



## Oases of the future? Springs as potential hydrologic refugia in drying climates

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### Abstract

Climate-change predictions in some water-limited regions, such as the southwestern US and central Australia, fore-cast increasing aridity and longer, hotter, and more frequent drought events (Chiew et al. 2011; Ahmadalipour et al. 2017). These projections and recent severe droughts have increasingly motivated efforts to find and conserve ecohydrologic refugia: that is, mesic microenvironments that are relatively buffered from climate change (McLaughlin et al. 2017). Some groundwater systems provide such buffering via water storage in deep aquifers for centuries or millennia, slow responses to precipitation changes, and relative protection from evapotranspiration (Cuthbert and Ashley 2014; Davis et al. 2017).

Springs are promising candidates as ecohydrologic refugia, making them increasingly important to freshwater and terrestrial biodiversity conservation in landscapes experiencing increasing aridification (Morelli et al. 2016; McLaughlin et al. 2017). However, even neighboring springs can respond idiosyncratically to climate signals, suggesting variable capacity to function as long-term hydrologic refugia (Weissinger et al. 2016; Cartwright and Johnson 2018). Moreover, many aquifers are threatened by groundwater withdrawals and some may be vulnerable to such changes in climate as snow-to-rain transitions in recharge zones (Taylor et al. 2013). Here, we discuss the importance of springs to regional and global biodiversity and their role as paleorefugia during previous climatic changes. We present a framework for integrating evidence from diverse disciplines to identify springs with the potential to provide future ecohydrologic refugia; to enhance inventory, monitoring, conservation, and restoration of springs; and to support adaptation of natural communities to changing environmental conditions.

### Springs as drought refugia and keystone ecosystems

Many springs serve as natural oases: important localized sources of surface water and soil moisture in water-limited regions (Figure 1). Despite their limited spatial extent, springs function as keystone ecosystems, exerting considerable ecological influence over disproportionately large geographic areas (Perla and Stevens 2008; Davis et al. 2017). This influence is partially because springs often act as present-day ecohydrologic refugia in dry landscapes by providing consistent resources (eg water, food, shade), a role that is especially important during droughts. Springs therefore provide ecological refugia over relatively short timescales (days to decades; ie “refuges” sensu Keppel et al. 2012). For example, ponderosa pines (*Pinus ponderosa*) near springs showed reduced drought sensitivity compared to those farther away (Fuchs et al. 2019), and evidence from East Africa suggests that springs provided drought refugia at key points in human evolution (Cuthbert and Ashley 2014).

The importance of springs to biodiversity stems from at least two well-documented ecological phenomena (Figure 2). The first is the occurrence of spring-obligate endemic taxa that are physically confined to spring-fed aquatic, wetland, or riparian habitats (Box et al. 2008; Cantonati et al. 2012; Davis et al. 2017). Such taxa include plants; fish and other vertebrates; and crustaceans, mollusks, insects, and other invertebrates (WebTable 1). Many spring-associated taxa are short-range endemics with naturally small distributions (ie <100 m<sup>2</sup>), and are threatened or endangered based on national or international criteria (Cantonati et al. 2012; Davis et al. 2017). Second, springs provide important and regionally scarce resources to wide-ranging animal species, such as birds and large mammals (Kodric-Brown and Brown 2007; Palacio-Núñez et al. 2007; Davis et al. 2017) and may extend the geographic ranges of some species into arid landscapes (Antos and Dann 2014).

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