed to develop a comprehensive understanding of subsurface water storage and predict its role in ecosystem development and function. The CZOs have expanded capacity to make predictions that bridge timescales—e.g., from daily fluxes of energy and matter to millennial changes in landform and ecosystems.

The Southern Sierra CZO is part of the U.S. National Science Foundation's CZO network. It has nested within it four focal measurement sites (Figure 1). These sites and their ecosystems span an elevation and climate gradient from low-elevation oak savannah to high-elevation subalpine forests along the western flank of the Sierra Nevada in California. This western flank contains watersheds that collectively serve as the primary source of surface water supplies and deep aquifer recharge for agricultural and municipal users within the Sacramento and San Joaquin Valley and across California (Figure 1).

In this paper, we present our view of how deep regolith storage may act as a mediating factor between the abiotic and biotic processes influencing the spatial and temporal evolution of the CZ. We review the topic of regolith water storage in mountain ecosystems with Mediterranean climates, and expand on it through specific examples and a review of findings from the Southern Sierra CZO (Figure 1). Through this, we address four main questions relevant to the prediction of water and storage capacity within the subsurface. First, what attributes of subsurface water storage capacities and held quantities are important? Second, what are the spatial and temporal patterns of these attributes across the steep climate gradients in a granitic mountain landscape? Third, what processes give rise to these patterns over short (days to years) to long (geologic) time scales? Fourth, how can improved prediction of the temporal and spatial patterns of these critical-zone attributes—and their controlling processes—advance current understanding in both critical-zone science and resource management? (Box 1)

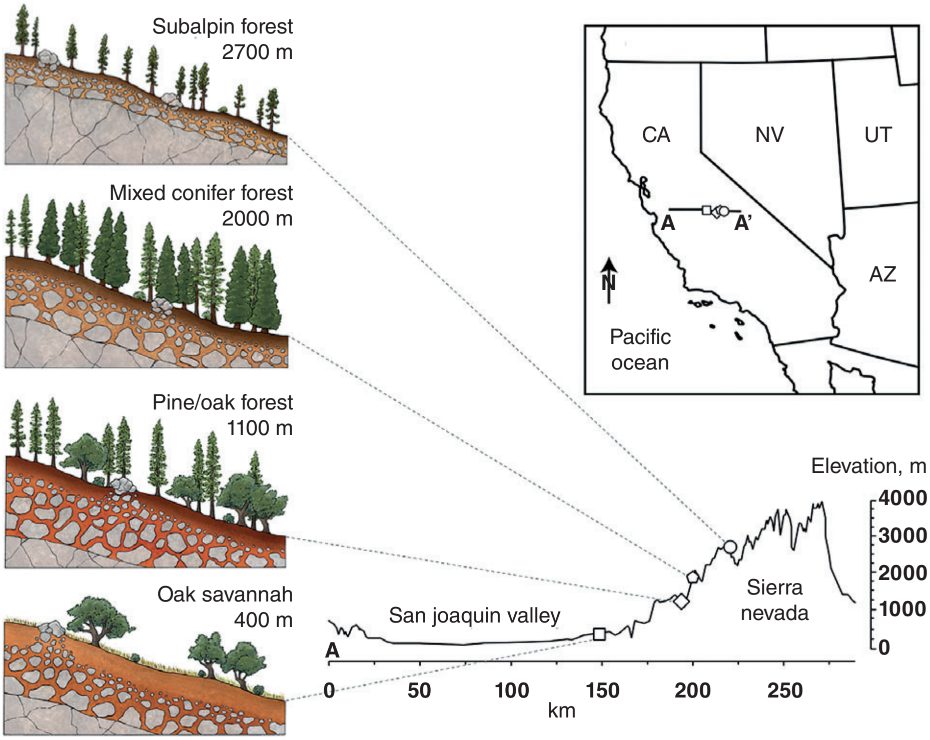

FIGURE 1 Study site locations and cross-sectional depictions of the Southern Sierra CZO and its ecosystems. The four focal sites of the CZO span an elevation and climatic gradient from low to middle elevations on the western flank of the Sierra Nevada of California, USA. Watersheds situated on the western flank provide surface water and groundwater recharge that support agricultural, municipal, and industrial water demands in the San Joaquin Valley and across California

BOX 1

IMPORTANCE OF PREDICTING PLANT-ACCESSIBLE WATER

Unlike climates where terrestrial water supply and demand are more closely synced (i.e., wet summers), in a Mediterranean climate the amount of water stored in the regolith is of comparable importance to mean annual amounts of precipitation and temperature, as well as human intervention, in determining many ecosystem attributes. In the Sierra Nevada, multiyear droughts occur with decadal frequency, and plant-accessible water storage from prior wet years must sustain the forest through multiple dry seasons. The 2011–2015 drought in California was warmer than past droughts, evaporative demand increased, and trees in some areas died as plant-accessible water was depleted.

Regolith water storage in the Sierra Nevada is a product of climate acting on granitic bedrock; and over time scales of regolith formation, heterogeneities in bedrock are amplified by the influence of climate and vegetation on weathering.

This review of our multiyear measurements of critical zone attributes, water storage, and water fluxes at four focal measurement sites provides a consistent picture of the feedbacks between climate, evapotranspiration, regolith water storage, and vegetation density. This integrated, critical zone approach to science explains how the existing forests at these four sites were sustained over past decades to centuries, and the vulnerability of these forests in a warmer and more variable climate.

Using satellite-derived indices of vegetation and climate data from across the Sierra Nevada, one can scale estimates of plant-accessible storage across the Sierra landscape. Our hypothesis is that, after accounting for precipitation and temperature, regolith properties are the primary determinant of what vegetation occurs where, how much annual evapotranspiration occurs, and the vulnerability of different sites to the effects of multiyear drought.

2 | PLANT-ACCESSIBLE WATER IN THE SUBSURFACE

The multiple definitions and measurements of regolith water quantities reflect a range of questions from different disciplines (McNamara et al., 2011). Those most relevant to plant-accessible water and critical zone science are illustrated in Figure 2. While some investigators have used the term “rock moisture” to refer to one or more aspects of the subsurface quantities in Figure 2 (Rempe & Dietrich, 2014a), we instead use more specific terms that emphasize the relationship of the water or the water storage element to the surrounding ecosystem.

