# **Title:** Toward climate change refugia conservation at an ecoregion scale in the Sierra Nevada

**Short running title:** Climate change refugia ecoregion scale

**Key words:** Climate change adaptation; conservation science; drought; natural resource management; Sequoia; snow refugia

**Target audience:** The target audience is land managers/conservation practitioners in both the Sierra Nevada and elsewhere, as well as scientists who work on the applied side of climate change adaptation.

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# ABSTRACT

Climate change uncertainty poses serious challenges to conservation efforts. One emerging conservation strategy is to identify and conserve climate change refugia: areas relatively buffered from contemporary climate change that enable persistence of valued resources. This management paradigm may be pursued at broad scales by leveraging existing resources and placing them into a tangible framework to stimulate further collaboration that fosters management decision-making. Here, we describe a framework for moving toward operationalizing climate change refugia conservation at an ecoregion scale with a review for the Sierra Nevada (California, USA). Structured within the Climate Change Refugia Conservation Cycle, we identify a preliminary suite of conservation priorities for the ecoregion, and demonstrate how existing mapping, data, and applications can be used for identifying, prioritizing, managing, and monitoring refugia. We focus on six conservation priorities, including meadows, old growth forests, giant Sequoia, and alpine ecosystems, and introduce the concept of ecosystem process-based refugia, including snow and fire. This pilot overview of concepts and resources provides a foundation of ideas for both near-term implementation and further discussion in moving from science to conservation practice. Such an approach may provide new practical insights for ecosystem management at ecoregion scales in the face of climate change.

# INTRODUCTION

Anthropogenic climate change poses severe threats to biodiversity and ecosystem function. Climate change adaptation aims to reduce vulnerabilities to these threats. One adaptation strategy is to conserve climate change refugia, defined as, “areas relatively buffered from contemporary climate change over time that enable persistence of valued physical, ecological, and socio-cultural resources” (Morelli et al. 2016). More resistant to climate change than surrounding areas, climate change refugia can be further supported and conserved in the short term by implementing best management practices to avoid degradation by immediate, non-climate-specific threats such as land use practices or invasive species. Knowledge of refugial status could motivate managers to direct extensive management or restoration efforts toward climate change refugia, where the return on investment is expected to last longer. Climate change refugia can be considered “slow lanes” -- areas where more gradual change shield valued resources from negative consequences of climate change in the near future (Morelli et al. 2020). Realistically, climate change refugia conservation represents a short- to medium-term management strategy on the scale of decades to a century, and many areas identified as refugia now may not remain so in perpetuity (Hylander et al. 2015, Morelli et al. 2016, Brown et al. 2020). Even so, managed refugial areas might act as “evolutionary cradles” that not only facilitate the persistence of valued resources, but potentially generate future biodiversity hotspots (Murphy et al. 2015), serving as havens from negative climate impacts to biodiversity and ecosystem function (Morelli et al. 2020).

Recent focus on operationalizing climate change refugia conservation calls for synthesis of regionally-relevant science and on-the-ground applications. The Sierra Nevada ecoregion (California, USA) (**Figure 1**) provides a compelling case study for a synthesis of climate change refugia science and application. The ecoregion is already experiencing profound impacts from the intersection of climate change and past management, with one of the largest wildfires ever recorded in the Sierra Nevada occurring in 2020 (CalFire 2020). Additionally, from 2012-2015, the ecoregion experienced its most extreme regional drought event in over a thousand years (which triggered massive tree morality) (Goulden & Bales 2019). Climate change threats interacting with current land management practices, invasive species, and pest dynamics portend continued loss of iconic species and ecosystems (Bentz et al. 2010, USFWS 2014, Spencer et al. 2015). Predicted changes to the Sierra Nevada climate -- which include end-of-century temperature increases that will continue to shift hydrologic and fire processes in the region, with decreased winter snowpack, earlier snowmelt, reduced summer flows, upslope biome shifts, and more frequent and severe wildfires (Diffenbaugh et al. 2015, Gonzalez 2016, Westerling 2016, Berg & Hall 2017, Reich et al. 2018) -- illustrate the urgency of climate adaptation planning in this ecoregion.

Nevertheless, the Sierra Nevada ecoregion also offers hallmarks of climate change refugia, such as steep elevational gradients and rugged topography that foster cold-air pooling (Wilkin et al. 2016) and microclimate diversity (Ackerly et al. 2010). Furthermore, some of the most advanced climate change, snowpack, and vegetative modeling, as well as extensive ecological studies, have occurred in California, including in the Sierra Nevada. Finally, consistent with the focus of climate change refugia conservation on “valued resources” (Wallace 2012, Morelli et al. 2016), the Sierra Nevada holds an exceptional degree of value to scientists, managers, the general public, and nearby population centers that depend on it for water and recreation (such as Los Angeles and the San Francisco Bay area)



Figure 1. Extent of Sierra Nevada Ecoregion, comprising the High Sierra and Sierra Nevada foothills subregions as defined by the Jepson Flora Project (Jepson Flora Project 2020).

Although refugia conservation approaches may have utility for practitioners both in the Sierra Nevada and elsewhere, major challenges remain. Taking refugia conservation from theory to implementation is demanding due to the difficulty of assembling relevant science, tools, and applications, and placing those resources within a clear framework for practical discussion and subsequent decision-making. This obstacle compounds at regional scales, where diversity in land tenure and organizational missions affects values and land management goals, as well as project implementation capacity. Because the lens through which conservation is considered and conducted varies, resulting land management objectives may be complementary or in conflict, but the capacity to develop and consider refugia conservation actions offers land managers the opportunity to make tangible decisions around climate change adaptation. Many agencies and organizations have missions to preserve valued natural resources for present and future generations. Climate change refugia conservation may help achieve objectives by promoting the persistence of endangered and rare species, ecologically important vegetation habitats (Thorne et al. 2020), or forest structure and function amid disturbance (Meigs et al. 2020), for example. However, without a concrete starting point for climate change refugia conservation, scientists and practitioners may lack the foundation to move toward ecoregion-scale climate change adaptation planning.

