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Hydrologic refugia, plants, and climate change

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Abstract

Climate, physical landscapes, and biota interact to generate heterogeneous hydrologic conditions in space and over time, which are reflected in spatial patterns of species distributions. As these species distributions respond to rapid climate change, microrefugia may support local species persistence in the face of deteriorating climatic suitability. Recent focus on temperature as a determinant of microrefugia insufficiently accounts for the importance of hydrologic processes and changing water availability with changing climate. Where water scarcity is a major limitation now or under future climates, *hydrologic microrefugia* are likely to prove essential for species persistence, particularly for sessile species and plants. Zones of high relative water availability – mesic microenvironments – are generated by a wide array of hydrologic processes, and may be loosely coupled to climatic processes and therefore buffered from climate change. Here, we review the mechanisms that generate mesic microenvironments and their likely robustness in the face of climate change. We argue that mesic microenvironments will act as species-specific refugia only if the nature and space/time variability in water availability are compatible with the ecological requirements of a target species. We illustrate this argument with case studies drawn from California oak woodland ecosystems. We posit that identification of hydrologic refugia could form a cornerstone of climate-cognizant conservation strategies, but that this would require improved understanding of climate change effects on key hydrologic processes, including frequently cryptic processes such as groundwater flow.

Keywords: climate change, conservation, fog, groundwater, hydrologic niche, hydrologic refugia, microrefugia, refugia

Introduction

Shifts in species distributions in response to the current era of rapid climate change (IPCC 2014) pose tremendous challenges for conservation planning, prioritization, and land protection decisions (Hampe & Petit, 2005; Ackerly *et al*., 2010; Anderson & Ferree, 2010). Predicting species distributional shifts is therefore a central focus of climate change ecology (Moritz & Agudo, 2013; Woodin *et al*., 2013; Valladares *et al*., 2014). Correlative species distribution models, widely used tools for making these predictions (Heller & Zavaleta, 2009), typically project poleward and upward elevational distribution shifts (e.g., Moritz *et al*., 2008; Bergamini *et al*., 2009; Felde *et al*., 2012; Scheffers *et al*., 2016), in which species track their thermal envelope as temperatures increase. Observed distributional responses, however, display great heterogeneity in latitudinal and elevational shifts across plant and animal taxa in response to 20th century climate change (Lenoir *et al*., 2010; Rapacciuolo *et al*., 2014; Lenoir & Svenning, 2015; Wolf *et al*., 2016). These observations suggest that species are not moving in response to regional temperature drivers alone.

The climatic conditions experienced by individual organisms or ecological communities typically arise from a cascade of climatic processes operating on different scales – the regional or mesoclimate, operating on scales of ~10^4–10^6 m, is modified by topography and elevation to form a topoclimate that varies on scales of ~10^2–10^3 m and is further mediated by small-scale environmental factors and vegetation cover, influencing the microclimate on scales of 10^1–10^2 m (Geiger *et al*., 2003). Including topoclimatic effects, such as cold air pooling, impacts the predictions of climate change models (Ashcroft *et al*., 2012; Flint & Flint, 2012; Potter *et al*., 2013; Hannah *et al*., 2014). Consequently, incorporating the impacts of a changing regional climate on microclimates might be expected to improve predictions of species distributional responses, especially at fine spatial scales, compared with predictions that rely on regional climatic changes alone (Dobrowski, 2011; Klausmeyer *et al*., 2011; Hannah *et al*., 2015; Keppel & Wardell-Johnson, 2015). In particular, climatic ‘microrefugia’ – locations on the landscape that support populations of a species while the surrounding climatic conditions become unsuitable for that species (Rull, 2009) – may provide opportunities for species persistence in the face of regionally deteriorating conditions. Relict populations not only contribute to regional biodiversity, but also harbor the potential to serve as climate nuclei (*sensu* Ferreira & de Melo, 2016; Väliranta *et al*., 2011) from which the species expand/disperse following a return to a more favorable regional climate (Grandcolas *et al*., 2014; Grandcolas & Trewick, 2016). Paleoecological studies show evidence of such climatically distinct microsites enabling species persistence during previous periods of climate change (Tzedakis *et al*., 2002; Rull, 2009, 2010; Stewart *et al*., 2010). In the context of contemporary climate change, such sites represent priority targets for conservation, yet their identification remains a challenging, poorly resolved, and interdisciplinary problem (Keppel *et al*., 2012; Corlett & Westcott, 2013; Hannah *et al*., 2015; Hylander *et al*., 2015), but see (Bátori *et al*., 2014).

Topographic locations that provide relief from temperature increases have been identified (Shoo *et al*., 2010; Ashcroft & Gollan, 2013; Gollan *et al*., 2014). Whether these sites will provide microrefugia requires consideration of how the microclimate interacts with species' physiological constraints, demography, dispersal, and community interactions. The recent focus on temperature in topographic and climatic microrefugia insufficiently accounts for the significance of changing water availability as a major stressor that is likely to be imposed by climate change, particularly in regions where contemporary ecosystems are water-limited (IPCC, 2014). The role of local hydrology in creating hydrologic microrefugia merits further exploration, particularly given observations of species distributional shifts that appear to be governed by water availability rather than temperature trends (Lenoir *et al*., 2010; Crimmins *et al*., 2011; VanDerWal *et al*., 2013).

For a site to form a hydrologic refugium, water availability at that site must be elevated compared with regional or local levels, creating a mesic microenvironment. Biotic communities in xeric ecosystems exploit such mesic microenvironments worldwide, dramatically illustrating the potential for these sites to support locally unique species assemblages in spite of extraordinarily dry regional climates. Figure 1 shows three desert environments with locally elevated water availability supported by distinct hydrologic processes. In each case, despite a dry regional climate, processes that supplement or concentrate water availability into these microenvironments support communities of relatively mesophytic plants (species with lower tolerance of water deficits, as determined by morphology, leaf stomatal responses, xylem vulnerability, or phenological strategies) than would be anticipated given regional climate.

Fig. 1 Examples of mesic microenvironments persisting in regionally arid climates. (a) Huacachina Oasis, Peru, (b) Shalala Cloud Forest, Oman, (c) Kings Canyon, Central Australia

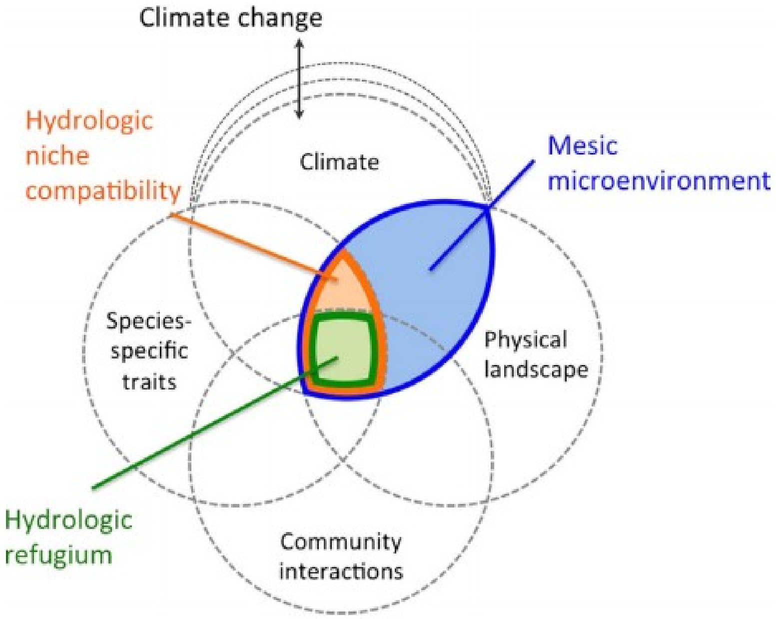

Fig. 2 This figure illustrates a hypothesized hierarchy of physical and ecological controls that would determine the suitability of a site as a hydrologic refugium for a given species. A mesic microenvironment is formed by the intersection of (shifting) climatic characteristics and the physical landscape that concentrates or disperses water resources. In a subset of such mesic microenvironments, the timing, form, and quantity of water available are compatible with the hydrologic niche requirements of a given species, meaning that the sites could support persistence of that species. To form a refugium, the site must also be available for colonization/persistence given biotic interactions. Shifting climate is likely to alter both physical and biotic processes and thus the identity and availability of hydrologic refugia.