Regolith extends from the land surface to unweathered bedrock and is broadly divisible into soil, saprolite or saprock, and weathered bedrock. Soil in mountain ecosystems consists of chemically and physically altered layers of material that have been mobilized downslope. Similar to soil, weathered bedrock and saprolite or saprock have also experienced chemical and physical processes that generate porosity; but unlike soil, these layers still retain the original rock fabric—indicating no downslope movement, bioturbation, or other types of in situ disruption. Within the regolith, porosity and pore connectivity decrease with depth as does biologic activity. Porosity, regulated by parent material and tectonics, as well as by biota, physical, and biogeochemical weathering over time, determines the water-holding capacity of the regolith (static storage capacities). However, the water balance, as controlled by the difference between precipitation, evapotranspiration, and net discharge, determines the actual availability of regolith moisture stores (seasonally dynamic stores of water).

3 | TOTAL POROSITY

“Total porosity”, or total void space, is the constraining limit to the maximum amount of water that can be stored in subsurface pore space and, if this pore space was completely full of water, it would be analogous to full saturation. It is governed by physical, chemical, and biological processes that create fractures and openings within the rock as it is transitions from unweathered bedrock at depth, to weathered and fractured rock, to saprolite or saprock, and then eventually to soil near the surface over millennial timescales.

3.1 | Available water storage capacity

The quantity “available water storage capacity” is less than total porosity and is governed by the connected pore-size distribution and resulting water-retention relationships (O’Geen, 2012). A large proportion of water in macro-pores (>75 μm in diameter) drains too rapidly under gravity to be available to plants, while a substantial amount of water in very small pores (<~0.2 μm in diameter) is held too tightly for plant root and associated mycorrhizal withdrawal. The smallest extractable

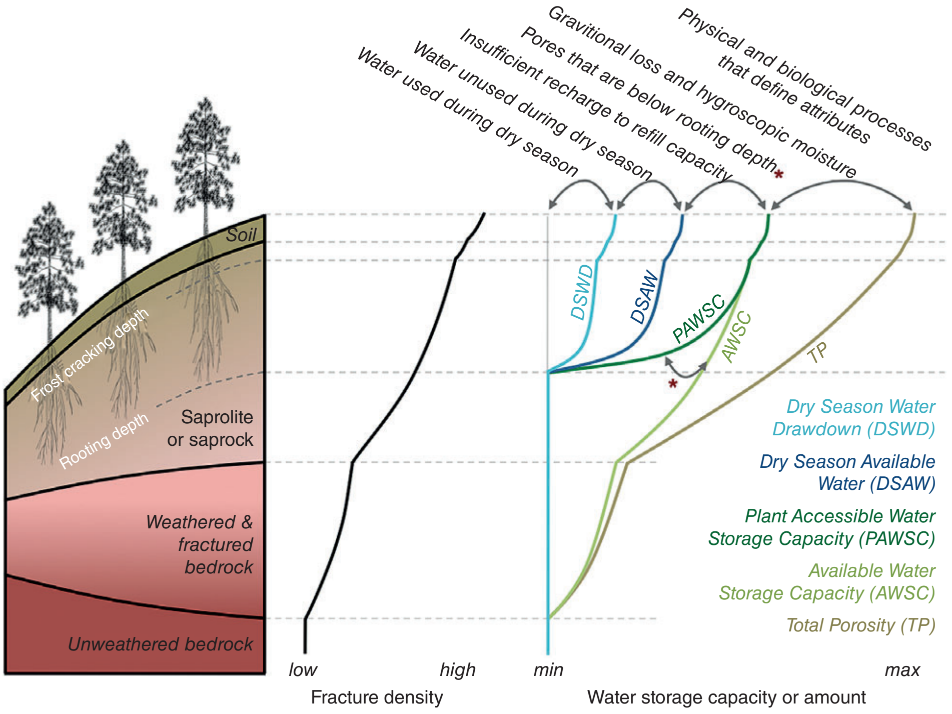

FIGURE 2 Conceptual model of critical zone architecture (left), fracture density (middle), and their relation to changes in subsurface attributes (right), both dynamic (blue) and static (earth tones). Processes (upper right) that control a decrease in water availability (from right to left) and define these attributes of storage capacity and stores of subsurface water. The attributes can be defined as follows: dry season water drawdown (DSWD) is the amount of water lost from storage during the dry season; dry season available water (DSAW) is the amount of plant-accessible water in storage at the beginning of the dry season; plant accessible water storage capacity (PAWSC) is the amount of void space available to hold water that is accessible to plants, and depends on rooting depth; available water storage capacity (AWSC) is the amount of void space available to hold plant-accessible water at amounts below field capacity and above wilting point, regardless of presence or not of rhizosphere; and total porosity (TP) is the total void space

pore size depends on the species present. The operational definition of available water storage capacity is the difference between field capacity and the permanent wilting point. Field capacity refers to water that is prevented from draining because it is retained against gravitational forces at water potentials of approximately −0.01 MPa in sandy soils and approximately −0.033 MPa in finer textured soils. Wilting point is defined by the reduction of stored water to the point where only tightly bound moisture that is believed to be unavailable to most plants and associated mycorrhizal communities remains; it often occurs at water potentials below approximately −1.5 MPa.

3.2 | Plant accessible water storage capacity

Consideration of subsurface root distribution leads to the idea of "plant-accessible water storage capacity." This reservoir is the subset of the available water storage capacity that is accessible for extraction by roots and mycorrhizal fungi; it is a physical and biological property of the critical zone that can vary through time as disturbance events alter biotic communities and their rooting depths. Plant rooting depth and distribution are poorly characterized in many natural ecosystems (Brantley et al., 2017; Mokany, Ash, & Roxburgh, 2008; Pawlik, Phillips, & Šamonil, 2016; Schwinning, 2010; Stone & Kalisz, 1991), but it is likely that portions of the critical zone are often devoid of roots, either because these portions lie beneath the maximum rooting depth needed to meet the resource demands of plants, or the areas are inaccessible to root exploration. Mycorrhizal fungi can extend the "reach" of the plant to access water and nutrients in pores beyond the physical extent of their root networks (Bornyasz, Graham, & Allen, 2005; Brantley et al., 2017; Egerton-Warburton, Graham, & Hubbert, 2003; Schwinning, 2010). Plant-accessible water storage capacity is highly relevant yet challenging to measure directly, and is defined through above-ground estimates of how much water is used by plants.

