



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

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Natural springs in water-limited landscapes are biodiversity hotspots and keystone ecosystems that have a disproportionate influence on surrounding landscapes despite their usually small size. Some springs served as evolutionary refugia during previous climate drying, supporting relict species in isolated habitats. Understanding whether springs will provide hydrologic refugia from future climate change is important to biodiversity conservation but is complicated by hydrologic variability among springs, data limitations, and multiple non-climate threats to groundwater-dependent ecosystems. We present a conceptual framework for categorizing springs as potentially stable, relative, or transient hydrologic refugia in a drying climate. Clues about the refugial capacity of springs can be assembled from various approaches, including citizen-science-powered ecohydrologic monitoring, remote sensing, landowner interviews, and environmental tracer analysis. Managers can integrate multiple lines of evidence to predict which springs may become future refugia for species of concern, strengthening the long-term effectiveness of their conservation and restoration, and informing climate adaptation for terrestrial and freshwater species.

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Climate-change predictions in some water-limited regions, such as the southwestern US and central Australia, forecast 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.

In a nutshell:

- Springs are biodiversity hotspots that supported species persistence during previous climatic changes
- Some springs may provide stable hydrologic refugia from future climate drying, becoming increasingly important to groundwater-dependent species, while other springs may be relative or transient refugia, undergoing major ecological shifts or eventual disappearance
- Identifying and categorizing refugial springs is challenging because of limited data and ongoing non-climate-related threats; however, interdisciplinary studies provide clues to the refugial potential of springs
- Consideration of the diverse responses of springs to climate change will improve the long-term effectiveness of their conservation and restoration

■ 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

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Figure 1. Springs support a highly diverse set of ecosystems in water-limited landscapes globally, including (a) spring pools; (b) hanging gardens; (c) stream and riparian ecosystems; and (d) spring-fed wetlands, such as fens.

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 m²), and are threatened or endangered based on national or interna-

tional 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).

■ Springs as evolutionary paleorefugia

Substantial evidence indicates that – in addition to providing short-term ecological refugia – springs functioned as paleorefugia (ie evolutionary refugia; *sensu* Keppel *et al.* 2012) on multiple continents over millennia (Sada and Pohlmann 2004; Davis *et al.* 2013; Murphy *et al.* 2015). Biogeographic relicts are species descended from once widespread taxa, whose habitats contracted over time due to environmental changes constraining present-day distributions (Habel *et al.* 2010). From a phylogeographic perspective, the presence of relict and narrowly endemic taxa are considered hallmark traits of climate refugia (Keppel *et al.* 2012; Davis *et al.* 2013). During periods of climate drying, desertification likely shrank the regional extent of aquatic and wetland habitats, as streams and other surface-water bodies transitioned from perennial to ephemeral



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Figure 2. Springs are hotspots of biodiversity, supporting (a) groundwater-dependent endemic fish (eg Salt Creek pupfish, *Cyprinodon salinus*); (b) plants (eg spring-loving centaury, *Zeltnera namophila*); and (c) invertebrates (eg New Mexico hot spring snail, *Pyrgulopsis thermalis*). Springs are also critically important water sources for terrestrial animals in water-limited landscapes, including (d) the American black bear (*Ursus americanus*).

and from ephemeral to dry. Over time, springs and other surface expressions of groundwater became the primary remaining sources of habitat for the evolutionary lineages of formerly widespread aquatic and wetland taxa (Perez *et al.* 2005; Box *et al.* 2008; Murphy *et al.* 2012).

As paleoreugia, some springs provided localized environmental stability (ie wetness and temperature decoupled from the changing regional climate), shaping the evolutionary trajectories of some lineages and creating “museums of biodiversity” (Murphy *et al.* 2015). Regional patterns of endemism have been linked to macroclimate stability (Keppel *et al.* 2012; Harrison and Noss 2017). Similarly, concentrations of endemic plants, invertebrates, fish, and other vertebrates in springs are related to localized environmental stability (Figure 2; WebTable 1; Murphy *et al.* 2012; Davis *et al.* 2013; Fattorini *et al.* 2016). This relationship is supported by the co-occurrence of multiple endemic species with highly specialized habitat requirements in springs with relatively stable hydrologic and thermal conditions (Erman 2004; Fattorini *et al.* 2016; Rossini *et al.* 2017).