Mesic microrefugia are likely to be most important in places where climate change causes regional water balance to shift toward more water-limited conditions. The regional water balance is influenced by evaporative demand (which is in turn mediated by atmospheric vapor pressure deficits and the land surface energy balance) relative to the availability of water to meet this demand (which is mediated by precipitation volumes and timing, snow melt timing, the storage capacity of soils/regolith, and plant rooting depths into this substrate, see the next Section). Thus, the response of the water balance to climate change is multifaceted, and varies through space in both its directionality and rate of change (Dobrowski *et al*., 2013). Similarly, the different components of the water balance are subject to varying degrees of certainty in terms of their response to anthropogenic climate forcing. Temperature increases are predicted with reasonable consistency across most climate model ensembles (Shiogama *et al*., 2016), meaning that related hydrologic variables such as snow–rain fraction and snow melt timing can also be predicted with some confidence (Krasting *et al*., 2013; Piazza *et al*., 2014). Conversely, uncertainty obscures predictions of regional rainfall patterns (Clark *et al*., 2016; Dai & Zhao, 2016). Other temperature-related variables such as potential evaporation – although expected to increase with climate change – actually declined over much of the globe during the 20th century, as measured by pan evaporation rates (Roderick & Farquhar, 2002; Roderick *et al*., 2009). Given this complexity, variability, and uncertainty, conclusions about the location, magnitude, and prevalence of regional climatic drying in response to anthropogenic climate change should be made cautiously. Nonetheless, an emerging consensus anticipates drying trends across regions that currently experience water-limited conditions (i.e., mediterranean-type climates, the semiarid subtropics, and the arid zone), equivalent to roughly 40% of the terrestrial land surface (Wiltshire *et al*., 2013; IPCC, 2014, Schewe *et al*., 2014; Gosling & Arnell, 2016). These regions include numerous biodiversity hotspots (e.g., the California Floristic Province, Mexico's Madrean Pine-Oak Woodlands, the Brazilian Cerrado, the Horn of Africa, South Africa's Succuluent Karoo, Cape Floristic Province and Maputaland-Pondoland-Albany regions, Southwest Australia, the Mediterranean Basin).

The confluence of probable drying trends in water-limited ecosystems (Flint & Flint, 2012) with the significance of many of these ecosystems for global biodiversity motivates this study. We use the breakdown of refugial capacity outlined above and illustrated in Fig. 2 to explore how mesic hydrologic refugia for plants are created and maintained. The physical processes and features that create mesic microenvironments (which may or may not ultimately function as hydrologic refugia) are described next. The following section considers how to identify potential hydrologic refugia, and addresses the requirements that hydrologic refugia be compatible with the hydrologic niche of a target species and accessible for species establishment and/or persistence. Then, a case study of hydrologic refugia in California oak woodlands is presented. Finally, the role and potential challenges of using hydrologic refugia in climate change adaptation planning are discussed.

A physical process basis for heterogeneity of plant-available moisture

From a hydrologic standpoint, mesic microenvironments arise from localized physical or biological processes that enhance water inputs or reduce water losses from the root zone. The resulting microenvironments exhibit high rates of vegetation water use, relative to the rest of the landscape (e.g., along a riparian corridor), high volumes of stored water available for exploitation by vegetation (e.g., near springs or seeps), or both. Important hydrologic processes altering the balance of water inputs, outputs, and storage are illustrated in Fig. 3. Descriptions of the processes, examples of their occurrence, and their relative importance and sensitivities to climate change are detailed in the text throughout this section, and in Table 1. These processes have differential sensitivity to climate change (Osborne *et al*., 1998; Johnstone & Dawson, 2010), and consequently, different implications for the persistence and behavior of mesic microenvironments (Ashcroft, 2010), and thus for species colonization, persistence within and utilization as microrefugia. As shown in Fig. 4, *stable* hydrologic refugia exist in places where water availability to plants is effectively unchanged (i.e., remains within the bounds of natural – or nonhuman influenced – climate variability) despite warming and drying trends in regional climate. *Relative* hydrologic refugia preserve differences in relative moisture availability between the microsite and the surrounding landscape, experiencing drying in absolute terms in concert with changes in regional climate. A relative refugium may also be *transient*, ceasing to function as a refugium over sufficiently long periods of drying. The hydrologic residence times for water associated with different hydrologic processes provide a proxy for the timescales of hydrologic response to climate change. These are used (in Table 1) to summarize the implications of hydrologic mechanisms for the behavior of refugia supported by each mechanism.

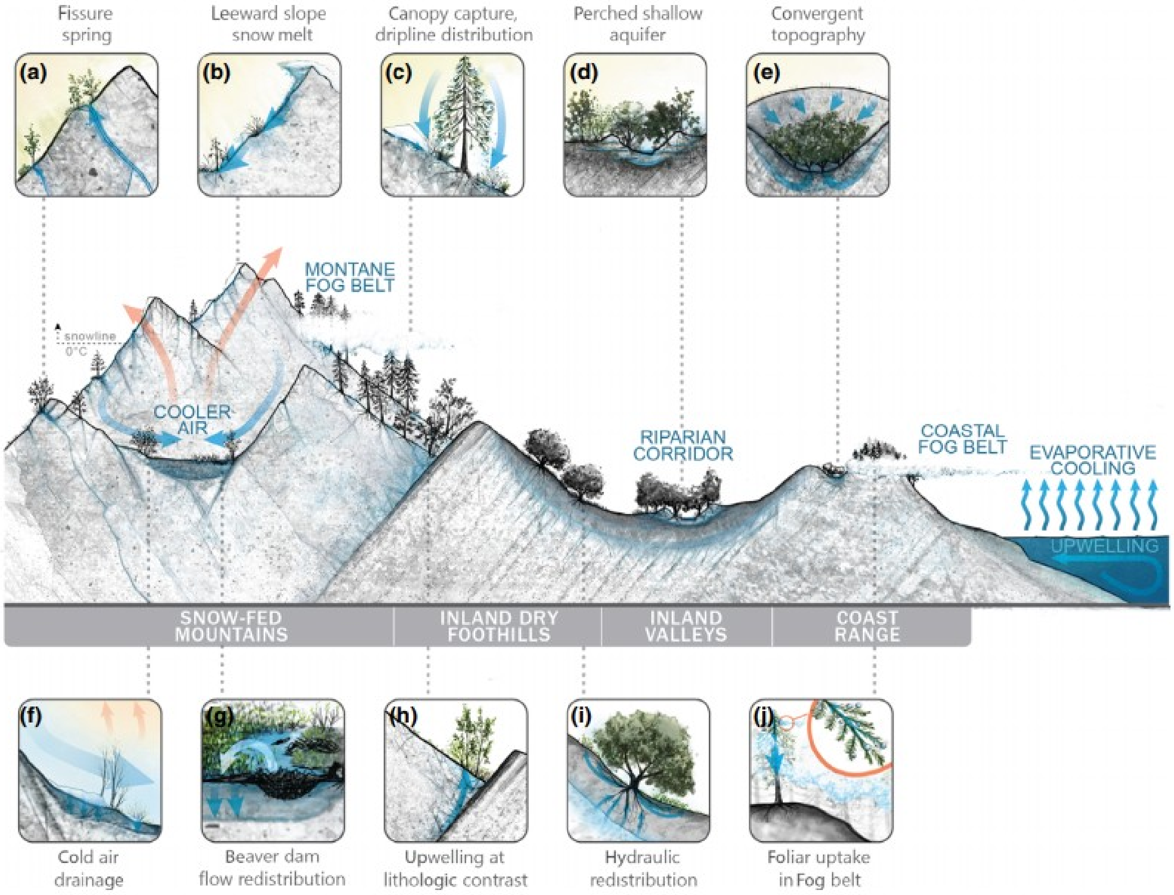

Fig. 3 Illustration of hydrologic processes and landscape features associated with potential mesic microrefugia. See discussion of hydrologic processes and different types of refugia below.

Table 1 Features associated with potential hydrologic refugia. The response times indicated are based on the range of timescales presented by Blöschl & Sivapalan (1995).