To address these challenges, the primary goal of this paper was to review how a climate change refugia conservation management paradigm can be pursued at an ecoregion scale in the Sierra Nevada. We produced a pathway toward refugia conservation in this ecoregion. Our objectives were to identify preliminary priorities for climate change refugia conservation in the Sierra Nevada, assess their climate change vulnerabilities, and review resources for identifying, validating, prioritizing, managing, and monitoring Sierra Nevada refugia. By creating a concrete landscape for practical discussion, efforts to assemble existing resources and arrange them within a clear framework for consideration may help leverage refugia conservation into a landscape conservation framework to confront the pressing challenges posed by climate change.

# METHODS

This work was catalyzed by a Climate Change Refugia Conservation workshop held at Yosemite National Park in 2019 through a collaboration among USGS scientists, the Northeast and Southwest Climate Adaptation Science Centers (CASCs), and the National Park Service (NPS; see [climaterefugia.org/sierra-nevada](https://www.climaterefugia.org/sierra-nevada)). The workshop organizers sought to bring together regional natural resource managers and scientists as part of a broader ongoing effort to integrate climate change refugia into existing management and climate change adaptation planning. Similar workshop efforts have been conducted regionally in the northeastern and northwestern United States (see [climaterefugia.org](https://www.climaterefugia.org/)). In pursuit of actionable science, the climate change refugia conservation workshops use translational ecology (Enquist et al. 2017) and knowledge co-production approaches (Wall et al. 2017) to connect refugia research with practitioner management priorities.

We extended and formalized the workshop efforts to move toward a refugia conservation roadmap for the Sierra Nevada ecoregion. Building on the ideas and resources identified in the workshop, we produced a review of existing ecological data resources and management frameworks that might be leveraged for climate change refugia conservation in this ecoregion. To forge a pathway toward Sierra Nevada refugia conservation, and illustrate an example of tangible refugia conservation planning more broadly, we sought to gather refugia-relevant data, mapping, tools, and applications that can be leveraged for identifying, prioritizing, managing, and monitoring refugia, framed within an abbreviated version of the Climate Change Refugia Conservation Cycle (CCRCC) (Morelli et al. 2016). The set of refugia priorities and resources outlined herein has been informed and constrained by the backgrounds of coauthors and workshop participants, and should not be considered comprehensive of the various conservation values and management objectives held by different land managers across the ecoregion.

The Sierra Nevada ecoregion boundary used for this refugia conservation review is based on the Sierra Nevada Region definition provided by the Jepson Flora Project (Jepson Flora Project 2020; **Figure 1**). This ecoregion covers a vast elevation range that includes the highest peak in the contiguous United States (Mt. Whitney) and the largest alpine lake in North America (Lake Tahoe). It boasts an abundance of endemic flora and fauna, ecological processes, and habitats, including foothill woodlands, conifer forests, alpine tundra, wetlands, meadows, lakes, and rivers (Millar 1996, NPS 2018). With over 60% of the ecoregion in public holdings (Millar 1996), implementing effective on-the-ground climate change refugia conservation approaches here is likely to entail substantial coordination among municipal, state, and federal government entities, tribal groups, private landowners, and non-governmental organizations (NGOs).

In this review, we organized the work into the following five sections for each priority resource:

1. **Define Planning Scope** defines and describes the priority resource.
2. **Assess Climate Change Vulnerability** describes the exposure, sensitivity, and adaptive capacity of the priority resource to climate change.
3. **Identify and Validate Refugia** describes mapping and modeling efforts relevant to delineating refugia for the priority resource.
4. **Prioritize Refugial Areas and Implement Management Actions** reviews resources for evaluating which identified refugial areas should be prioritized for management, as well as management actions to support the priority resource.
5. **Monitor Effectiveness of Refugia** describes existing monitoring efforts that may be leveraged to assess whether refugia are functioning as desired.

**Figure 2** uses one priority resource, Sierra Nevada meadows, to illustrate this organization style within the context of the Climate Change Refugia Conservation Cycle. Although the Sierra Nevada Climate Change Refugia Workshop touched upon these steps, this paper represents the first attempt to formally arrange existing resources within the lens of the Climate Change Refugia Conservation Cycle.