3.3 | Dry season available water

Of great interest in Mediterranean climates is the actual subsurface water available to vegetation during the dry season, or "dry-season available water." In a wet year, it will equal plant-accessible water storage capacity, but in a dry year can be much lower, as mountain regolith may not be fully recharged during the wet season. That is, dry-season available water may be thought of as the minimum of two values: (a) plant-accessible water storage capacity in the subsurface and (b) the sum of the remaining subsurface store from the previous water year and the amount of water recharged into the subsurface from the most recent wet season.

3.4 | Dry season water drawdown

"Dry-season water drawdown" or actual dry-season evapotranspiration drawn from storage is controlled by either dry-season available water or the evaporative demand. Dry-season water drawdown is the minimum of dry-season available water (after accounting for dry-season precipitation) and dry-season evapotranspiration demand, as controlled by potential evapotranspiration and the transpirational capacity of the vegetation. This attribute can be valuable in discerning the contributions of lateral subsurface flow in settings where root-accessible water may be low but utilization is nonetheless high.

4 | OBSERVED PATTERNS IN PLANT-ACCESSIBLE WATER

Vertical and spatial patterns of water within the subsurface critical zone are hidden from view and thus often challenging to access and study. As a result, the architecture and function of below-ground water storage has remained poorly understood (Brantley et al., 2017; Graham et al., 2010; Riebe et al., 2016). Direct excavation can provide important observations, but is often limited in scope to only a few sites due to costs and complicated logistics. The Southern Sierra CZO has several focal measurement sites spanning a range of elevations and climates. Excavations at each show differences in subsurface architecture that are captured conceptually in Figure 1. They also show how the subsurface varies with elevation and the associated gradient in climate. These excavations, or similar drilling processes, are often too invasive, destructive, or costly to accomplish on scales relevant for fully quantifying subsurface complexity. To overcome this limitation, the Southern Sierra CZO has used a variety of in-situ, geophysical, and remotely sensed techniques to quantify patterns and processes within the critical zone (Figure 3). Observations suggest that weathered and fractured bedrock in the Southern Sierra CZO can extend to depths of 35 m or more (Holbrook et al., 2014), and the subsurface exhibits marked horizontal heterogeneity over both landscape (10 km) and hillslope (100 m) scales (Figures 4 and 5). Comparison between the focal sites of the Southern Sierra CZO demonstrates the spatiotemporal variation in attributes and subsurface water that can vary both by depth within sites and more broadly across the landscape. Combining these findings with results from the larger CZO network, which spans a more diverse array of bedrock lithologies and climate zones, provides a basis for improved prediction of the key critical zone processes controlling ecosystem services worldwide.

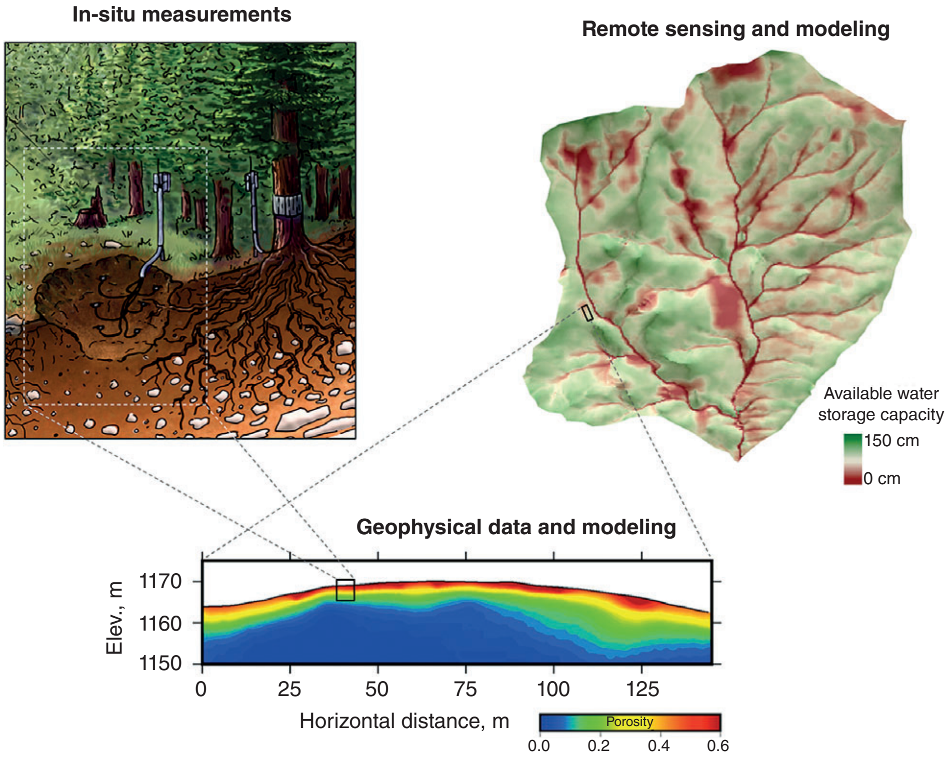

FIGURE 3 Types and scales of measurement that can be integrated to understand the temporal and spatial variations of subsurface water-related attributes in mountain ecosystems