Landscape or ecological feature		Hydrologic response time scales	Sensitivity to local climate change
Subsurface water			
Shallow/perched aquifer			
Abiotic – local precip. dependent (Fig. 3, D, E&H)	Drainages and channels Topographic convergence/ break in slope Permeability contrasts: Aquicludes, Aquitards, Clay/caliche lenses, Permafrost, Soil/ regolith/bedrock transitions	Days – Years Months – Decades Months – Decades	Medium – High *Likely to support relative refugia* Climate-independent topographic / geologic mechanisms concentrate water resources: water resource availability depends on local precipitation and evaporation (storage in aquifer slows responses to local climate change)
Abiotic – Non-local precip. dependent (Figure 3, D)	Riparian areas Floodplains, wetlands	Days – Years	Low-Medium *Likely to support stable and relative refugia* Water availability *may* be nonlocal (for riparian zones, floodplains and wetlands associated with high stream order)
Biotic (Fig. 3, G&I)	Deep rooting systems – hydraulic redistribution Beaver dams Rodent mound/pool complexes	Hours – Decades Years – Decades Years – Decades	High *Likely to support transient refugia* Species may be climatically sensitive; water resource availability depends on local climate
Deep groundwater			
Abiotic (Fig. 3, A&H)	Fractures/Faults Lithologic contrasts Seeps/Springs/Discharge sites	Months – Centuries	Low *Likely to support stable refugia* Separation of recharge and discharge reduces sensitivity to *local* climate; response timescales increase with increasing scale of aquifer and decreasing permeability of aquifer substrate; geologic features independent of climate
Spatially variable water inputs (throughfall, stemflow, runoff and infiltration)			
Abiotic	Rocky outcrops/soil texture contrasts	Months – Centuries	Medium *Likely to support relative refugia* Rock and soil type independent of climate; sensitive to local rainfall
Biotic (Fig. 3, C)	Canopy structure – precipitation capture and redistribution Infiltration capacity contrasts (vegetation or soil crust induced)	Hours – Years	High *Likely to support transient refugia* Biotic processes climatically dependent; sensitive to local rainfall
Occult precipitation			
Abiotic (Fig. 3, F&J)	Coastal proximity/orientation Fog belts, high elevation areas of fog concentration Canyons and valleys – cold air and fog drainage/shading (dew)	Hours – Months	Medium *Likely to support stable refugia* Conflicting predictions about coastal fog response to climate change; upwelling relatively insensitive to climate; cloud ceilings rising

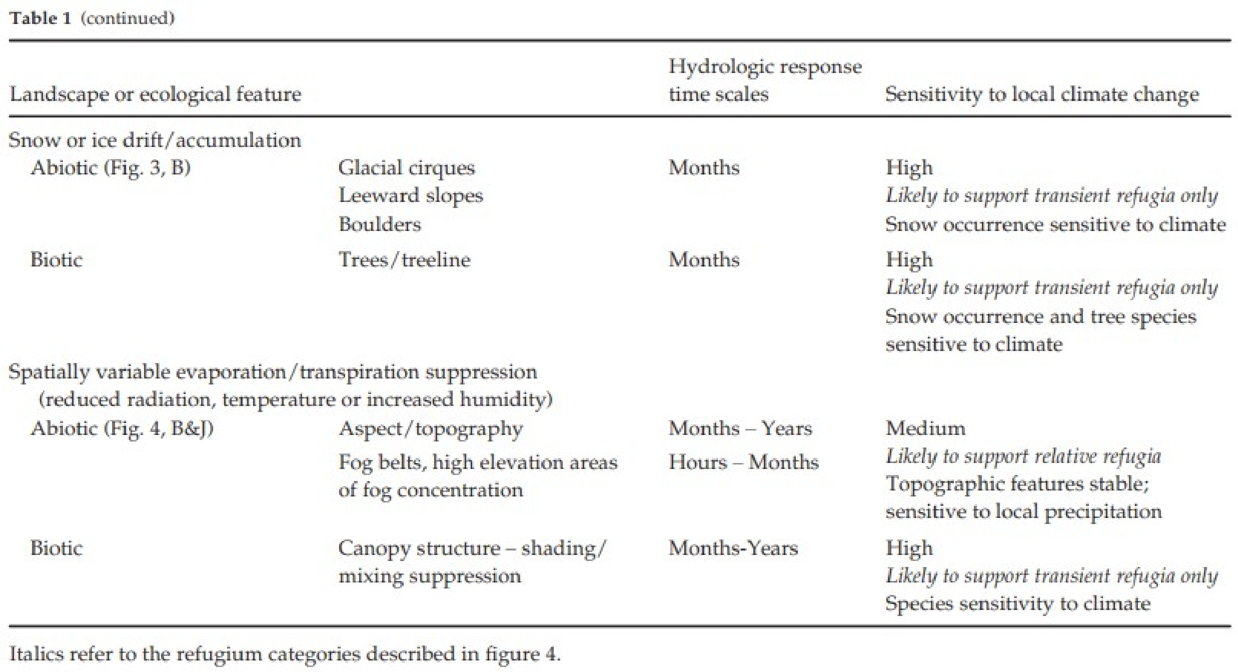

Table 1 (continued)

Landscape or ecological feature		Hydrologic response time scales	Sensitivity to local climate change
Snow or ice drift/accumulation			
Abiotic (Fig. 3, B)	Glacial cirques Leeward slopes Boulders	Months	High *Likely to support transient refugia only* Snow occurrence sensitive to climate
Biotic	Trees/treeline	Months	High *Likely to support transient refugia only* Snow occurrence and tree species sensitive to climate
Spatially variable evaporation/transpiration suppression (reduced radiation, temperature or increased humidity)			
Abiotic (Fig. 4, B&J)	Aspect/topography	Months – Years	Medium *Likely to support relative refugia* Topographic features stable; sensitive to local precipitation
	Fog belts, high elevation areas of fog concentration	Hours – Months	
Biotic	Canopy structure – shading/mixing suppression	Months-Years	High *Likely to support transient refugia only* Species sensitivity to climate

Italics refer to the refugium categories described in figure 4.

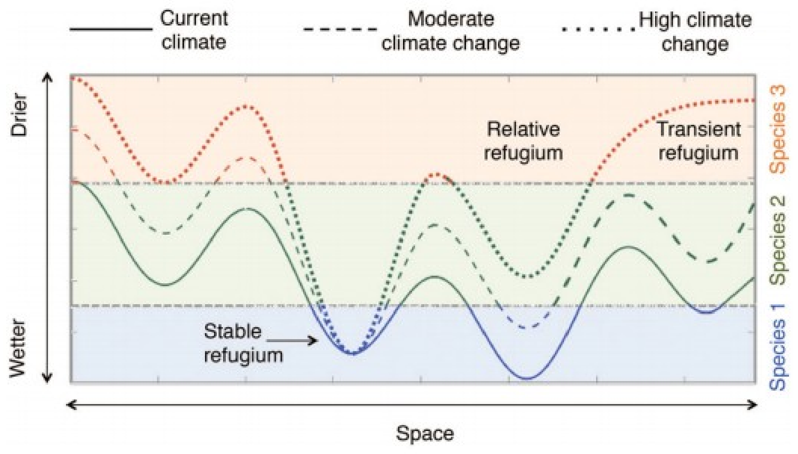

Fig. 4 Schematic illustration of stable, relative, and transient refugia generated as a climate moves from contemporary conditions (solid lines) through a period of moderate warming and drying (dashed line) to a significantly hotter and drier state (dotted line). Stable refugia maintain wet conditions suitable for mesophytic species such as 'Species 1' under all scenarios. Relative refugia remain wet compared with the remainder of the landscape for all climate scenarios, but may dry sufficiently that mesophytic species are replaced by more xerophytic types (Species 2) under warming scenarios. The remainder of the landscape becomes suitable primarily for truly xeric species (Species 3) as strong warming and drying continues. Temporary persistence of mesophytic species in the warming climate may arise in transient refugia, although these refugia may only exist as long as a water store remains in the landscape, and as such may disappear if dry conditions persist. A detailed discussion of community interactions in stable, relative, and transient refugia is provided below.