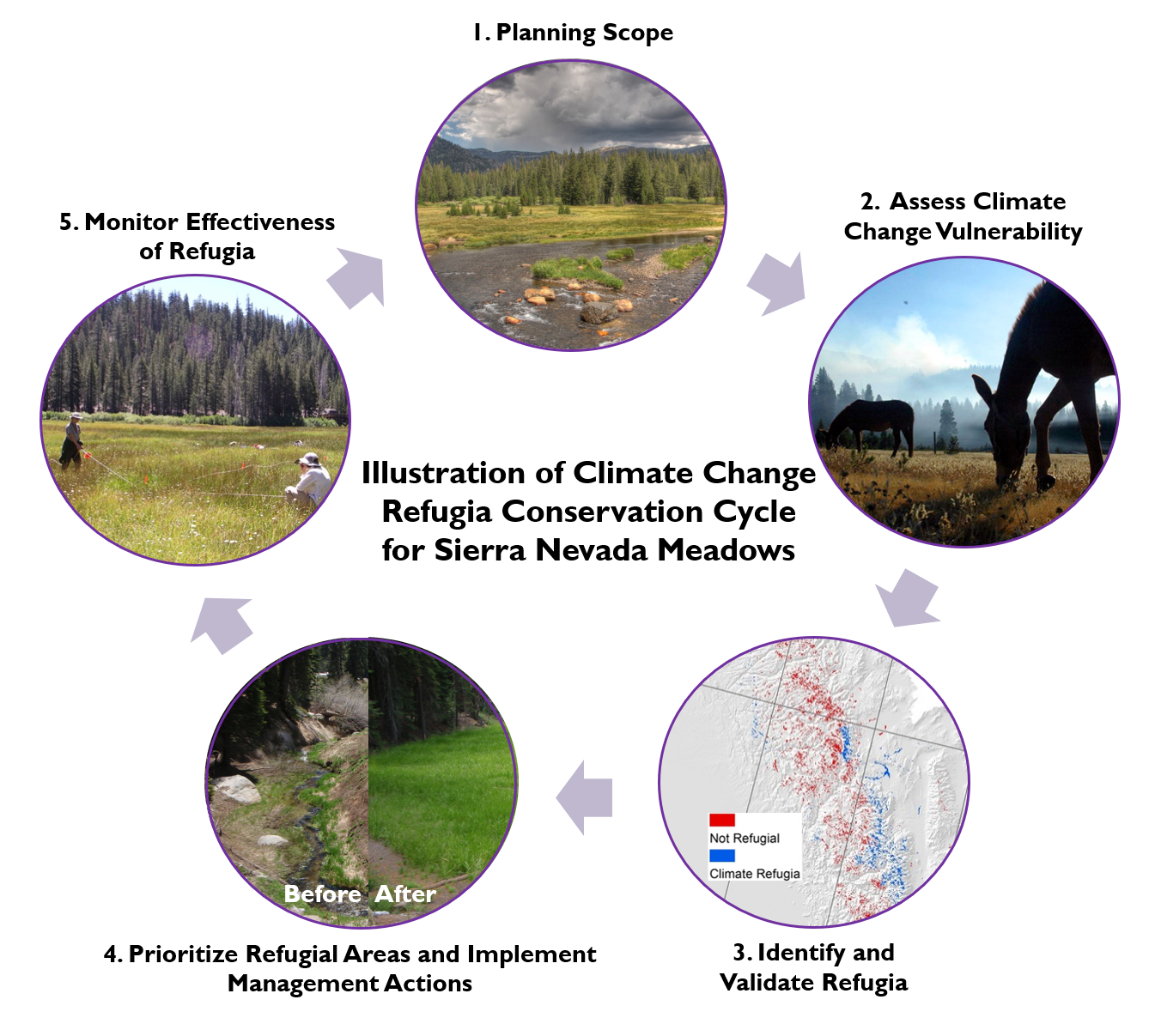


Figure 2. The Climate Change Refugia Conservation Cycle (Morelli et al. 2016) provides a framework for approaching climate change adaptation. This work uses a condensed formulation of the cycle to provide a preliminary roadmap toward refugia conservation in the Sierra Nevada ecoregion. Here, the Meadows Priority resource illustrates the organization of the paper. For each priority resource, sections are organized into 1. Define Planning Scope (e.g., protect refugial meadows), 2. Assess Climate Change Vulnerability (e.g., meadows are vulnerable to climate-driven hydrologic changes, exacerbated by livestock grazing and trampling), 3. Identify and Validate Refugia (e.g., mapping and modeling efforts relevant to the priority resource, such as Sierra Nevada meadow refugia mapping by Maher et al. 2017), 4. Prioritize Refugial Areas and Implement Management Actions (e.g., restoration efforts at Halstead Meadow at Sequoia and Kings Canyon National Parks provide an example of management action that can be taken for refugial areas), and 5. Monitor Effectiveness of Refugia (e.g., a vegetation monitoring plot at Soda Springs Meadow in Devils Postpile National Monument provides an example of existing monitoring practices that might help assess refugia effectiveness).

Photo credits: 1. National Park Service/B.Blackburn; 2, 4, 5: National Park Service; 3. Maher et al. 2017.

Herein, we use language like “priorities” and “resources”, but acknowledge that indigenous-led discourse might favor terms such as “relatives” and “beings” (Tribal Adaptation Menu Team 2019, Long et al. 2020), in recognition of animals, plants, and water as full citizens within the community (Aldern & Goode 2014). The Sierra Nevada is considered sacred and within the ancestral homelands of many tribal communities, and for indigenous people who have stewarded these lands since time immemorial, protecting these areas in the face of climate change is a critical responsibility. Cultural resources, such as cultural burning to foster regeneration of food-providing plants like sourberry and oaks (Aldern & Goode 2014), are not currently represented in the priorities detailed here, but could be a focus of Sierra Nevada climate change refugia conservation. Cultural burning practices in the Sierra Nevada serve to balance ecosystem health, and are likely to provide further resilience in a refugia framework (Aldern & Goode 2014, Tribal Adaptation Menu Team 2019, Long et al. 2020).

# RESULTS

The priority resources identified at the workshop fit broadly into two categories. First, *Process-based Refugial Priorities,* such as snow and fire,focus on ecosystem processes that support or promote the persistence of valued ecosystems, habitats, or species. Second, *Ecosystem-based Refugial Priorities* focus directly on the valued ecosystems, habitats, or species themselves, and include meadows, alpine ecosystems, giant sequoia (**Refugia S1**), and old growth forests (**Refugia S2**) (**Figure 3**). Although each priority is reviewed and discussed separately below or in the supplementary material, there is often clear overlap between process- and ecosystem-based priorities (e.g., meadows overlap with snow and hydrologic processes). Some priority sections illustrate sub-priorities in greater detail, demonstrating that sub-priorities – like Pacific fisher (*Pekania pennanti,* **Inset S1**) in old growth forests, or whitepark pine (*Pinus albicaulis,* **Inset S2**) in alpine systems – may have their own refugia cycles.