The role of springs as paleoreugia hints at their potential as future ecohydrologic refugia (Davis *et al.* 2013; Cartwright and

Johnson 2018). However, refugia from present-day anthropogenic climate change will not necessarily be spatially or functionally congruent with paleoreugia because of differences in the nature and rate of climate change, and landscape differences such as habitat fragmentation (Keppel *et al.* 2015; Mokany *et al.* 2017). Landscape features that function as both paleoreugia and future refugia are likely to be critically important for biodiversity conservation (Mokany *et al.* 2017). Also, although springs harboring endemic and relict taxa exist throughout a variety of humid regions globally, we anticipate that springs in water-limited regions hold particular importance as potential hydrologic refugia. Conservation of groundwater-dependent biodiversity in these regions may be strengthened by identifying, protecting, and restoring the subsets of springs that are most likely to maintain stable ecohydrologic conditions in these regions.

■ Identifying and classifying future hydrologic refugia

As climates dry in certain parts of the world, we anticipate considerable variability in the ecohydrologic responses of

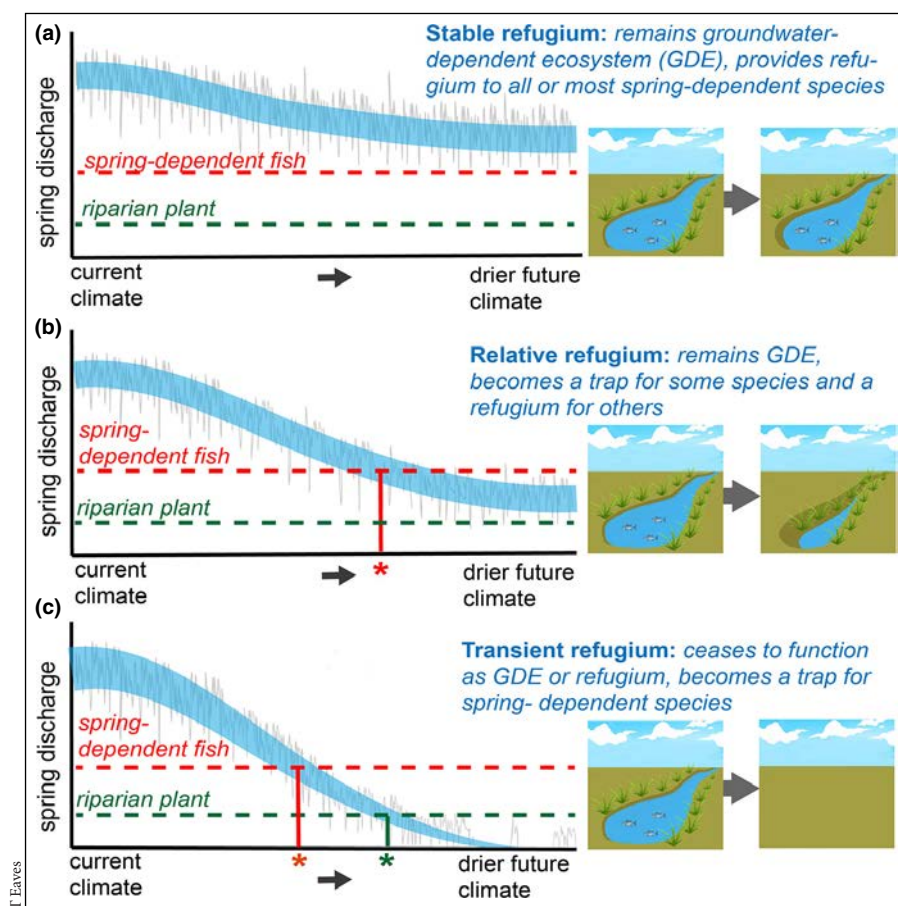


Figure 3. Conceptual model of spring discharge responses to climate drying. (a) Discharge from springs supporting stable hydrologic refugia may decrease slightly over time but does not fall below critical ecohydrologic thresholds for most spring-dependent species (illustrated by hypothetical fish and riparian plant species). (b) In relative refugia, discharge crosses thresholds for some species but not others (asterisks represent stages of climate change at which species experience extirpation). (c) Transient refugia are springs that eventually dry entirely and are sites of extirpation or extinction for all spring-dependent species at various points in time.

many springs (Weissinger *et al.* 2016). Subsets of springs are likely to become “oases of the future”, providing the kinds of hydrologic refugia needed to maintain groundwater-dependent biodiversity in the coming decades. McLaughlin *et al.* (2017) identified three distinct types of hydrologic refugia – stable, relative, and transient – based on different ecohydrologic responses to climate change. We adapted this framework to examine changing spring discharge (ie the rate of groundwater flow from a given spring) relative to critical ecohydrologic thresholds (Figure 3). Examples of situations in which spring discharge crosses species- and habitat-specific ecohydrological thresholds could include: (1) transitions from surface water (perennial spring-brooks and pools) to zones of saturated soil without inundation; (2) shifts in seasonal timing of water availability (eg perennial springs that become seasonally intermittent); and (3) reductions in the size or connectivity of spring-fed wetlands and riparian zones below thresholds required for viable populations.