Subsurface fluxes: groundwater flow and hydraulic redistribution

Fluxes in the subsurface environment are dominated by saturated groundwater flow in deep or shallow aquifers. Shallow groundwater is accessible to plants over 7–17% of the globe (Fan *et al*., 2013) and is used by vegetation in a wide range of ecosystems (Canadell *et al*., 1996). Although salt or oxygen stress can be increased by saturated soils (Gill & Jackson, 2000; Jackson *et al*., 2000; Rengasamy *et al*., 2003;

Araya *et al*., 2011), access to groundwater is typically beneficial to plants. Access can be enhanced by hydraulic redistribution – where roots act as conduits between soil layers – allowing deep-rooted plants to supply water to shallow roots and shallow-rooted nearby individuals (Peñuelas & Filella, 2003). Hydraulic redistribution is ubiquitous, especially in seasonally dry ecosystems (Dawson, 1993; Caldwell *et al*., 1998), and plays a significant role in sustaining vegetation through droughts (Bauerle *et al*., 2008), supporting ecosystem transpiration (Lee *et al*., 2005) and maintaining dominance of mesophytic communities in seasonally dry regions (Wang *et al*., 2011). Analogously, laterally spreading root systems, common in clonal individuals, allow water transport across the radially spreading plants and facilitate the colonization of dry sites, supplied by water transported from distant (~10+ m), wetter locations (Barbier *et al*., 2008).

Biotic agents can alter groundwater availability by changing the physical environment (Reed & Amundson, 2007; Cramer & Barger, 2014). Pocket gophers (*Geomys* spp.) shape surface microtopography by burrowing (Reichman & Seabloom, 2002), creating a mound-pool landscape with dry mounds surrounded by seasonally flooded depressions (Cox & Gakahu, 1986; Cox & Roig, 1986; Lovegrove & Siegfried, 1986; Cox & Scheffer, 1991; Horwath & Johnson, 2006). Inundation gradients created by the mound-pool complex define local plant distributions (Bauder, 1987, 2005; Barbour *et al*., 2005).

Groundwater may be present near the soil surface due to impeded vertical drainage, due to rock, clay, hydrophobic soil, or permafrost layers, causing perched aquifers or surface lakes to form (Shannon & Brezonik, 1972; Dingman, 1994; Woo *et al*., 2008) (also see Fig. 1a, Fig. 3 panel d). Groundwater may be forced toward the surface by obstructions to horizontal flow, so seeps and springs form upslope of the obstruction (Engel *et al*., 1987) (Fig. 3, panel h). Bedrock depressions or fractures can store additional water (compared with shallow or unfractured bedrock), enhancing plant water availability (Miller *et al*., 2010). Such idiosyncratic and localized processes support extensive plant groundwater use but are difficult to predict at larger scales (Lewis & Burgy, 1964; Dawson, 1993; Thorburn *et al*., 1993; Zencich *et al*., 2002; Gries *et al*., 2003; Hultine *et al*., 2003; Peñuelas & Filella, 2003; Chimner & Cooper, 2004; Jewett *et al*., 2004; Kurz-Besson *et al*., 2006; Bleby *et al*., 2010; Miller *et al*., 2010; Doody & Benyon, 2011; Jobbágy *et al*., 2011).

The distribution and surface expression of groundwater are often topographically dictated. For instance, the widely used *topographic wetness index* (TWI, the log of the ratio of upslope catchment area to local land surface slope gradient) represents the balance between the shallow groundwater volumes routed to a given location, and the rate of drainage from that location (Beven & Kirkby, 1979). TWI predicts groundwater expression (as channels, seeps, or riparian water tables) in convergent topographies with large upslope catchment areas (Fig. 3, panel e), and at the toes of hillslopes where slope gradients drop dramatically (Eamus & Froend, 2006); at a landscape scale, variation in TWI can be a strong predictor of vegetation density (Deng *et al*., 2007; Hwang *et al*., 2011).

Surface water bodies such as rivers or lakes can also supply groundwater to plants. Vegetation lines desert rivers and oases (Snyder & Williams, 2000; Lamontagne *et al*., 2005; O'Grady *et al*., 2006a; Butler *et al*., 2007; Lautz, 2008; Scott *et al*., 2008), supported by groundwater seeping from the surface water body (Fig. 3 panel d). Increased volumes and residence times of surface water in the landscape tend to increase the influence of the surface water bodies on surrounding plant communities. Damming of streams by beavers (*Castor* spp., Fig. 3 panel g) may sustain high water tables and wetlands (Baker *et al*., 2005; Westbrook *et al*., 2006, 2011; Wolf *et al*., 2007), even in relatively dry climates (Westbrook *et al*., 2006).

The groundwater processes discussed above all relate to shallow aquifers recharged directly by local precipitation, which are often responsive to climate [with hydraulic residence times of months to years (Blöschl & Sivapalan, 1995)]. These water stores are likely to be diminished by warming and drying conditions, while still representing wet sites on the landscape (Vörösmarty *et al*., 2000). Shallow groundwater is likely to be associated with relative hydrologic refugia. Conversely, deep and confined groundwater aquifers may contain ancient water (up to 10^6 years old), and be largely decoupled from local climatic fluctuations. Deep groundwater aquifers are often larger in extent than shallow aquifers and can connect geographically distinct recharge and discharge sites. Surface expression of deep groundwater in the form of seeps, springs, and desert oases, and their associated plant communities[(Faunt, 1997; Jobbágy *et al*., 2011), Fig. 3 panels a and h] may thus provide stable hydrologic refugia.

Water inputs and losses across the soil atmosphere boundary

A local increase in water entering the root zone, or a local reduction in evaporation and transpiration losses to the atmosphere can also form mesic microenvironments. In the atmosphere, rainfall, snowfall, and fog/dew occurrence vary through space, not only over large gradients (such as those induced by orographic rainfall), but also locally. For instance, higher wind speeds on ridges reduce precipitation volumes compared with adjacent valleys (Sevruk, 1997; Watson *et al*., 2008).

Small-scale changes in snow water inputs are reflected in the pattern of available meltwater and infiltration (Essery *et al*., 1999; Essery & Pomeroy, 2004; Barnett *et al*., 2005), influencing soil moisture (Billings & Bliss, 1959), individual plants’ water status and use (Thilenius, 1975; Sturm *et al*., 2001; Walker *et al*., 2001; Sugimoto *et al*., 2002; Wipf & Rixen, 2010), and community composition (Billings & Bliss, 1959; Edmonds *et al*., 2006; Helm, 1982; Walker *et al*., 1993; Wipf & Rixen, 2010, Fig. 3 panel b). Snow scouring and drifting cause snowpack to accumulate on the leeward side of ridges and vegetation (Sturm *et al*., 2001). Snowpack persists longer into the growing season on poleward-facing slopes (Green & Osborne, 1998; Osborne *et al*., 1998; Essery *et al*., 1999; Sturm *et al*., 2001; Essery & Pomeroy, 2004). Again, these spatial differences increase soil water during the growing season and support locally mesophytic vegetation (Walker *et al*., 2001). The persistence of rare mesic species during past interglacial warming periods in Central Europe is attributed to such locations (Jeník, 1959). Processes of snowfall variation, snow scour, and accumulation are largely independent of climatic warming and drying, although snowpack areas and snow volumes may be reduced. Thus, these processes could create both relative and stable hydrologic refugia.