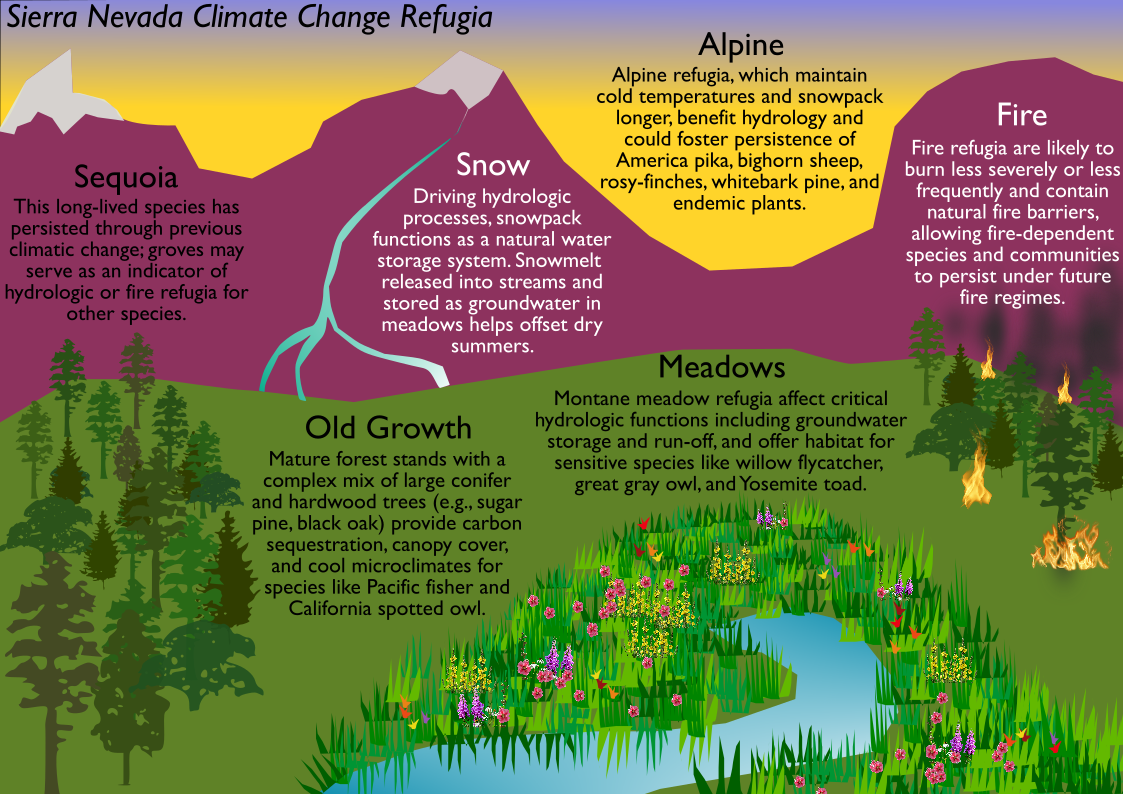


Figure 3. Overview of preliminary Sierra Nevada Climate Change Refugia priorities identified at the 2019 refugia conservation workshop. Process-based priorities are denoted with white text and include Snow and Fire. Ecosystem-based priorities are denoted with black text and include Meadows, Old Growth, Sequoia, and Alpine.

# PROCESS-BASED REFUGIAL PRIORITIES

## Snow

*Planning Scope*

Snow refugia are areas predicted to sustain late season snow on the landscape even in the face of climate change. Snow is a primary driver of hydrologic processes in the Sierra Nevada, and snowpack functions as California’s largest natural water storage system. Snowmelt is slowly released into streams and stored as groundwater in meadows, offsetting the typically dry summer season. Drought stress in the ecoregion is precipitated largely by deficient winter snowfall or inadequate snowpack (Edwards & Redmond 2011). Runoff from snowmelt contributes up to 80% of annual streamflow (Rice et al. 2011), with alpine regions of the Sierra Nevada serving as water sources for downstream agriculture and municipal uses. Due to tight linkages with hydrological processes, snow refugia can overlap with and support other refugial priorities, such as old growth forest, the high water needs of Giant Sequoia (*Sequoiadendron giganteum*) (Ambrose et al. 2016), and other critical ecosystems (e.g., montane meadows, alpine areas).

*Assess Climate Change Vulnerability*

In the past century, climate change has shepherded a shift to more rain and less snow (Knowles et al. 2006, Safeeq et al. 2016, Hatchett et al. 2017), with decreases in snow water equivalent (e.g., Moser et al. 2009, Biondi & Meko 2019), April 1st snowpack (Moser et al. 2009), and snow depth at low elevations (e.g., Grundstein & Mote 2010). Snow drought has been linked to extreme early season precipitation, frequent rain-on-snow events, and low precipitation (Hatchett & McEvoy 2017). In the latter half of the 21st century, increases in precipitation and temperature have led to decreases in snowpack at low-to-mid elevations, with increases in snowpack at higher elevations (Howat & Tulaczyk 2005). Additionally, whitebark pine (*P. albicaulis*) is invading formerly persistent snowfields (Millar et al. 2004); concomitant forest canopy snow interception diminishes snow accumulation (Helbig et al. 2019).

Warming temperatures are expected to shift snowmelt timing earlier by approximately one week per °C in the Sierra Nevada (Rice & Bales 2013), with snowmelt occurring up to 50 days earlier by the end of the century (Reich et al. 2018). An increase of 2°C could decrease average spring snowpack by 30-50% (Mote et al. 2005, Reich et al. 2018), with the loss of snow albedo feedback causing increased warming at mid-elevations (~1500-2400m) (Reich et al. 2018). Climate change is predicted to increase the proportion of winter precipitation falling as rain, and lead to a shift in peak snow mass to earlier in the year, reduced water tables, reduced summer base flows, and drying of perennial streams (Theobald et al. 2009, Thorne et al. 2015, Reich et al. 2018, NPS 2019).