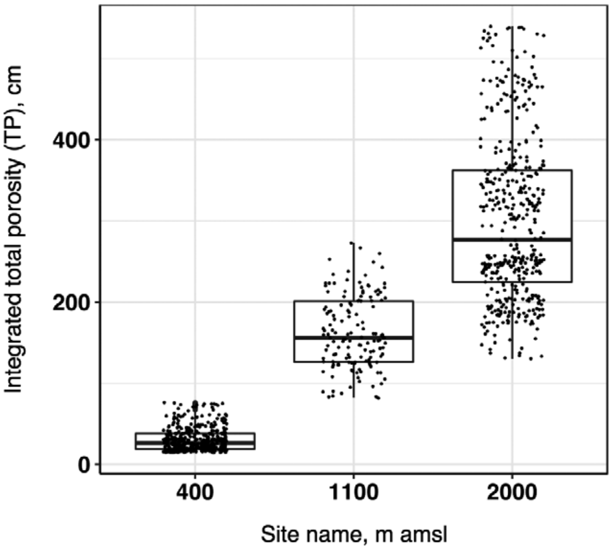

FIGURE 4 Geophysical estimates of depth-integrated total porosity (which is a minimum due to assumptions about saturation) across the three lowest-elevation measurement sites of the Southern Sierra CZO (see text for methods). Total integrated porosity, in cm, quantifies the depth-integrated volume-per-unit-area (i.e., the effective thickness) of void space in the subsurface below any given 1 cm^2 area on the land surface. Similar total porosity data for the 2700 m site is not available

4.1 | Variation at an individual site

The combined thickness of soil, saprock, and weathered bedrock at the Southern Sierra CZO can range from 2 to 35 m across a broad range of landscape positions. These regolith thickness measurements are derived from a combination of geophysical observations and data from hand and engine-driven augers, drills, and corers. Measurements of bulk density in samples from volumetric cores show that porosity generally increases with proximity to the surface (Holbrook et al., 2014). Traditionally, porosity measurements of deeper regolith have required these types of physical samples. Drilling or excavation in mountain environments can be challenging and often fails to capture the spatial distribution of porosity over large scales, especially at depths greater than a few meters.

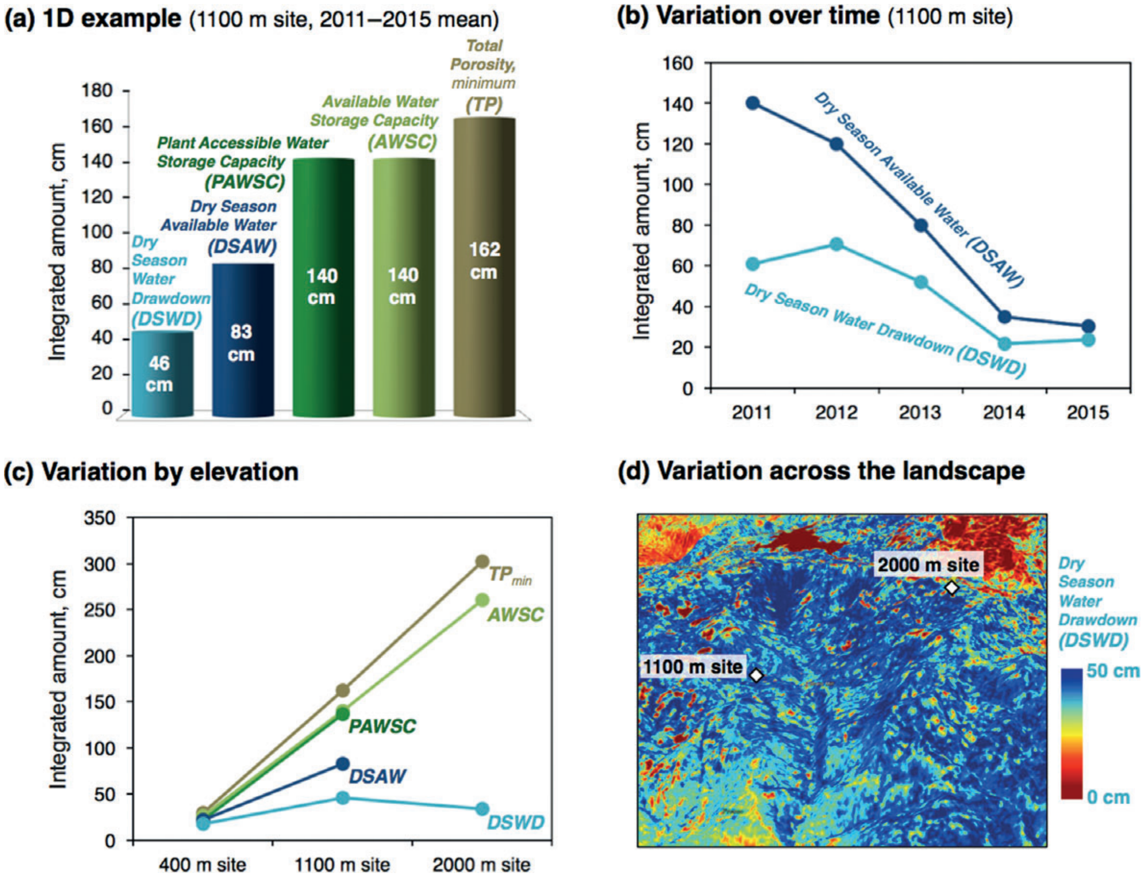

FIGURE 5 Examples from the Southern Sierra CZO showing quantitative estimates for actual stores and storage capacities of subsurface water integrated across the entire regolith depth at an individual site for (a) a single instant in time and (b) across several years; (c) across elevation; and (d) across the landscape. There is insufficient data to accurately estimate plant-accessible water storage capacity or dry-season available water at the 2000 m site (c)

An alternative approach for estimating total porosity is to use near-surface geophysical methods, specifically P-wave velocities obtained from shallow seismic refraction surveys, in conjunction with a modeled rock-physics relationship (Bachrach & Nur, 1998; Holbrook et al., 2014; Mota & Santos, 2010). P-Wave velocities are controlled by lithology, porosity, fracture density, and the fluid in the pore space (Andersen & Johansen, 2010; Dvorkin, Mavko, & Nur, 1999; Nur, Mavko, Dvorkin, & Galmudi, 1998). In an environment where parent lithology is uniform, the dependence on porosity can be exploited using a rock-physics relationship. Previous work in the Southern Sierra CZO demonstrated that the Hertz-Mindlin rock-physics model (Hashin & Shtrikman, 1962; Holbrook et al., 2014; Mavko, Mukerji, & Dvorkin, 2009; Mindlin, 1949) worked well to predict measured porosities (Holbrook et al., 2014). The level of water saturation influences the observed velocities and must be accounted in the rock physics model (Bachrach & Nur, 1998; Kahraman, 2007; Mavko & Mukerji, 1998) and in practice saturation is difficult to quantify in the field due to limited direct access to the deep regolith. If nothing or little is known we assume zero saturation. In that case, the geophysical analysis provides lower limits on total porosity (Figure 4). Together, geophysical data and rock physics modeling (Holbrook et al., 2014) indicate a mean value for minimum depth-integrated total porosity at the 1100 m site of 162 cm (Figures 4 and 5a).