Important water-quality parameters related to discharge may also be subject to ecological thresholds. These include water temperatures rising beyond species’ thermal limits, or changes in dissolved oxygen, salinity, or pH that turn springs into unsuitable habitat (Morrison *et al.* 2013; Jyvasjarvi *et al.* 2015). The concepts depicted in Figure 3 can be adapted to any variable that defines habitat viability in spring-dependent ecosystems. Dewatering experiments have shown that, for some springs, even small reductions in discharge produce substantial changes in habitat quality and quantity (Morrison *et al.* 2013), suggesting that ecohydrologic thresholds may vary not only among species but also between sites, depending on spring geomorphology, soil conditions, and ambient temperature. In some cases, reduced discharge might benefit some species; for instance, aquatic invertebrates in spring-brooks may experience reduced mortality if fish predation declines due to hydrologic disconnection between the spring and nearby streams.

Stable refugia

Springs that are stable ecohydrologic refugia provide relatively constant environmental conditions despite regional climate drying (Figure 3a; McLaughlin *et al.* 2017). Spring discharge may vary somewhat over short timescales (eg seasonally), and the typical discharge range may decrease slightly, but critically important ecohydrologic thresholds are not crossed. For example, a spring pool might sustain a modest reduction in size, but as long as the pool persists and water-quality parameters remain relatively constant, the spring can provide a stable ecohydrologic refugium. In a drying climate, such settings may provide the only remaining habitat for obligate aquatic spring endemics as other nearby springs become desiccated. For wide-ranging birds and mammals that rely on springs for key stopover resources, stable spring refugia will likely be sites of increasing competitive stress as more individuals congregate at fewer remaining oases (Cuthbert and Ashley 2014; McLaughlin *et al.* 2017). Springs with characteristics indicating their potential as stable refugia would be high priorities for conservation and restoration. Springs that maintain stable year-round flow are likely to be of prime ecological importance; however, some currently intermittent springs could also function as stable refugia if they maintain relatively constant seasonal timing and magnitude of flow under future climate, and do not cross critical ecohydrologic thresholds for species that depend on them.