Snow refugia may be less vulnerable due to features such as topographic shading and cold-air pooling, wherein cold, dense air collects in topographic depressions to reduce snowmelt (Curtis et al. 2014). Higher elevations (Howat & Tulaczyk 2005) and snow drifts that are especially deep, on north-facing slopes, or are related to persistent glaciers may have a higher capacity to persist (Morelli et al. 2016).

*Identify and Validate Refugia*

Quantifiable measures of features that reduce exposure (e.g., high elevation, topographic shading, north-facing slopes) can help in identifying snow refugia. **Table S1** summarizes a sampling of relevant tools and research products for snow refugia identification, such as future snow residence time and snow water equivalent (Rice et al. 2011, Luce et al. 2014, Lute & Luce 2017). In the validation stage, independent data are used to test predictions for desired ecological characteristics to ground-truth whether an identified refugium is functioning to conserve the valued resources (Barrows et al. 2020). Though refugia validation is often difficult, the validation of identified snow refugial locations may be straightforward. Snow refugia validation efforts can use the automated, sensor-based snow telemetry (SNOTEL) network, which collects sub-daily data such as snow depth, precipitation accumulation, and snow water equivalent, with approximately 30 sensors located within the Sierra Nevada (<https://www.wcc.nrcs.usda.gov/snow/>). SNOTEL data are supplemented by the California Cooperative Snow Surveys (CCSS) program, which comprises an automated network of 130 snow sensors and manually-collected data from 265 snow courses (CDWR 2020). **Table S1** contains additional resources.

*Prioritize Refugial Areas and Implement Management Actions*

Refugial status is just one of many priorities for choosing an area for management or conservation action. However, it can provide an extra layer of information by which to select a finite number of areas for management, necessary given limited opportunities and resources for action. Management actions to protect snow refugia include strategic forest management to retain snow on the landscape (Lundquist et al. 2013), such as creating canopy gaps that improve snow retention and fire resilience (Schneider et al. 2019). Reduction or modification of recreation or development activities that compromise snowpack may also help (Rixen & Rolando 2013). Management actions to protect meadow refugia (see below section: **Meadows**) may overlap to preserve snow refugia function. For example, functional wet meadows can act like a sponge, absorbing snowmelt in groundwater and surface water sources and releasing groundwater slowly throughout the dry season (Hunt et al. 2018).

*Monitor Effectiveness of Refugia*

Monitoring efforts for snow refugia may be driven by an adaptive management approach that uses the normalized difference snow index (NDSI), SNOTEL, and CCSS sensor data, paired with sub-basin-specific scenario planning for temperature, precipitation, snowpack, snowmelt, and streamflow (Rice & Bales 2013). National Park Service hydrology inventory and monitoring efforts and existing data (e.g., Andrews 2012) can track the status of snow refugia by assessing downstream hydrologic function. Additionally, effectiveness may be assessed using monitoring methods directly relevant to the ecosystems with which snow refugia are closely linked – for example, by looking at normalized difference water and/or vegetation indices (NDWI, NDVI) available via ClimateEngine (Huntington et al. 2017), wherein a lack of decline in these metrics may provide further evidence of effective snow refugia.

## Fire

*Planning Scope*

Fire is a natural ecosystem process in the Sierra Nevada; it protects meadows from forest encroachment, supports the establishment and regeneration of fire-dependent species like giant sequoia, and affects and maintains forest structure and composition (Agee 1996, Sugihara et al. 2006). Prescribed burns and natural and managed wildfires have long been used by indigenous groups to promote the persistence of valued species and ecosystems (Kimmerer & Lake 2001, Hankins 2015, Anderson and Rosenthal 2015), and cultural burning remains in practice today (Long et al. 2016, Long et al. 2017). However, the region is recovering from over a century of Euro-American fire suppression that enabled excess vegetation growth, fuel accumulation (Stephens et al. 2007), and ecosystem homogenization (Koontz et al. 2020).

Fire refugia are patches disturbed less severely or frequently by fire relative to the surrounding vegetation matrix (Krawchuk et al. 2016, Meddens et al. 2018), thereby preserving habitat persistence and connectivity for plants and wildlife (Hylander & Johnson 2010, Robinson et al. 2013, Thompson et al. in review). Areas less frequently or severely disturbed by fire compared to surrounding areas act as legacies, conserving variation in structure, function, and genetics to promote post-fire recovery (Krawchuk et al. 2020). In a fire-adapted landscape like the Sierra Nevada, fire refugia may also be considered as areas that are not highly departed from the natural fire regime.

*Assess Climate Change Vulnerability*

The Sierra Nevada is already experiencing more stand-replacing fires and higher proportions of area burned at high severity due to interactions between past land management and climate change (Westerling et al. 2006, Miller et al. 2009, Miller & Safford 2012, Steel et al. 2018, Westerling 2018). For example, the 2020 Creek Fire, the largest single source wildfire to burn in the Sierra Nevada, had already burned nearly 380,000 acres at the time of this writing (CalFire 2020). Wildfires have been occurring at higher elevations in the Sierra Nevada over the past century (Schwartz et al. 2015). As disturbance regimes shift due to climate change and land use practices, fire refugia are expected to decline in their capacity to support priority resources (Krawchuk et al. 2020). Changing vegetation dynamics – such as invasion by fire-prone species – may fundamentally alter fire regimes by shortening fire return intervals, and by carrying fire into sparse-vegetation environments that normally do not burn (Barrows et al. 2020). Additionally, under extreme heat and drought conditions, areas identified as fire refugia may ultimately burn more severely due to accumulated fuel loads (Safford & Harrison 2008, Krawchuk et al. 2016, Kolden et al. 2017). Thus, rather than binary styling as refugia or non-refugia, fire refugia may be best conceptualized in a gradient, varying along a continuum as climate and disturbance regimes change through time (Krawchuk et al. 2020).