Occult forms of precipitation (fog, mist, dew) can also be spatially localized. For example, fog interception and drip are concentrated on ridges, at low elevation (Whiteman *et al*., 2001) and at forest edges (Dawson, 1998; Ewing *et al*., 2009; Simonin *et al*., 2009); dew preferentially forms in cold air drainages ((Baier, 1966; Kidron, 1999, 2005; Pypker *et al*., 2007), Fig. 3 panel f) and wherever condensation surfaces are plentiful. Again, these patterns of input drive the pattern of soil moisture availability (Dawson, 1998), and plant water status over tremendously diverse climates (Lancaster *et al*., 1984; Dawson, 1998; Kappelle *et al*., 2004; Limm *et al*., 2009; Goldsmith *et al*., 2012, 2013; Hesse, 2012; Hiatt *et al*., 2012; Eller *et al*., 2013). Fog can increase water input to plants through direct foliar uptake of water (Limm *et al*., 2009), Fig. 3 panel j). Foliar water uptake relieves leaf-level water stress (Burgess & Dawson, 2004; Limm *et al*., 2009) and can result in sap flow reversals throughout the plant, even replenishing soil moisture reserves (Eller *et al*., 2013). Fog, mist, and clouds suppress transpiration from leaves and reduce evaporative losses by providing persistently dim, cool, and humid conditions (Barradas & Glez-Medellín, 1999). Fog cover reduces transpiration in cloud forests by 30% or more compared with nonfog conditions (Ritter *et al*., 2009; Goldsmith *et al*., 2012, 2013). Transpiration suppression by fog improved seedling recruitment in a California coastal grassland (Kennedy & Sousa, 2006), and is responsible for approximately one-third of the water balance of coast redwood (*Sequoia sempervirens*) (Burgess & Dawson, 2004). Dew can have similar effects (Duvdevani, 1964; Matimati, 2009, Hill *et al*. 2015). The combined effects of fog drip, leaf uptake, and transpiration suppression can sustain species through drought: in *Pinus muricata* forests, these processes reduced drought stress by 50%, and buffered against drought mortality (Fischer *et al*., 2009). Fog is essential to the persistence of coast redwoods throughout much of their range, and supports many plant communities in low rainfall environments (Corbin *et al*., 2005; Dawson, 1998; Hiatt *et al*., 2012; Lancaster *et al*., 1984). The sensitivity of fog/cloud/mist occurrence to shifting climatic conditions is likely to be variable: Cloud ceilings, for instance, are likely to rise, potentially reducing cloud forest ranges. Although the refugia created by clouds are likely to retain high levels of water availability and are thus ‘stable’ in the sense that absolute water availability is retained, the spatial extent of such stable refugia is likely to shrink to those elevations where frequent cloud cover persists. Coastal fog caused by upwelling of cold water may be more independent of local climate, potentially generating stable hydrologic refugia over a constant area in space.

Even when rain/snow/fog water input is uniform in space, canopy interception or surface runoff can concentrate (or dissipate) this water before it enters root zones. Canopy interception induces small-scale randomness in throughfall fluxes across the canopy (often concentrated at a canopy drip line, Fig. 3 panel c), and highly directed stemflow. Stemflow directs water fluxes toward the root zone (Levia & Frost, 2003, 2006; Johnson & Lehmann, 2006) and may disproportionately drive deep recharge. Arid plant species often exhibit particularly high proportions of stemflow (Martinez-Meza & Whitford, 1996).

Spatial variations in infiltration capacity may cause rapid spatial organization of water availability through ‘runoff–runon’ mechanisms (Ludwig & Tongway, 1995; Thompson *et al*., 2011). Runoff is generated on low infiltration capacity sites (e.g., crusted or rocky areas), flows downslope, and subsequently infiltrates in areas with high infiltration capacity [e.g., macroporous soils often associated with vegetation (Belnap, 2006; Thompson *et al*., 2010a; Trimble & Mendel, 1995)]. Runoff–runon mechanisms can enhance infiltration volumes by a factor of eight times compared with rainfall (Galle *et al*., 1999; Niemeyer *et al*., 2014). These mechanisms are often essential for the maintenance of vegetation in otherwise arid regions (Thompson *et al*., 2010b; Assouline *et al*., 2015). They are often biologically mediated, primarily through the formation of biological soil crusts (Belnap, 2006). In particular, ‘smooth’ microphytic crusts forming in arid deserts may reduce infiltration rates by a factor of 10 (Thompson *et al*., 2011), resulting in concentrated runoff formation (Belnap *et al*., 2001; Maestre *et al*., 2002). In cool deserts, microbiota can form ‘rugose’ microphytic crusts that add roughness to the desert surface, enhancing rainfall infiltration, increasing dew formation and capture, reducing evaporative losses, and promoting the formation of mesic microsites (Schulten, 1985; West, 1990; Baker *et al*., 2005; Belnap, 2006; Ram & Aaron, 2007; Liu *et al*., 2009; Su *et al*., 2009; Li *et al*., 2010; Warren, 2014). As an abiotic example, runoff from a large granite outcrop supplies water to a relict vegetation population of jarrah (*Eucalyptus marginata*) in Western Australia (Abbot, 1984). Although located 100s of kilometers beyond the species’ contemporary distribution, the runoff mechanism creates a stable hydrologic refugium in an otherwise arid landscape. Most redistribution mechanisms incorporate biotic processes however, making them vulnerable to changes in local climate. By creating a positive feedback in which water availability to plants depends on the extent and health of plant cover, runon–runoff mechanisms can place ecosystems at risk of threshold-like collapse if increased drought causes vegetation mortality – as this mortality undermines the mechanism sustaining the refugium (Kéfi *et al*., 2007a,b, 2011). Consequently, runon–runoff mechanisms will likely support transient hydrologic refugia.

Topography, particularly aspect, has well-known effects on temperature, humidity, and light, causing large differences in evaporation rates and annual energy balance that can impact tree transpiration. Most importantly, slopes that face the equator receive elevated solar radiation relative to pole-oriented slopes, increasing evaporative demand, and causing sharp differentiation in available water storage and water losses between different slope aspects, associated with differences in slope gradient, soil textural properties, and soil depths (Hanna *et al*., 1982; Stephenson, 1998; Geroy *et al*., 2011). Unsurprisingly, these physical variations also result in sharp differentiation in plant communities by aspect. More subtly, atmospheric mixing is weaker in valleys than on ridges, increasing valley humidity and reducing evapotranspiration rates (Mackay *et al*., 2002, 2007; Loranty *et al*., 2008). Vegetation canopies shade the land surface and impede gas transfer from land to atmosphere, generating distinct understory and canopy environments that depend strongly on canopy structure (Rambo & North, 2009; Ma *et al*., 2010). Old growth forests may buffer understory communities from the effects of regional warming (De Frenne *et al*., 2013; Stevens *et al*., 2015) and provide microrefugia (Olson *et al*., 2012). Biotically mediated low-evaporation environments are likely to be sensitive to local climate change, and perhaps more pressingly, to human pressures such as deforestation and land-use change (Hansen *et al*., 2013), suggesting forest conservation and management – already essential for direct conservation of species and their habitat – may also be important to protect the biophysical processes that support refugia, and the climatic resilience of forests and the moist microsites they contain. Conversely, topographic-based differences in evaporative demand are likely to persist. Topographic shading is thus a likely mechanism to form relative hydrologic refugia, which will respond to a regional drying and warming climate, while remaining more mesic than exposed or equatorially facing slopes (Gutiérrez-Jurado *et al*., 2013).

Intersecting physical processes

Multiple drivers of spatial variation in local water balances arise in real landscapes, and occur on top of temporal patterns of precipitation occurrence and evaporative demand. Figure 5 shows how the formation of perched water tables in the valley floors during the early growing season (Fig. 5 panel a) interacts with elevation controls on humidity and fog frequency (Fig. 5, panel b) to create strong ecological contrasts between the dense riparian woodlands in the valleys (Fig. 5 panel c) and open grasslands on the hillslopes (Fig. 5 panel d). Although the trend of increasing water availability at lower elevations is clear, many site-specific, idiosyncratic features in the landscape (such as variable bedrock depths and seismic faulting) influence local water availability in a less predictable fashion.