Relative refugia

Springs that function as relative refugia will continue to be relatively wet sites in otherwise dry landscapes and will continue to be classified as groundwater-dependent ecosystems. However, as climate drying progresses, their typical discharge range will eventually fall below critical ecohydrologic thresholds for some spring-dependent species, causing profound and irreversible biodiversity losses and ecosystem changes. For example, sufficient reduction in discharge will transform a spring pool into a mesic depression supported by near-surface groundwater. This site may provide an ecohydrologic refugium for certain wetland plants that colonize moist soil as the pool disappears, maintaining viable populations in an increasingly arid climate. However, the same disappearing pool will become a site of local extinction (ie extirpation) for obligate aquatic species (Bogan and Lytle 2011). Springs that transition from year-round flow to seasonally intermittent flow may also function as relative refugia. In general, springs providing relative refugia are expected to provide temporary refugia to a limited suite of species whose ecohydrologic niches are maintained in the changing environmental conditions (McLaughlin *et al.* 2017). Such springs may become sites of considerable ecological change (Bogan and Lytle 2011) and priorities for conservation, restoration, and long-term monitoring. These springs may play a critical role in buying time for terrestrial wildlife to adapt to changing climate conditions and may extend population longevity for some spring-dependent species, creating opportunities for them to be rescued from extinction and relocated to alternative habitats.

Transient refugia

Springs that eventually run dry will provide transient ecohydrologic refugia. With sufficient climate drying, these sites will cease to qualify as groundwater-dependent ecosystems, will be associated with the extirpation of all groundwater-dependent species, and in some cases may be sites of extinction for rare, range-limited species, analogous to documented cases of springsnail (*Pyrgulopsis* spp) extirpations and extinctions at springs that were dewatered by groundwater extraction and surface flow diversions (Hershler *et al.* 2014). Transient refugia may be relatively low priorities for conservation and restoration investment, but they may provide important temporary habitat for “holdout” populations (*sensu* Hannah *et al.* 2014) or – for species with high mobility or dispersal capacity – could serve as temporary “stepping stones”, facilitating range shifts. Scientific understanding of important processes (eg ecosystem collapse) can be improved by long-term monitoring at such sites.

Data sources and methods for identifying stable hydrologic refugia

Predicting ecohydrologic change in springs requires integration of multiple lines of evidence from a number of disciplines (Figure 4; WebTable 2). Present-day characteristics

of springs can be used to infer their potential to provide stable hydrologic refugia. For example, long groundwater-residence times are associated with hydrologic and thermal stability through time and muted responses to climatic warming and drying (Jyvasjarvi *et al.* 2015; Solder *et al.* 2016). Importantly, present-day discharge alone does not guarantee refugial capacity, because many springs with comparatively large discharge are karstic (ie discharging from large conduits or caves in carbonate rock), with short flow paths and rapid recharge, suggesting potentially strong climate-change impacts.

Climatic, edaphic (soil-related), geologic, and topographic characteristics – at broad scales for recharge zones and at microscales for discharge sites – are likely to shape spring ecohydrology and help identify stable refugia. Bedrock permeability is an important regulator of recharge rates and groundwater transit time to springs. Large recharge zones allow for mixing of groundwater from different sources. Recharge zones with slower climate-change velocities (eg slower evapotranspiration increases) may promote recharge stability over time. In water-limited landscapes globally, ephemeral streams and lakes are focal areas that concentrate recharge (Scanlon *et al.* 2006). Compared to low-elevation deserts, mountainous recharge areas generally provide greater overall recharge with more infiltration derived from snowmelt, supplying “water subsidies” to adjacent lowland springs (Jobbágy *et al.* 2011). High-elevation recharge zones that are projected to maintain snowpack may be more effective in buffering groundwater from climate change than recharge zones characterized by snow-to-rain transitions. In some high-gradient groundwater systems, elevation differences between recharge zones and spring sites (ie hydraulic head) may also buffer against short-term drought impacts on spring discharge. Where such recharge zones can be identified, they may indicate springs that are potentially stable refugia. Moreover, springs’ microclimates – as related to elevation, aspect, and geomorphic setting – can maintain locally cooler temperatures and reduced evapotranspiration, which facilitate the persistence of rare species (Morelli *et al.* 2016; Weissinger *et al.* 2016; McLaughlin *et al.* 2017).