*Identify and Validate Refugia*

Fire refugia are typically defined in post hoc fire analyses as areas that have persisted through multiple wildfires, forming as a consequence of topography, fuels, and weather, which control fire spread and intensity (Meddens et al. 2018). Riparian zones, wet meadows, topography, and soil characteristics can help predict fire refugia occurrence (Krawchuk et al. 2016), with refugia more likely to occur in valley bottoms, gullies, and local concavities, potentially due to cold-air pooling and soil moisture (Wilkin et al. 2016, Meddens et al. 2018). Refugia may also be identified on low productivity soils like serpentine (Safford & Harrison 2008) or areas where exposed bedrock or boulders protect vegetation rooted therein (Hylander and Johnson 2010, Koontz et al. 2020). In the fire-suppressed Sierra Nevada, areas with restored (or less departed) fire regimes may also act as a form of fire refugia through perpetuation of fine-scale heterogeneity (Koontz et al. 2020). Such areas are correlated with higher lightning strike densities in the Sierra Nevada (Jeronimo et al. 2019).

One way to validate areas identified as fire refugia is to assess the persistence or (timely) return of target species post-fire. For example, after the 2013 Rim Fire, spotted owls (*Strix occidentalis*) were recorded within certain areas of the fire perimeter at rates similar to those observed pre-fire, suggesting that forest characteristics remained consistent with owl habitat requirements (Schofield et al. 2020). See **Table S1** for additional region-specific tools and research products to identify and validate fire refugia.

*Prioritize Refugial Areas and Implement Management Actions*

Management of fire refugia can involve managing other stressors, such as addressing competing vegetation during post-fire reforestation (North et al. 2019), and preventing development or heavy visitor use. Fire refugia management decisions could fit into existing fire management frameworks, such as National Park Service resource stewardship strategies and U.S. Forest Service fire management plans in the region, wherein landscape-scale management approaches are combined with scenario planning, vulnerability assessments, and structured decision making (e.g., Nydick & Sydoriak 2011). Emerging frameworks for near real-time predictions of wildfire severity may inform management strategies for mitigating negative impacts (Huang et al. 2020). Management action can influence or reinforce fire refugia, for example by building fire breaks around valued resources (Meddens et al. 2018) or maintaining restored fire regimes. See **Table S2** for a sample of additional research products to support prioritization and management of fire refugia.

*Monitor Effectiveness of Refugia*

Post-fire severity mapping tools, such as the Rapid Assessment of Vegetation Condition after Wildfire (RAVG), provide a direct means for evaluating whether identified fire refugia overlap with recent wildfires (RAVG: <https://fsapps.nwcg.gov/ravg/>, Miller & Quayle 2015). Long-term data collection efforts tracking tree mortality factors, like the Yosemite Forest Dynamics Plot and the Sierra Nevada Forest Dynamics Plot Network (e.g., Lutz 2015, Das et al. 2016), may be invoked to monitor the effectiveness of fire refugia for protecting forests. Evaluating persistence of target species post-fire provides another means for monitoring refugia effectiveness (e.g., spotted owls: Schofield et al. 2020, Pacific fisher: Blomdahl et al. 2019). Monitoring that considers interactions between different process-based refugial priorities could also be fruitful: for example, drought increases wildfire activity (Abatzoglou & Williams 2016), and severity (i.e., kills more trees) (van Mantgem et al. 2013), so hydrology-focused monitoring, modeling, and mapping (e.g., Flint et al. 2014) may provide indirect indicators for fire refugia effectiveness.

# ECOSYSTEM-BASED REFUGIAL PRIORITIES

## Meadows

*Planning Scope*

Meadows are a rare ecosystem in the Sierra Nevada, making up 2% of the ecoregion (Drew et al. 2016). Meadow ecosystems intersect strongly with hydrologic and snow processes in the Sierra Nevada, potentially acting as hydrologic refugia where water availability is greater than that of the surrounding landscape (McLaughlin et al. 2017). Meadows provide ecosystem services including groundwater recharge, surface water retention and runoff, carbon sequestration, water quality improvements, and late season base flow (Micheli & Kirchner 2002, Loheide et al. 2009, Norton et al. 2011, Drew et al. 2016, Ankenbauer & Loheide 2017). Identifying and protecting refugial meadows can improve the chances of conserving a wide diversity of flora and fauna, including federally-threatened Yosemite toad (*Anaxyrus canorus*), Cascades frog (*Rana cascadae*), California state-endangered Willow Flycatcher (*Empidonax traillii*), California state-endangered Great Gray Owl (*Strix nebulosa*), California Golden Trout (*Oncorhynchus aguabonita*), and a host of other birds, fish, and amphibians. Meadow management, restoration, and monitoring in the Sierra Nevada is a multi-agency collaboration (Drew et al. 2016). The Sierra Meadows Partnership ([www.sierrameadows.org](https://www.sierrameadows.org/)) aims to restore and protect 30,000 acres of meadow habitat by 2030 and to provide climate-informed guidance for restoration projects (Vernon et al. 2019). This partnership can be leveraged to identify, validate, manage, restore, and monitor meadow refugia.

*Assess Climate Change Vulnerability*

Current climate change-based threats to meadow persistence have been magnified by past land use practices. California has lost over 90% of its wetland area since 1780 (National Research Council 1992), and a period of high intensity grazing and burning in the late 1800s produced long-lasting impacts on herbaceous vegetation in Sierra Nevada meadows (McKelvey & Johnston 1992). Meadows have also been historically degraded or lost due to intensified livestock grazing during the gold rush, drainage for railway and road placement, home construction, introduced non-native species, surface and groundwater diversions, fire suppression, agricultural conversion, and recreation (Kattelmann & Embury 1996).