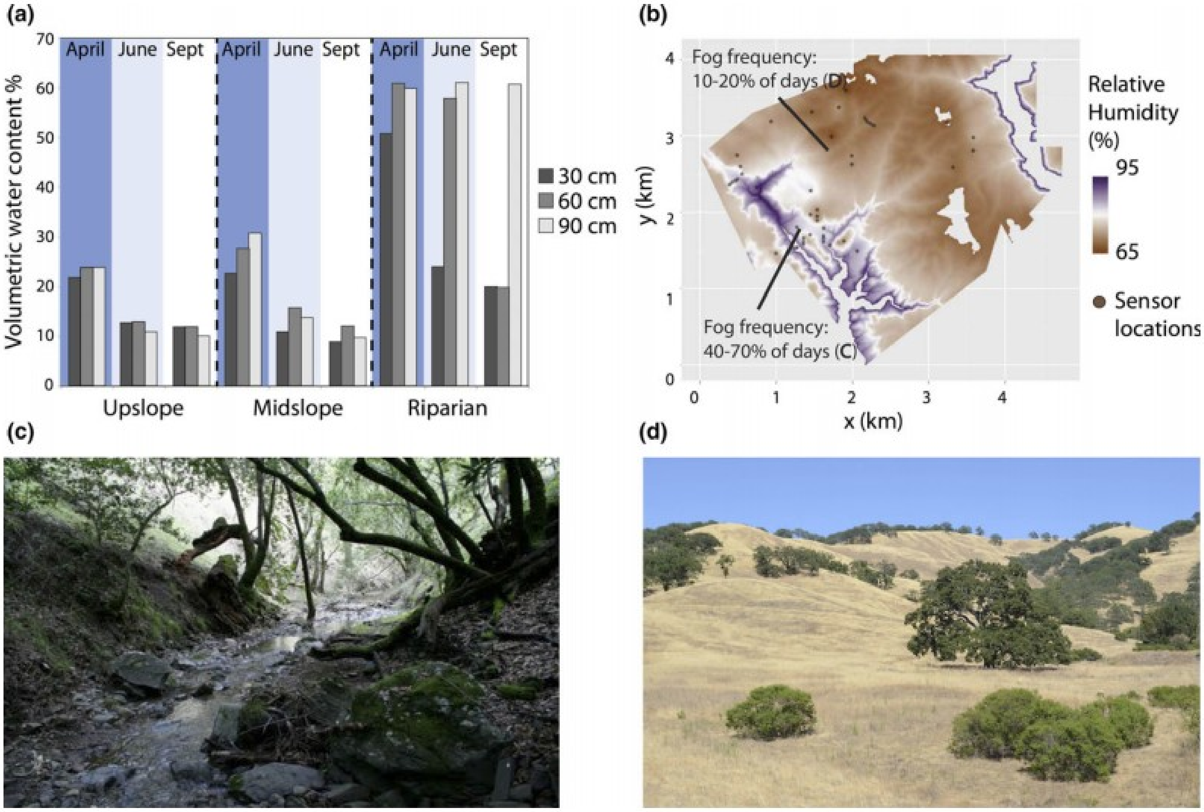

Fig. 5 Processes associated with the creation of mesic microenvironments at the Blue Oak Ranch Reserve in central California (oak savanna). (a) Late winter soil moisture forms a perched water table along hillslopes, receding during the summer, but sustaining wet conditions in riparian habitats. (b) In low-lying areas, fog occurs as often as 3 days out of 4, but less than once every 5 days on the ridges. Mean relative humidity (interpolated from a network of 30 sensors across the site) varies by 30% between the valley and ridge locations, indicating large differences in mean evaporative demand. (c) Low-lying areas support riparian forests, drawing on subsurface water and with relatively lower evaporative demands than the (d) ridge environments, which, with low water availability and high evaporative demand, support mostly annual grasses and little primary production during summer. Photo credit: Michael Hamilton.

Predicting the locations of hydrologic refugia

Elevated water availability at any site is sufficient to form a mesic microenvironment, but is not a sufficient criterion to claim that the site could act as a hydrologic refugium. This is because, as illustrated in Fig. 2, refugia must also meet biological requirements. For the mesic site to support a given plant species, the hydrologic characteristics of the site, including the quantity of water available, the form and location of this water, and the timing of its availability, must be compatible with the requirements of the species. The site must also be available for colonization or otherwise support the persistence of the species in the face of competitive, facilitative, and other biotic interactions with a changing community. A refugium must also protect the species from other threats associated with climate change, such as thermal stress or natural disturbances associated with fires (Wilkin *et al*., 2016) or floods.

Species-specific effects: moisture accessibility, synchrony, and complementarity

Plants adjust differently to the stresses and benefits conferred by particular local hydrologic and climatic regimes. These species-specific effects (Fig. 4) result in niche partitioning of space along aeration and dryness gradients (Dawson, 1990). They also result in the partitioning of water consumption among different species, and separation of recruitment patterns in time, as water supplies vary (Silvertown *et al*., 2015). These effects are referred to as *hydrologic niche segregation*. Different species' locations in the landscape separate along aeration/wetness axes, indicating that hydrologic niche requirements can structure plant communities through space (Silvertown *et al*., 1999, 2015). Compatibility between the characteristics of a species' hydrologic niche and the physical hydrology of a mesic site is essential for that site to provide a hydrologic refugium.

Morphological, physiological, phenological, and biochemical adaptations determine the hydrologic niche requirements of different species by dictating which water sources can be used, how each species uses them, and what trade-offs might be associated with such use. For example, deep root systems facilitate the uptake of subsurface water stores (Canadell *et al*., 1996; Oshun *et al*., 2016), and morphological and physiological adaptations of some leaves can enhance foliar uptake of water (Limm *et al*., 2009) or the efficiency of fog capture and drip (Burgess & Dawson, 2004; Limm *et al*., 2009; Ritter *et al*., 2009; Goldsmith *et al*., 2012). Individuals without these adaptive features may not be able to access, or efficiently exploit the additional water associated with the presence of groundwater or the occurrence of occult water sources like fog (Dawson, 1998). Use of this additional water, however, exposes plants to risks that would not be present in drier sites. For instance, deep root systems are likely to experience inundation and aeration stress (Jackson & Colmer, 2005), plants in riparian environments are exposed to disturbance during flood events (Muneepeerakul *et al*., 2007), and plants growing in fog belts could be exposed to an elevated risk of foliar disease due to persistent leaf wetness (Jones, 1986). For a mesic microenvironment to provide a refugium for a given species, the species' traits must allow for the exploitation of the benefits and tolerance of the costs of inhabiting that microenvironment.

The timing of moisture availability in the microenvironment must also be compatible with the needs of a target species. Plant water demands vary through time due to changes in leaf area (e.g., in deciduous species, Vico *et al*., 2014), the timing of germination (e.g., in annual species, Kemp, 1983), and changes in energy availability. For example, peaks in radiation lead to Northern Californian evergreen tree species maximizing water use during summer (Link *et al*., 2014), which is also the period of highest landscape-level climate water deficit in this mediterranean-type climate. A mesic microenvironment that sustained water supplies to trees during this period would be expected to have a strong influence on species persistence (Miller *et al*., 2010). Complementary timing of peak snow melt and peak radiation enables montane meadow plants to make use of meltwater resources (Godsey *et al*., 2014), which would not be as efficiently used if melt occurred earlier in the season. Plasticity in the phenology of peak water use, observed in some invasive grassland species (Wolkovich & Cleland, 2014), may enable species to adapt to a wider array of potential climate refugia by adjusting phenology so that peak water demands coincide with peak water availability.

On longer timescales, similar synchronies between plant water requirements and environmental water availability in refugia may enable plants to survive drought-vulnerable life stages (Liu *et al*., 2009). The ‘ecological ratchet’ theory (Jackson *et al*., 2009) argues that seedlings establish in narrower environmental windows compared with those in which adults persist. The availability of hydrologic refugia during a drought-vulnerable young life stage may thus impact the distribution of adult populations. Temporary hydrologic conditions, such as flooding, can raise the water table and create ephemeral regeneration refugia, allowing the roots of young life stages to initially reach and then follow the descending water table to its typical depth (Mahoney and Rood 1998), creating a long-term population-level effect from a temporary hydrologic condition. For example, *Populus* regeneration in the Taklamakan Desert occurs during rare flood events and is tied to high groundwater availability (Bruelheide *et al*., 2003; Gries *et al*., 2003).

Hydrologic refugia that overlap or complement thermal and fire refugia may be particularly important in drying, warming climates. Many of the features associated with mesic microenvironments (lower elevation, shading, fog) also are associated with cooler microclimates (Dobrowski, 2011) and fire refugia (Mackey *et al*., 2002, 2012; Wilkin *et al*., 2016), so such complementarity may be widespread. For example, in addition to providing mesic microenvironments, forested riparian areas (Dwire & Boone, 2003) and forests on northeast- and north-facing slopes (Taylor & Skinner, 2003; Alexander *et al*., 2006) may maintain lower fire frequency and severity relative to the surrounding landscape, and provide cool microclimates.