We estimate available water storage capacity using an indirect approach that couples measurements of depth to unweathered bedrock with water release curves for regolith. At the 1100 m site, mean available water storage capacity is approximately 0.20 cm^3 cm^{-3} in the upper regolith (0–5 m depth). Based on the observed decrease in porosity at greater depths (Holbrook et al., 2014), mean available water storage capacity could decrease to 0.05 cm^3 cm^{-3} or less in the lower regolith (below 5 m depth), implying that available water storage capacity can be as high as approximately 150 cm for a regolith thickness of 15 m, and is likely closer to approximately 140 cm at our 1100 m site based on the estimates of plant-accessible water storage capacity (Figure 5a,b). Using this value and the total porosity value noted above, the ratio of available water storage capacity to total porosity in the substrate is about 0.86. However, since our estimate of total porosity is a minimum estimate (as discussed above), the difference between available water storage capacity and total porosity is likely greater.

The recent severe drought and widespread tree mortality across the Southern Sierra CZO provides the means to estimate plant-accessible water storage capacity based on the maximum cumulative net withdrawal of subsurface moisture. Integrated measurements of evapotranspiration based on eddy-covariance observations indicate a net depletion (i.e., evapotranspiration-precipitation) during the four-year drought of approximately 140 cm at the 1100 m site (Figure 5a). This value for plant-accessible water storage capacity approaches our estimate of available water storage capacity, implying that roots may extend to the base of the weathered rock profile approaching depths of 15–20 m.

Dry-season available water varies annually and seasonally with precipitation (Figure 5b). Over time, it is governed by the net recharge of water to the regolith, which—disregarding lateral flows and deep percolation—is total precipitation minus wet-season evapotranspiration. The 2011 through 2015 mean precipitation minus wet-season evapotranspiration was between 80 and 100 cm year^{-1}, which we use to estimate mean dry-season available water for the 1100 m site (~83 cm year^{-1}, Figure 5a). Similarly, dry-season water drawdown varies over time (Figure 5b) and is comparatively well known at local scales based on integrated eddy-covariance observations of evapotranspiration. Dry-season precipitation is minor for these sites. The mean estimate of dry-season water drawdown for the 2011–2015 period at the 1100 m site is approximately 46 cm year^{-1} (Figure 5a).

Measurements from the Southern Sierra CZO provide quantitative estimates of the important attributes describing subsurface water; and other nodes in the greater network of CZOs are well poised to assemble similar measurements in the near future. This leads to the first research challenge highlighted by this review, which is to explore subsurface water storage across a suite of sites, particularly across sites at end members in gradients of lithology and climate (Box 2).

BOX 2

RESEARCH CHALLENGES IN ENHANCING THE UNDERSTANDING OF PLANT-ACCESSIBLE WATER IN THE SUBSURFACE

Challenge 1: Test, explore, and establish consistent terminology to define differences in subsurface attributes across sites, focusing on locations that represent end members in gradients of lithology and climate.
Challenge 2: Quantify landscape patterns of water storage from regional to global scales.
Challenge 3: Understand processes that control water storage across sites, focusing on locations that represent end-members in gradients of lithology and climate.
Challenge 4: Understand the implications of subsurface water storage in assessing the vulnerability of forests and run-off to climate and land use change.
Challenge 5: Model the critical zone as a coupled system to improve predictive ability across hydrologic, ecological and geologic timescales.

4.2 | Variations across the landscape

Seismic refraction surveys and rock physics modeling (Holbrook et al., 2014) at three different elevations within the Southern Sierra CZO show that total porosity increases with elevation (Figure 4). Moreover, the geophysical data correspond to a marked increase in both regolith thickness and available water storage capacity with increasing elevation from 400 to 2000 m (Figures 4 and 5c). Previous work in the region has shown, however, that the thickness of regolith and the density of overlying vegetation can vary markedly at mid elevations due to small variations in granite bedrock geochemistry (Hahm, Riebe, Lukens, & Araki, 2014). Hence, the overall altitudinal trend in regolith properties is likely modulated to some extent by variations in underlying bedrock.

Although we did not quantify total porosity, available water storage capacity, or regolith thickness at elevations above 2000 m, we hypothesize they would all decline with further increases in elevation above approximately 2300 m, the lower limits of Pleistocene ice cover along the transect (Gillespie & Zehfuss, 2004), due to the effects of glaciation. This prediction is consistent with flux tower data and visual observations from the 2700 m elevation site (Fellows & Goulden, 2015). Thus, we expect that regolith storage capacity and total regolith thickness both decrease with increasing elevation in the uppermost elevations of the Sierra Nevada (Figure 1).