Additionally, sensitive species composition dynamics and hydrologic structure make meadows highly vulnerable to climate change (Viers et al. 2013, Hauptfeld et al. 2014). Meadows are formed and maintained by feedbacks between hydrologic processes, vegetation, and soils (Wolf 2017). If lost or degraded under climate change, new meadows are unlikely to form on timescales meaningful for the persistence of valued resources they support, and recovery from disturbance may be slow (Maher et al. 2017). Montane meadow ecosystems are sensitive to projected decreases in spring snowpack, particularly in areas with limited subsurface storage (Albano et al. 2019), where reduced water availability in summer and fall may enable transition toward upland vegetation communities (Drexler et al. 2013). Meadows are at risk from encroachment by upland shrubs and trees due to past fire suppression, overgrazing, shifts to competitive interactions, and climate change, which interact to degrade hydrologic function (Millar et al. 2004, Darrouzet-Nardi et al. 2006). Climate change impacts on hydrology are further exacerbated by livestock grazing and trampling, which affects channel morphology and soil and nutrient dynamics (Ostoja et al. 2014, Vernon et al. 2019). Meadow-dependent wildlife species are directly vulnerable due to loss of suitable habitat from hydrologic degradation, livestock grazing and trampling, and conifer encroachment (Green et al. 2003, Kalinowski et al. 2014, USFWS 2014, Brown et al. 2015).

Meadows with higher watershed subsurface water storage capacity are likely to be more resistant to climate change; likewise, meadows for which more precipitation historically occurs as rain rather than snow (i.e., not dependent on snowpack) may also be less vulnerable (Albano et al. 2019). Such features may serve as hallmarks of meadow refugia.

*Identify and Validate Refugia*

Sierra Nevada meadow refugia have been mapped using a species-agnostic approach (Maher et al. 2017). This work can be integrated with species-specific data to identify refugial meadows for prioritized wildlife – for example, using great gray owl landscape habitat suitability modeling in Yosemite (e.g., Keene et al. 2011). To validate meadow refugia, independent data can be used to test whether an identified refugial meadow is functioning as anticipated. To assess whether a refugial meadow is supporting prioritized species, the refugium can be cross-referenced against species survey or genetic data (e.g., Belding’s ground squirrel, Morelli et al. 2017). Validation of refugial meadow hydrologic function might be accomplished by using the Climate Engine meadow monitoring tool (Albano et al. 2019, Gross et al. 2019). See **Table S1** for additional resources.

*Prioritize Refugial Areas and Implement Management Actions*

Meadow refugia can be ranked for management based on existing prioritization and decision-making tools for Sierra Nevada meadows. The Sierra Meadow Prioritization Tool (Vernon 2019) has been used to identify areas where refugial meadows overlap with priority species, ecosystem services, or other management goals. The Meadow Decision Support Framework (Albano et al. 2019, Gross et al. 2019) can evaluate climate change vulnerability and inform where conservation and restoration actions should be focused. For some management entities, the top priority management action in the face of climate change is to restore, support, and protect functional meadow hydrology. Managers can protect meadow refugia by removing livestock (Vernon et al. 2019), rerouting recreational trails that undermine meadow hydrological and ecological function (*sensu* Yosemite’s Lyell Canyon, Yosemite Conservancy 2020), restoring incised streams (Drew et al. 2016, Long et al. 2020), and raising the water table with controlled burns that stave off encroaching vegetation (Aldern & Goode 2014, Meddens et al. 2018). See **Table S2** for additional prioritization and management approaches for meadow refugia.

*Monitor Effectiveness of Refugia*

Depending on their goals, refugia managers can adopt adaptive management-driven monitoring plans, assessing metrics such as grass height at the end of the growing season, percent willow cover, plant species composition, bank stability, groundwater levels, floodplain inundation, focal bird species richness and abundance, and percent cover of bare soil (Vernon et al. 2019). The Climate Engine meadow monitoring tool can be used to assess meadow responses to climate change and refugia management actions in near-real time (Albano et al. 2019, Gross et al. 2019). Monitoring data about meadow ecosystem characteristics can then be combined with monitoring efforts for prioritized species. For example, great gray owls have previously been monitored in Yosemite under an occupancy monitoring design that may inform future monitoring (Keene et al. 2011, Wu et al. 2016).

## Alpine

*Planning Scope*

Threats posed by climate change are expected to impact high elevation alpine communities (Santos et al. 2015), which support flora and fauna endemic to the area. Alpine refugia priorities include the subalpine whitebark pine community (*P. albicaulis*) (**Inset S2**), and the High Sierra Sky Islands – high elevation vegetation communities found on unglaciated plateaus. Alpine systems also support a diverse array of alpine fauna, several of which we highlight in this section: the American pika (*Ochotona princeps*), bighorn sheep (*Ovis canadensis*), Sierra Nevada Gray-crowned Rosy-Finch (*Leucosticte tephrocotis dawsonii*), proposed endangered Sierra Nevada red fox (*Vulpes vulpes necator*), federally-threatened Yosemite toad (*Anaxyrus canorus)* and federally-endangered mountain yellow-legged (*Rana muscosa*) and Sierra Nevada yellow-legged (*Rana sierrae*) frogs.

While lower elevation species may adapt to warming climates by migrating upward or northward, high-altitude species are thought to be at risk of climate-induced extinction because range shifts are often not possible -- a phenomenon termed the “escalator to extinction" (Hayhoe et al. 2004, Ackerly et al. 2010, Freeman et al. 2018). Nevertheless, anticipated upslope shifts for lower-elevation species have not always occurred as expected (Crimmins et al. 2011, Tingley et al. 2012, Alexander et al. 2018), so specific topographical and ecological features of alpine ecosystems might promote short-term persistence of valued alpine resources (Millar et al. 2016).