Responses of springs to past climate fluctuations can provide insights about possible impacts of future climate change (Weissinger *et al.* 2016; Cartwright and Johnson 2018). Where repeated discharge or water-quality measurements exist under a range of climate conditions (eg before, during, and after major droughts), past hydrologic stability may suggest future refugial potential. Such data are commonly lacking, but time-series analysis of remotely sensed spring-dependent vegetation can allow inferences about hydrologic history (Cartwright and Johnson 2018). Examination of spring-dependent species can also provide indicators of a long history of environmental stability. Such indicators include a rich diversity of dispersal-limited endemic and relict taxa (Erman 2004; Blinn 2008; Rossini *et al.* 2017) and population genetic indicators for obli-

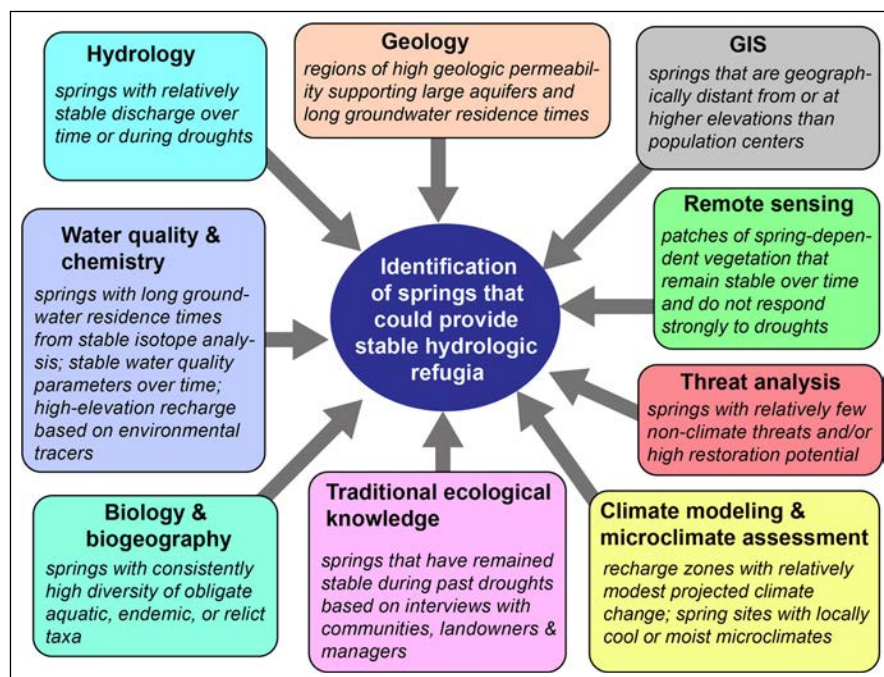


Figure 4. Identifying and classifying the refugial potential of springs requires integration of multiple lines of evidence from diverse disciplines. Within each category of investigation (colored boxes) are examples of spring characteristics (in italics) that could suggest greater capacity to provide stable hydrologic refugia. See WebTable 2 for additional details and a list of data sources and methods for investigation.

gate aquatic species exhibiting long periods of isolation without population bottlenecks (Finn *et al.* 2009).

Notably, characteristics that could allow certain springs to provide stable hydrologic refugia can be offset by a range of non-climate-related human threats, such as aquifer depletion. In some cases, trade-offs might exist between characteristics conferring climate resistance and other sources of risk. For instance, although springs discharging from large, deep, ancient aquifers might be relatively resistant to hydrologic and thermal impacts of climate change (Jyvasjarvi *et al.* 2015; Solder *et al.* 2016), many such aquifers face not only unsustainable rates of groundwater extraction but also contamination from mining, and may be more difficult to protect than smaller, more localized aquifers (Davis *et al.* 2017). Climate effects on springs must therefore be considered within the larger context of challenges and opportunities for conserving groundwater-dependent biodiversity.