Approaches to determining water storage using remotely sensed or physically modeled data are not as well developed at landscape scales as they are for local measurements from excavations, boreholes and geophysics. Nonetheless they do provide spatially gridded storage estimates that are consistent with evapotranspiration at the individual focal measurement sites (Figure 2; Fellows & Goulden, 2015). Moreover, they can be readily coupled with catchment-scale predictions of regolith thickness obtained using terrain analysis together with digital regolith mapping (Figure 3; Beaudette & O'Geen, 2016; Tesfa, Tarboton, Chandler, & McNamara, 2009). Dry-season drawdown (Figure 5d) is quantified using remote sensing and a simple water balance model to partition annual evapotranspiration into the portion that occurs during the wet season (which is presumably supported by the rapid turnover of recent precipitation), and the portion that occurs during the dry season (which is mainly supported by the net withdrawal of subsurface moisture from storage; Fellows & Goulden, 2015). When coupled together these observations should permit comparisons between the remotely sensed, gridded estimates of water storage and the overlapping direct measurements of local storage made at individual focal measurement sites (Figure 3). This helps us identify the second research challenge in Box 2, which is to quantify landscape patterns of water storage from local to global scales. Gridded quantitative estimates of water storage are ultimately needed to predict the controls on spatial patterns of water storage across landscapes, and to drive predictive models for hydrology, ecosystem health, landscape management, and the evolution of the critical zone (Riebe et al., 2016).

5 | PROCESS CONTROLS ON PLANT-ACCESSIBLE WATER

Although data displayed in Figure 5 represent a step towards quantifying the water storage attributes highlighted in this article, much more work is needed to develop a predictive, process-based understanding of how they vary across landscapes. Our first-order prediction is that the patterns can be explained by a combination of Jenny's five state factors—time (i.e., degree of pedogenesis and history of glaciation), parent material (i.e., bedrock lithology), climate (i.e., precipitation and temperature), topography (i.e., landscape position, slope, and aspect), and the biota (i.e., surface plants). We therefore propose that it should be possible to take the next step towards a more predictive understanding by using a combination of spatially gridded estimates of storage from remotely sensed data and complementary datasets of climate, topography, vegetation, rock type, and history of glaciation (Jenny, 1941; Jenny, 1980). This should lead an empirical interpretation—based on millions of pixels of landscape data—of factors that influence storage capacity within deep regolith.

However, simple empirical correlations in the Jenny framework are unlikely to predict variations at hillslope scales that are driven by factors such as lateral water flows. Lateral water flows and heterogeneous snowpack accumulation may be the dominant source of water in some locations (Safeeq & Hunsaker, 2016; Thompson, Harman, Troch, Brooks, & Sivapalan, 2011). Within the Sierra Nevada of California, riparian meadows are clearly supported by upslope contributions (Lowry, Loheide, Moore, & Lundquist, 2011), and studies show that estimates of subsurface water can be 25% higher if lateral redistribution is considered (Tague & Peng, 2013). This helps explain how available water storage capacity can be low in valleys (Figure 3) even though corresponding dry-season water drawdown is high (Figure 5d). Linking critical zone evolution with spatial patterns of lateral connectivity and snowmelt heterogeneity remains an important but challenging research need (Brooks et al., 2015). Plant allocation of carbon to roots (i.e., atmospheric CO_2 to below-ground C conversion) and the influence this has on carbon sequestration also remain poorly understood (Asbjornsen et al., 2011; Fischer, Hart, LeRoy, & Whitham, 2007; Franklin et al., 2012). Recent advances in remote sensing of root distributions (Cui, Guo, Chen, Chen, & Zhu,

2013) and isotopic measurements (Alstad, Hart, Horton, & Kolb, 2008; Wang et al., 2012) to assess sources of plant water can contribute to improved understanding.

To move beyond the empirical, correlative predictions of gridded datasets it will be crucial to develop a more process based understanding of how attributes of below-ground water—both its stores and capacities for storage—are regulated by the physical, chemical, and biological processes that generate fractures and porosity in soil and weathered rock. This leads to the third research challenge highlighted in this review: understanding the process controls on water storage across the landscape, with a particular focus on locations that represent common endmembers in gradients of lithology and climate (Box 2). Although several exciting hypotheses have recently emerged from the CZO network on how the architecture of the deep critical zone is shaped by fracturing (St. Clair et al., 2015), bedrock drainage (Rempe & Dietrich, 2014b), frost cracking (Anderson, Anderson, & Tucker, 2013), tree fall (Brantley et al., 2017; Gabet & Mudd, 2010), and chemical weathering (Lebedeva & Brantley, 2013), these hypotheses have rarely been tested (Riebe et al., 2016). Moreover, they have not been assimilated into a comprehensive framework for predicting how the different attributes vary with factors such as climate (precipitation and temperature regime), vegetation (species and cover), and lithology (bedrock chemistry and structure). Figure 2 provides a simple conceptual model for the distribution of fractures, grain-scale porosity, and plant accessibility of stored water in the subsurface critical zone that may help in developing specific hypothesis about how different processes influence different water storage attributes.

In the conceptual framework of Figure 2, we adopt the perspective of Earth material as it evolves on its journey through the critical zone. In this perspective, we assume that erosion of material at the surface outpaces deposition, such that material from depth (relative to land surface) is effectively exhumed towards the surface, where it is increasingly exposed to the influences of biota and reactive throughflow of meteoric water. The starting point on this conveyor is unweathered rock, referred to here as “unweathered bedrock,” at the base of a vertical column of the critical zone (Figure 2). This unweathered material actually lies below the base of the CZ, which, in the parlance of geochemists, is the depth where the water-rock system grades from disequilibrium near Earth’s surface into a state of chemical equilibrium at depth (Brantley et al., 2011; Riebe et al., 2016). Although it is unweathered by definition, unweathered bedrock can harbor abundant fractures, inherited when it was deep in the crust (Molnar, Anderson, & Anderson, 2007). Nevertheless, chemical equilibrium dominates in unweathered bedrock, because flow of reactive water from the surface is slowed by overburden pressures and tectonic forces that keep existing fractures closed (St. Clair et al., 2015).

Unweathered bedrock grades into “weathered and fractured bedrock” as erosion lowers the land surface and exposes new unweathered bedrock to reactive fluids at depth (Figure 2). This reflects increased fracture porosity as lithostatic overburden pressures decrease (St. Clair et al., 2015). Here, flow rates of reactive meteoric water are faster, pushing the water-rock system away from equilibrium and thereby initiating chemical weathering in minerals exposed at fracture surfaces (Lebedeva & Brantley, 2013). On average, chemical alteration of rock—and the resulting generation of new grain-scale porosity within it—are still minimal here, but fractures can nevertheless provide plant-accessible water storage capacity if roots extend deeply enough and if water does not drain away too quickly. To the extent that roots are present, they likely promote additional fracturing through the transfer of energy from the wind to the rock, with tree sway possibly creating a “crowbar effect” that can weaken rock over time (Brantley et al., 2017; Roering, Marshall, Booth, Mort, & Jin, 2010). They may also promote chemical weathering through the action of associated microbial communities (Balogh-Brunstad, Keller, Gill, Bormann, & Li, 2008) and mycorrhizal fungal networks (Bonneville et al., 2009).