Community interactions

Species interactions and their response to changing climate and hydrology (Gilman *et al*., 2010; Blois *et al*., 2013; HilleRisLambers *et al*., 2013) will also influence the function of mesic sites as microrefugia. However, predicting specific trajectories of such interactions under climate change remains challenging. Studies that manipulated hydrologic conditions and examined the effects on community structure reveal complex transient conditions and intricate trophic interactions. For example, Suttle *et al*. (2007) found that increases in spring moisture availability in an experimental grassland initially favored growth of native plant species, but the increase of a nitrogen fixer increased soil nitrogen, leading to a subsequent increase in invasive plants. As species’ dispersal into an *ex situ* refugium outside their original distribution may create novel species interactions, including priority effects

(Moorcroft, 2006), ecological release (Tilman, 1994), and competitive suppression (Grime, 1973), capacity to predict community dynamics is limited. Dispersal processes themselves also can be climatically mediated (Thompson & Katul, 2013), so there is substantial uncertainty around which species may disperse into *ex situ* refugia and the impacts on species interactions.

Certain biotic interactions in mesic microenvironments are likely to intensify in a drying climate, and could provide important monitoring targets as part of efforts to anticipate hydrologic refugia. In systems where water is already a limiting resource, both facilitation and competitive interactions around water already exist and may influence community responses to drying in relative and stable microrefugia. In relative microrefugia, communities would be expected to shift in parallel along hydrologic niche axes, as individual species simultaneously track their hydrologic niches through space. With climatic drying, the most mesophytic species in the community would be expected to be extirpated first as the wettest conditions disappear, analogously to the frequently projected loss of mountain-top species with warming temperatures. Stable microrefugia, conversely, preserve the hydrologic niche for mesophytic species within the refugium. As the surrounding landscape dries, competitive interactions likely would become intensified as species tracked their hydrologic niches along hydrologic gradients toward the refugium, increasing competitive stress on species present in the mesic microenvironment. Species that previously partitioned water use among different moisture sources may converge on common sources, changing hydrologic niche partitioning within the community. Transient versions of this type of competitive resource use pattern occur between species that use complementary moisture sources during nondrought conditions, but compete for the same sources during drought (Schwinning, 2008), and would be strong indicators of where competitive interactions would intensify with climate change. Subject to more persistent drought, such competition could drive competitive exclusion.

Positive interactions between species could either amplify or constrain the role of a refugium. Shallow-rooted nurse plant associates and understory or juvenile plants that benefit from hydraulic redistribution or driplines may indirectly benefit from elevated water availability in refugia. In contrast, mutualistic relationships could also alter the suitability of refugia for partner species, as both species would need to be successful within the refugium (Joël *et al*., 2007; Memmott *et al*., 2007). Large asymmetries in each species' dispersal rate, physiological tolerances, or other ecological constraints might inhibit establishment of mutualist pairs within potential refugia (Schweiger *et al*., 2008; Dunn *et al*., 2009).

Identifying locations of potential refugia

As outlined above, identifying mesic microenvironments from physiographic, landscape, and vegetation features (such as aspect, TWI, or extant vegetation communities) is feasible in many cases. Further screening of these sites as potential hydrologic refugia could be based on an assessment of the relevance of the microenvironment to the ecology of a target species. Current or historical relationships between the target species and the potential refugial environment could provide further indications of the potential for wet sites to become refugia. Differential water stress across space and time and life stage, including site- or regional-scale dryness gradients, historical, annual, or seasonal variation in climate, or differential drought vulnerability of seedlings versus adults may be used as ‘proxies’ to anticipate a species’ response to future drier climates, and give insight into the potential role of hydrologic refugia.

Potential refugia should have a realistic association with the species’ hydrologic niche. For instance, obligate use of a high groundwater microenvironment by a phreatophytic species suggests that the microenvironment is already contributing to persistence of that species in the contemporary landscape. Facultative adjustment of water use, for example, shifts to groundwater utilization as soils become drier (Thomas & Sosebee, 1978; Flanagan *et al*., 1992; Thorburn *et al*., 1993; Chimner & Cooper, 2004; Lamontagne *et al*., 2005; O'Grady *et al*., 2006b; Oshun *et al*., 2016), as climate increases in aridity through space or time (Meinzner, 1927; Dawson & Pate, 1996; Zencich *et al*., 2002; Chimner & Cooper, 2004; O'Grady *et al*., 2006b; Nippert & Knapp, 2007a,b), or as groundwater availability increases (Yang *et al*., 2015), suggesting that groundwater availability might provide a hydrologic refugium under drying conditions.

Relict or remnant distributions of species, representing a subset of a more widespread historical distribution, may also indicate where and in what form future refugia from anthropogenic climate change could occur. For example, the current distribution of coast redwood (*Sequoia sempervirens)* is constrained within the ‘coastal fog belt’ between California and Oregon (Johnstone & Dawson, 2010). The species’ current distribution is considered to be relict of a much more extensive historical distribution associated with a more mesic and stable climate in western North America (Raven & Axelrod, 1978; Noss, 2000). Under the present mediterranean-type climate, fog appears to have provided the hydrologic conditions necessary for regional coast redwood persistence. Fog might be expected to play a similar role on local scales with projected climatic drying (Fernández *et al*., 2015).

Current biogeographic patterns under relatively dry conditions – for example, at the xeric edges of species distributions or during drought – also may be used as proxies for future drier climates, and give insight into the role of hydrologic refugia. For example, at the southern, drier areas of the coast redwood distribution, coast redwood communities are generally located in low, north-facing (Henson & Usner, 1993) or ocean-facing slopes, or the bottoms of small canyons within a matrix of xerophytic vegetation (Noss, 2000). Redwood occurrence mirrors the local spatial pattern of high fog accumulation, indicating that fog microenvironments play a critical role in redwood survival in relatively dry sites – and might be expected to do so more widely across the species distribution as regional drying progresses.

Proxy indicators also may include selective recruitment of drought-vulnerable life stages within mesic microenvironments. For example, at sites near the southern range of *Pinus muricata*, recruitment was limited to areas of high fog presence during severe drought (Fischer *et al*., 2009), suggesting that fog could act as a long-term microrefugium under a drier climate.

The proxies identified above can be combined to explore hydrologic refugia potential for selected species. We illustrate this approach in the next case study section, focusing on two closely related, geographically overlapping oaks, valley oak (*Quercus lobata)* and blue oak (*Quercus douglasii)*.

Case study of California oak woodlands

Valley and blue oak trees, endemic to the mediterranean-type climate region of the California Floristic Province, form the structural backbone of California deciduous oak woodlands. While projections for future precipitation are uncertain, rising temperatures will lead to drying of terrestrial ecosystems in California (Flint *et al*., 2013; Ackerly *et al*., 2015). The persistence of oak ecosystems under a drier regional climate will be closely tied to the viability of these keystone trees. Both species are projected to experience extensive distributional losses with climate change (Kueppers *et al*., 2005; Zavaleta *et al*., 2007). Recent extraordinary drought in California confirms the vulnerability of these oaks to a future drier climate, with dieback recorded in over 150 000 ha of blue oak and 700 ha of valley oak woodland in summer 2015 (US Forest Service, 2015). These oaks are ideal target species for exploring the role of hydrologic refugia in a drying environment. This case study synthesizes research on these oaks as relevant to hydrologic refugia, and explores challenges to enacting refugia-oriented conservation.

California oak ecosystems meet many of the criteria for anticipating hydrologic refugia with the frameworks described above. Their distributions cross wide regional climatic and local microenvironmental gradients, and experience strong seasonality and interannual variability in rainfall. With multicentury lifespans and relatively drought-sensitive young life stages (Mahall *et al*., 2009; Stahle *et al*., 2013), current tree stand structure creates a living record – local adult distributions record historical recruitment limitation and survival, and young life stage distributions provide comparative insights into current limitations on recruitment. This creates ideal conditions to observe the interactions between oak performance, climate and mesic microenvironments, and anticipate future hydrologic refugia. Given these oaks' deep-rooted morphology (within range of the groundwater table in many locations, Griffin, 1973; Lewis & Burgy, 1964), winter-deciduous habit, and the climate in which peak photosynthetic demand coincides with the protracted summer dry season, we would anticipate the following microenvironments to be particularly important for these species’ persistence in a drying climate: (i) areas where summer water sources supplement shallow soil moisture reserves that are largely depleted by late summer, and (ii) areas with water to support episodic recruitment. Across much of the species’ current range, groundwater appears to fulfill this role.