■ Integrating refugia identification with spring conservation and management

Efforts to inventory, research, conserve, and restore springs are ongoing in some water-limited landscapes around the world. However, existing frameworks for spring monitoring and management – including prioritization of springs for conservation and restoration investment – rarely include processes for evaluating their responsiveness to climate change (Thompson *et al.* 2002; Barquin and Scarsbrook

2008; Giardina 2011); for an exception see Stevens *et al.* (2016). Because springs that function as stable, relative, or transient refugia likely will have very different ecological trajectories in the coming decades (Figure 3), long-term conservation of spring-dependent biodiversity will benefit from consideration of factors that affect the refugial capacity of springs.

Springs under threat

Both site-level and regional threats to springs must be evaluated in the context of refugia identification (WebTable 2), because springs with characteristics conferring climate resistance cannot serve as refugia if they are destroyed by non-climate-related threats. The many ongoing, interacting threats to springs have been reviewed extensively (Barquin and Scarsbrook 2008; Unmack and Minckley 2008; Davis *et al.* 2017), and include aquifer depletion and pollution, surface-water diversion, channelization of spring-brooks, livestock trampling, recreation, invasive species, and effects from surrounding landscape disturbances. Groundwater extraction is a global

phenomenon with the potential to severely impact springs, especially if aquifer recharge simultaneously declines due to climate change (Taylor *et al.* 2013). While some site-level threats may be ameliorated by management interventions, such as cattle exclusion or rerouting of trails, regional-scale threats to aquifers require coordinated efforts across multiple sectors of society and sometimes across jurisdictions (Davis *et al.* 2017). Comprehensive efforts to address threats to springs across landscapes have been relatively rare (Paffett *et al.* 2018), in part because springs are typically not included in national regulations to protect lakes, streams, and wetlands (Giardina 2011; Lehosmaa *et al.* 2017).

Linking refugia identification to inventory and monitoring

Improved mapping and monitoring of springs are needed if potential ecohydrologic refugia are to be identified and conserved. Many springs remain unmapped and unsampled (Springer *et al.* 2008; Giardina 2011) and long-term monitoring is rare (Weissinger *et al.* 2016). However, innovative approaches using citizen science (Panel 1), multidecadal remote sensing (Cartwright and Johnson 2018), dendrochronology (Fuchs *et al.* 2019), or accumulation curves of spring density (Junghans *et al.* 2016) can generate the kinds of information required to evaluate the refugial capacity of springs at the landscape scale (Figure 4; WebTable 2). Monitoring can reveal which springs retain discharge, water quality, wetland area, and ecohydrologic integrity during dry years. In a drying climate,

Panel 1. “Adopt a Spring”: citizen science for spring monitoring in the Sky Islands

Springs are vitally important to biodiversity in the Sky Islands region of the US and Mexico, yet they remain poorly studied. Sky Island Alliance, a bi-national non-profit conservation organization, combines citizen science and expert assessment for inventory and monitoring of springs across hundreds of square kilometers. Data from county, state, and federal agencies were compiled using the Springs Online database (<https://springsdata.org>) to create a central repository that transcends national and jurisdictional boundaries. Through the “Adopt A Spring” monitoring program, volunteers collect additional data on spring discharge, water quality, soil moisture, and biota, and monitor wildlife use of springs with remote cameras (Figure 5).

This approach demonstrates how volunteer efforts and compiled data can be leveraged to anticipate and monitor climate-driven changes to spring-dependent ecosystems and species. Base-line inventories and repeat monitoring can reveal how springs are changing over time, potentially helping to identify stable ecohydrologic refugia. A centralized database and standardized monitoring protocols help ensure data quality, accessibility, and consistency. Trained citizen scientists also monitor the effectiveness of restoration projects and help to prioritize springs for future restoration investment.