As Earth material rises still higher in the column, the head gradient between the hillslope location and the local channel eventually grows to the point that it drains the weathered and fractured bedrock of any remaining chemically equilibrated water (Rempe & Dietrich, 2014b). This opens minerals to increased exposure from reactive water from the surface. This leads to a marked increase in chemical alteration (Lebedeva & Brantley, 2013), a corresponding increase in grain-scale porosity (Navarre-Sitchler et al., 2013), and a transition from weathered and fractured bedrock to “saprolite” (literally rotten rock) or “saprock.” The distinction between saprolite and saprock is defined by the degree to which weatherable minerals (e.g., plagioclase, biotite, etc.) are pseudomorphically altered to clay minerals, with a low proportion of alteration indicating saprock, and a high proportion indicating saprolite. Within granitic lithologies, field techniques have been developed to distinguish these grades of weathered bedrock (Clayton & Arnold, 1972). Both total porosity and available water storage capacity may increase sharply at this transition from weathered and fractured bedrock to saprolite or saprock (Figure 2). To the extent that roots and mycorrhizal fungi are present, this reservoir then becomes plant-accessible water storage capacity. As exhumation continues through saprolite or saprock, fracturing, chemical weathering, and porosity all increase while lithostatic pressures continue to decline as contact with reactive meteoric water increases (Brantley et al., 2011; Riebe et al., 2016). Chemical alteration, often leading to mineral expansion and alteration (e.g., biotite into vermiculite), generates mechanical forces that cause new porosity to propagate inward from fracture surfaces into the interiors of still mostly coherent but friable rock fragments (Girty, 1991; Navarre-Sitchler et al., 2013). Root networks can extend many meters into this layer (Arkley, 1981; Graham et al., 2010), making available water storage capacity therein accessible to plants—thus creating plant-accessible water storage capacity (Figure 2). Creation of porosity in saprolite or saprock can therefore be vital to ecosystem function (Brantley et al., 2017; Graham et al., 2010), providing crucial supplements to water stored in the soil. In the uppermost layers of saprolite or saprock and soil, frost cracking (Anderson et al., 2013), salt and pedogenic calcite precipitation (Hirmas & Graham, 2011), and biological activity are likely to exert important controls on fracturing and porosity generation, which in turn promotes biological activity by providing storage space for life-sustaining water (Figure 2). This biologic activity includes plant root and associated microbial and mycorrhizal mediated chemical weathering (Balogh-Brunstad et al., 2008; Bonneville et al., 2009; Kelly, Chadwick, & Hilinski, 1998; Moulton, West, & Berner, 2000), and physical mixing and root wedging (Gabet & Mudd, 2010; Pawlik, 2013; Roering et al., 2010). Porosity in the uppermost layer, the soil, evolves through time as pedogenic processes generate and translocate secondary clay minerals (Girty, 1991), forming micro-porosity. Clay minerals also aggregate into structural units to form macro- and meso-porosity.

Porosity production in these described layers of the subsurface critical zone architecture forms through mechanisms that result in a variety of pore space sizes. It is not possible to categorize which processes correspond to which pore size classes, since there is no agreed upon designation of what size ranges constitute different pore size classes (Cameron & Buchan, 2006; Brewer, 1969; Mazurier et al., 2016; Rossi & Graham, 2010). It is however agreed upon that macro pores are large enough to promote free drainage by gravity and micro pores are pores that retain water against gravity by capillary action. Thus, most differentiate micro porosity as water filled pore space at field capacity, with diameters less the 30 μm (typically inter-grain pores in soil), and macro porosity as air-filled pore space at field capacity, with diameters greater than 30 μm (typically inter aggregate voids in soil). Because weathered bedrock, saprock, and saprolite have no identifiable aggregates, but can have large voids based on mineral grain size and fractures, as well as microcrack and macrocrack structures (Mazurier et al., 2016), we have defined pore size distribution here as micro pores: less than 30 μm; meso pores: 30–75 μm; and macro pores: >75 μm. Examples of mechanisms that form these different size classes of porosity are: tectonically formed joint fractures and microfractures; microfractures formed and expanded by weathering (e.g., stress fracturing induced by biotite expansion); and pores generated by chemical dissolution and resulting material loss (Mazurier et al., 2016; Rossi & Graham, 2010).