Even during nondrought years, these oaks use subsurface water during the dry season (Griffin, 1973; Miller *et al*., 2010), indicating that the species’ hydrologic niche requirements are compatible with groundwater refugia. In a blue oak woodland site, where groundwater depth averaged 8 m, Miller *et al*. (2010) attributed 80% of total summer evapotranspiration to the use of groundwater, after shallow soil moisture was depleted in spring.

In drought years, groundwater availability can impact adult performance. In a historical study of valley oak survival, the highest adult mortality was coincident with the period of years with the lowest groundwater levels (Brown & Davis, 1991). In response to California's 2014–2015 drought, we saw a significant correlation between blue oak adult canopy condition and utilization of stored winter precipitation [typically deep water, indicated by the stem water oxygen-18 and deuterium isotope composition (Ehleringer & Dawson, 1992)] in the xeric section of the species distribution (B.C. McLaughlin, unpublished results). Across a site-scale microenvironmental gradient, oaks that grew in areas with persistent groundwater availability appeared more likely to survive multiple years of drought. These findings may portend a future constriction of adult oaks at the xeric distributional edge around hydrologic refugia where groundwater remains high.

Valley oak adults did not experience a similar extent of dieback as blue oak during the 2014–15 drought (US Forest Service, 2015), potentially because the lowland and riparian distribution of these trees coincides with areas of higher groundwater availability (Pavlik, 1991). However, young valley oaks experience higher drought stress than proximate adults (Mahall *et al*., 2009), and spring recruits must survive a summer dry season as their roots race to tap the water table. In studies on the local spatial distribution and size class structure of blue and valley oak, young life stages associated with more mesic microclimates than adults in the thermally and drought-stressed margin of the species’ distributions (McLaughlin & Zavaleta, 2012; McLaughlin *et al*., 2014). Valley oak saplings recruited in closer proximity to groundwater sources than established adults in sites along this *‘trailing edge’*. No such effect arose in sites where valley oak range is projected to persist or expand (McLaughlin & Zavaleta, 2012). Similar patterns were found for blue oak seedlings (McLaughlin *et al*., 2014).

Based on these findings, near-surface groundwater would be expected to provide relative hydrologic refugia for oaks under projected climatic drying. New generations of oaks would form locally in microenvironments with high water tables accessible to young plants, for instance near springs, or along stream courses and flood plains. Adult oaks would also persist in these environments, and in stable hydrologic refugia formed by deeper groundwater.

Blue oak (and perhaps other deep-rooted Californian oak species) support hydraulic lift (Ishikawa & Bledsoe, 2000; Querejeta *et al*., 2007), likely influencing water availability to the surrounding plant community. They also influence population dynamics of consumers, such as the specialized predator/mutualist acorn woodpecker (*Melanerpes formicvorous*), through acorn masting (Hannon *et al*., 1987) and habitat provisioning. Hydrologic refugia for oaks are therefore likely to support indirect refugia for other species. As groundwater is likely to be critical as a hydrologic refugium for California oaks and the ecological communities, groundwater conservation and management within oak ecosystems should be a priority. Such management is challenged by ongoing and projected future land-use change in these systems from relatively low water use rangeland to irrigated agriculture and residential development (Cameron *et al*., 2014). These changing land-use patterns generally result in higher local groundwater withdrawals and reduced opportunity for recharge into deep soils (Byrd *et al*., 2015). Irrigated areas, however, may serve as anthropogenic hydrologic refugia for oaks, which frequently grow at the edges of cultivated lands. Efforts to encourage oak-friendly agricultural practices to maximize the conservation benefits of irrigated lands may become an important complement to groundwater conservation.

To date, there has been little groundwater mapping or monitoring in oak ecosystems. Widespread lack of knowledge about groundwater systems in these areas limits the identification of potential refugia and effective management of groundwater for conservation. Groundwater systems are likely to vary dramatically across the species distribution – for example, between the Sierra Nevada foothills, where mountain block recharge to groundwater (derived from snow melt at high elevations) supports 20% of streamflow (Conklin & Liu, 2008) and presumably local water tables, and the western extent of California's Central Valley where groundwater is primarily recharged by winter rain (Cain & Walkling, 2006; Parrish, 2011). Lithologies of oak systems are also highly variable, and different rock types that support oaks can provide strong contrasts in the rates of groundwater recharge and opportunities for groundwater storage (Booth *et al*., 2011). Given the complexity and variability of the hydrology of oak woodlands, hydrogeological investigations may be a necessary step to protect these ecosystems in a future dryer climate.

Conclusions

Species may evolve, acclimate, and/or move in response to climate change. For long-lived, sessile species with limited dispersal and long generation times, whose physiological tolerances do not change on timescales relevant to climate change, persistence within refugia may be the most important option for survival. Many climatic (temperature) refugia are anticipated to disappear in biologically relevant timeframes under most future climate change scenarios (Hannah *et al*., 2015). However, some forms of hydrologic refugia are decoupled from the regional climate or buffered in terms of how fast they will respond to changes in climate. Long-lived species may persist for centuries in such refugia. Such stable refugia would arguably provide the most significant protection from a biophysical standpoint; however, the features that create stability, for example, deep groundwater, are often highly attractive for human exploitation, which places this stabilizing function at risk (Wada *et al*., 2010). Relative and transient refugia would provide more temporary but important protection. They would temporarily maintain seed production and dispersal, maintenance of mutualist or facilitative relationships (MacNally *et al*., 2000), collectively ‘buying time’ for climate change conservation strategies (i.e., assisted migration) to mature. Relative and transient refugia may be particularly important for sustaining current populations at the ‘trailing edge’ of species distributions, prime targets for conservation given the likelihood that these subpopulations may be genetically distinct from the main distribution and relatively adapted to warmer/dryer climates (Hampe & Petit, 2005).

Protecting ‘topographic’ or ‘landscape’ diversity has emerged as a recent conservation strategy based on the theory that areas with high topographic diversity (i.e., mountainous areas) likely will provide high climate heterogeneity and climatic refugia (Davis & Shaw, 2001; Luoto & Heikkinen, 2008; Randin *et al*., 2009; Seo *et al*., 2009; Ackerly *et al*., 2010; Mosblech *et al*., 2011; Anderson *et al*., 2014). This strategy underrepresents lowland regions in conservation planning (Merenlender *et al*., 2004), often excluding locations of potential hydrologic refugia such as groundwater discharge, floodplains, and riparian areas. Similarly, accessible topographic approaches, such as TWI, may fail to account for the role of biota in modifying local micrenvironments. While remote identification of some ecosystem engineers (e.g., beavers, gophers, or soil crusting) is challenging, other effects, such as those induced by forest cover, could be readily mapped. Including hydrologic diversity, whether physically or biotically mediated, as well as topoclimatic drivers in conservation planning, would create a more balanced and comprehensive strategy for conservation and climate change refugia management (Morelli *et al*., 2016).

Complementing a focus on fine-scale topoclimates (Flint & Flint, 2012) and climatic microrefugia (Ashcroft, 2010; Dobrowski, 2011; Ashcroft *et al*., 2012; Keppel *et al*., 2012; Keppel & Wardell-Johnson, 2015), conservation planning needs to be informed by coupled hydrologic, climatic, and species distribution modeling efforts, and should motivate ongoing improvements in these modeling techniques. Ecohydrological modeling frameworks are available on a variety of scales to assess the interplay between plant water use and environmental water availability, with a variable climate (Tague & Band, 2004; Ivanov *et al*., 2008; Feng *et al*., 2017); however, groundwater resources represent a frontier for prediction. Despite new theories that may improve predictions of physical boundaries [e.g., depth to bedrock (Rempe & Dietrich, 2014)], and climate vulnerability assessments that use basic proxies for ground water availability (Klausmeyer *et al*., 2011), *de novo* predictions of local groundwater dynamics are challenging. As in the case of oak systems, described above, hydrogeologic investigations may need to become part of the repertoire of conservation biology.

Despite challenges associated with coupled predictions of climatic, hydrologic, and ecological responses to climate change, such joint predictions are essential. By ensuring that the roles of water in climate change projections are not limited to precipitation totals, but also address fog and dew, shallow and deep groundwater, meltwater and redistributed water resources, and other examples discussed here, we can improve the identification of refugia. In doing so, we will improve estimations of species distributional shifts and identify critical opportunities for conservation in the face of rapid climate change.

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