Figure 5. In the Sky Islands region of Mexico and the US, citizen scientists (a) monitor springs seasonally using established protocols and a centralized database, supplemented with remote cameras to document (b) wildlife use of springs.

these springs can be identified as potentially stable refugia, especially if other lines of evidence suggest hydrologic resistance to climate change (Figure 4; WebTable 2). Monitoring after disturbances, such as wildfires, also may reveal whether some springs function as fire refugia (WebPanel 1; WebFigure 1).

Inventory and monitoring efforts for springs are most effective where they leverage existing frameworks to classify springs and archive data (Barquin and Scarsbrook 2008). For example, Springer and Stevens (2009) classified 12 “spheres of discharge” based on hydrogeology and geomorphology, and Thompson *et al.* (2002) and Paffett *et al.* (2018) proposed multiple ranked categories for spring conservation potential. At a landscape scale, comparison of characteristics that indicate refugial capacity (WebTable 2) can be conducted within and across spring types. Comprehensive databases, such as Springs Online (<https://springsdata.org>), hosted by the Springs Stewardship Institute at the Museum of Northern Arizona, allow efficient and secure entry, archiving, and retrieval of important baseline information.

Spring restoration to maximize future refugia

Depending on site history and desired outcomes, restoration of degraded spring-dependent ecosystems can include removal

of flow-diversion infrastructure, exclusion of livestock, reduction of other human impacts, geomorphic restructuring, invasive species removal, controlled burns, and planting of native vegetation (Stacey *et al.* 2011; Stevens *et al.* 2016; Paffett *et al.* 2018). Resources are typically limited relative to restoration needs, and managers must therefore prioritize springs for restoration by considering such factors as water rights ownership, ease and cost-effectiveness of restoration, presence of endangered or exotic species, and the cultural or historical importance of the springs (Barquin and Scarsbrook 2008). Where aquifers are intact, efforts to restore springs are often successful in meeting short-term objectives, and spring ecosystems can prove remarkably resilient once human impacts are ameliorated (Stevens *et al.* 2016; Lehosmaa *et al.* 2017). However, the scarcity of pre- versus post-restoration monitoring data complicates efforts to assess long-term restoration effectiveness (Stacey *et al.* 2011; Lehosmaa *et al.* 2017).

Although not commonly considered in the restoration planning process, projections of ecohydrologic resistance to future climate change might be valuable to long-term spring restoration effectiveness at the landscape scale. If groundwater extraction and pollution are the only threats to aquifers considered in the restoration planning process, then springs discharging from

aquifers located far from (or at elevations high above) areas of intensive human land use might be considered “safe investments”, in that they would be expected to maintain their post-restoration ecohydrologic and water-quality integrity over time. However, even springs in remote or mountainous areas may be vulnerable to climate change (Jyvasjarvi *et al.* 2015; Weissinger *et al.* 2016). Springs anticipated to provide stable refugia based on multiple characteristics (Figure 4; WebTable 2) might prove to be better conservation and restoration investments than springs that display warning signs of desiccation under a drying climate (transient refugia). The long-term success of restoration efforts in springs will require careful consideration of multiple indicators of refugial capacity (Figure 4; WebTable 2) and investment in post-restoration monitoring over decades as climate-change impacts are realized.

■ Conclusions

Only subsets of springs in any region are likely to function as future oases (stable hydrologic refugia under drier future climates). Identifying these refugia is critical for conserving spring-dependent biodiversity and prioritizing management actions in view of scarce conservation resources. Where multiple lines of evidence suggest a spring or spring complex has potential to provide a stable long-term refugium, mitigation of non-climate threats (eg groundwater extraction or contamination, disturbance from grazing) may be especially important. To help anticipate and plan for major shifts in spring-dependent ecosystems, managers should also consider relative and transient refugia, which could provide warning signs of impending population extirpations or species extinctions.

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