6 | INFLUENCE OF DEEP REGOLITH ON HYDROLOGIC AND ECOLOGIC SUSTAINABILITY

Improved understanding of subsurface attributes of plant-accessible water will have important implications for documenting the vulnerability of semi-arid ecosystems to climate change (fourth research challenge noted in Box 2; Bales et al., 2018). The recent California drought (2012–2016) was the most severe drought in at least the past 120 years (Williams et al., 2012), in part due to climate warming-induced increases in evaporative demand. Future droughts are likely to be even more severe, as temperatures in the southern Sierra Nevada are expected to rise about 2°C by 2050, with associated declines in snowpack of 10–25% at high elevations and 70–90% at low elevations (Climate, 2013). Warming temperatures have already caused a doubling of mortality rates in Sierra Nevada forests over the past few decades (Van Mantgem & Stephenson, 2007); and a recent remote-sensing-based study estimated that more than 58 million trees experienced critical canopy water loss, a likely indicator of mortality (Asner et al., 2016). Work at the Southern Sierra CZO highlights the role played by subsurface attributes in moderating these impacts of climate change, and allows us to predict which areas are most vulnerable, and which may be refugia into the future (McLaughlin et al., 2017). For example, we predict greater forest mortality during drought in areas with less subsurface water storage capacity after controlling for possible confounding factors such as vegetation type and density and snowpack heterogeneity. Climate warming can increase plant stress and mortality through increased evaporative demand. Vegetation at locations with larger subsurface water storage capacity may be comparatively resistant to warming because the vegetation has more water available to meet this increasing evaporative demand. Under climate warming, we predict locations with less subsurface storage will see little decrease in runoff. In contrast, we predict that locations with more water storage will experience greater water deficits due to increases in plant water use and evapotranspiration of stored water resulting in a subsequent decrease in runoff (Safeeq & Hunsaker, 2016; Tague & Peng, 2013). We expect the ecological and hydrologic effects of warming may often be a win-lose trade-off, and that the balance between the trade-offs—i.e., whether the ecological or hydrological effect will be greater—will be controlled in part by the subsurface water storage capacity. As a general example, areas with less subsurface storage (e.g., the 1100 m site vs. the 2000 m site) will tend to see a larger impact of climate warming on vegetation health and a comparatively smaller impact on streamflow runoff, and vice versa. The pronounced spatial heterogeneity in subsurface storage across the Sierra Nevada means that the consequences of warming and how these win-lose trade-offs play out will also vary in space. To predict how ecosystem

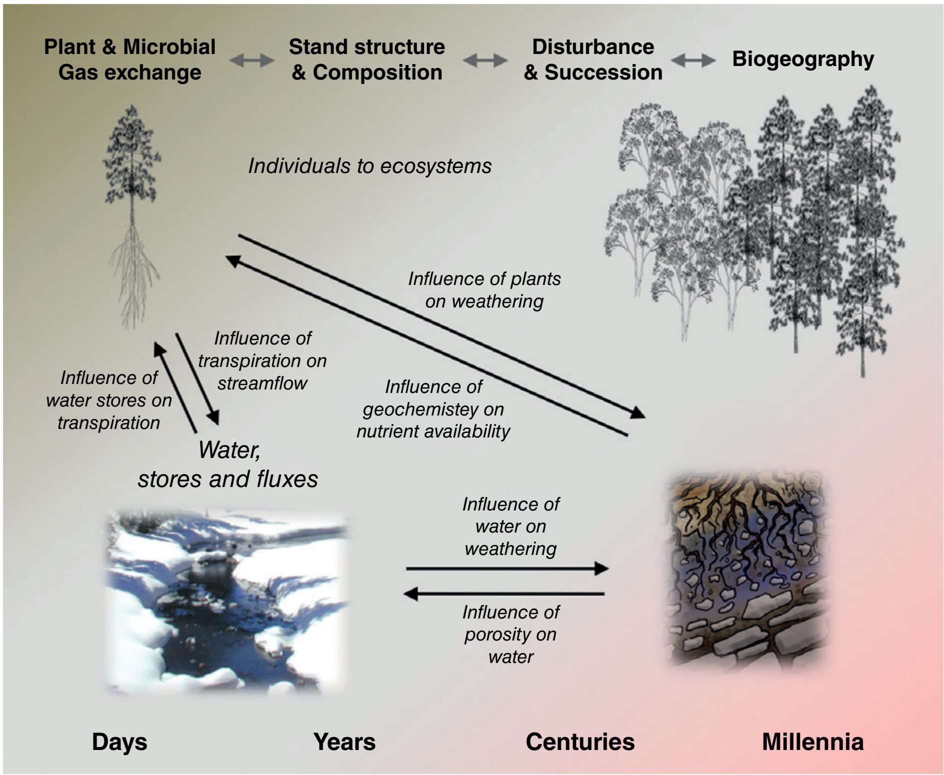

FIGURE 6 Conceptual overview of key integrated physical–biological–chemical processes in the critical zone in need of quantitative investigation through new predictive coupled-modeling frameworks that span temporal scales from days to millennia

health and water resources are likely to change with warming, we will need to be able to better characterize subsurface storage attributes. The critical zone research summarized above is a first step.

The complexities and trade-offs are built into our fifth research challenge (Box 2), which is the need for a modeling approach that explores the critical zone as a coupled system of interacting processes through time that can serve as a predictive tool for decision support or future research in semi-arid regions globally (Szabo et al., 2016). This modeling approach needs to be coupled to predict how surface vegetation, rooting structures, weathering processes, pedogenic processes, and subsurface properties interact to control the evolution of the critical zone over time scales from days to millennia (Figure 6). Ecohydrologic modeling has matured in recent decades and there are a number of models that provide estimates of the interaction between climate forcing, vegetation water use, and plant-accessible water storage capacity (Fatichi et al., 2016; Wang & Dickinson, 2012). Fewer of these models account for dynamic interactions between vegetation growth and plant-accessible water storage (Fatichi et al., 2016), and of those, parameterizing allocation of carbon and water resources to roots for growth remains a key uncertainty. In both classic hydrologic models and coupled ecosystem models, subsurface parameters are major sources of uncertainty and are poorly constrained. A step forward would be to link terrestrial ecohydrologic models with process models of critical zone evolution. Coupling terrestrial hydrology and ecohydrologic models with landform evolution and geochemical models would improve estimates of vegetation water use and productivity, and provide predictive tools that could contribute to understanding how critical zone processes coevolve across multiple temporal scales (Figure 6).

7 | CONCLUSION

Stores and storage capacities of plant-available water in mountain landscapes both control and are controlled by the subsurface critical zone architecture and its coupled plant communities. Research at the Southern Sierra CZO highlights the importance of water stores at depths greater than typical soil thickness, reaching up to 20 m deep into highly weathered regolith. Data from the Southern Sierra CZO suggest that elevation, and its associated gradient in climate, helps explain variations in the thickness and capacity of these subsurface attributes of water and storage, with the highest amount of storage existing at mid elevations within the Sierra Nevada. Future research in critical zone science needs new ways of working across timescales to predict subsurface water storage and use. This will allow improved understanding of how daily to decadal timescales of ecohydrologic processes are linked with the century to millennial timescales of the physical and biogeochemical processes that control landscape evolution.

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CONFLICT OF INTEREST

The authors have declared no conflicts of interest for this article.

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