Understanding mechanisms that both limit these extreme environment specialists and control their responses to change is fundamental to anticipating species conservation threats (Şekercioğlu et al. 2008, Tingley et al. 2012). Mobile, generalist-diet mountaintop animals can serve as focal surrogates for alpine communities, their responses to directional change, and intervention needs (Epanchin et al. 2010). Federally-endangered Bighorn sheep use upland, montane, and rocky alpine areas along the eastern slope of the Sierra Nevada, living at higher elevations in summer and moving to lower elevations in winter for forage (CDFW 2020). American pika inhabitat mid to high elevation peaks and talus ridges (Kellermann et al. 2019). Rosy-Finches breed at some of the highest known altitudes of any birds in North America, and are among the least studied due to remote and inaccessible nests (MacDougall-Shackleton et al. 2020). Once believed extirpated but rediscovered in 2010, the rare Sierra Nevada red fox is found only in high elevation alpine and subalpine zones year round primarily at elevations above 2750m (Runcie et al. 2020). Meanwhile, three federally listed Sierran amphibians have life histories tied to alpine habitats; Sierra Nevada and Mountain yellow-legged frogs breed exclusively in alpine lakes and ponds (Pope & Matthews 2001, Brown et al. 2014) and Yosemite toads breed in montane and subalpine wet meadows, and ephemeral ponds (Brown et al. 2015).

*Assess Climate Change Vulnerability*

Accelerated warming (Cordero et al. 2011), decreased snowpack, and earlier spring snowmelt threaten alpine faunal communities dependent on snow for many aspects of life history, including foraging and reproduction (Theobald et al. 2009, Rice and Bales 2013, NPS 2019). Changes in snow quantity, quality, and timing of snowmelt drive shifts in species distributions, both in terms of upslope movement of lower elevation species and modified habitat use by high elevation specialists, resulting in alterations in animal behavior, community composition, interspecific interactions, and competition. For example, gray fox (*Urocyon cinereoargenteus*) have shown a 25-30% increase in occupancy above 2000m during the 2012-2015 drought in California, potentially increasing competition for prey and resources in high elevation habitats (Tucker et al. 2019). Meanwhile, pika -- sensitive to high temperatures and found to alter behavior to avoid hyperthermia -- have already been extirpated from portions of their range due to climate change (Moritz et al. 2008, Stewart et al. 2017).

Changes in snow and alpine climates can also impact wildlife reproduction. Rosy-Finches breed above treeline, largely nesting in cracks or holes in cliffs, in boulder fields, and talus slide zones; habitat loss with upslope movement of lower-elevation communities may pose the greatest threat (Johnson et al. 2020). Sierra Nevada yellow-legged frogs require multiple years to complete metamorphosis; increases in pond and lake drying thus threaten recruitment (Lacan et al. 2008). Conversely, Yosemite toads have a rapid reproductive cycle in which metamorphosis is completed entirely during the short alpine summer in wet meadows and shallow ephemeral breeding pools (<30 cm). These breeding conditions make the species vulnerable to climate change if breeding pools dry too early due to inadequate snow levels and increased drying (Brown et al. 2015, Liang et al. 2017).

Additionally, many wildlife species have foraging strategies tied to snow conditions. A warming climate is predicted to cause deterioration of the subnivean environment, a thermally stable area beneath the snow surface (Pauli et al. 2013). Rosy-Finches feed on insects and seeds in snowbanks, often following the snowmelt line while foraging (MacDougall-Shackleton et al. 2020). Changes to precipitation and fire regimes may impact bighorn sheep forage quantity in high alpine meadows (Wehausen 1992, Greene et al. 2012) or loss of foraging habitat for Yosemite toad (Brown et al. 2015). Consequently, shifting hydrology and snowpack dynamics could lead to phenological mismatches for faunal forage dynamics.

*Identify and Validate Refugia*

To identify alpine refugia, species-specific data might be combined with terrain (e.g., USGS 2007) and/or landscape resiliency data based on land facet mapping and topoclimate diversity (e.g., Buttrick et al. 2015). The CDFW Sierra Nevada Bighorn Sheep Recovery Program has mapped both historical distribution and current distribution in 16 “herd units” identified as appropriate for Sierra bighorn based on habitat suitability modeling, 13 of which are currently occupied (CDFW 2020), while survey and mapping efforts in the Sierra Nevada have investigated both pika range and habitat features driving pika occurrence (Millar and Westfall 2010, Stewart & Wright 2012, Stewart et al. 2017). Occupancy and distribution modeling for Sierra Nevada rosy-finch species is currently in progress, which can be compared with spatially explicit mapping that assessed rosy-finch vulnerability under climate change (Siegel et al. 2014).

*Prioritize Refugial Areas and Implement Management Actions*

Alpine refugia might be prioritized for management based on areas where rare or sensitive species are currently found, or where habitat is projected to be suitable. Due to their low population and endangered status, translocations are a fundamental management method for bighorn sheep (USFWS 2007, CDFW 2020). Most pika habitat in the Sierra Nevada falls under the management auspices of public agencies, but little statistical evidence exists about impacts to pika from human land use (e.g., grazing, recreation), limiting knowledge about potential management options (Stewart & Wright 2012). Removal of non-native trout species may benefit alpine-dependent amphibians (Knapp & Matthews 2000) and rosy-finches (Epanchin et al. 2010).

*Monitor Effectiveness of Refugia*

Existing population monitoring efforts may be adapted to evaluate whether alpine refugia are adequately conserving prioritized species. In addition to extensive habitat modeling, the CDFW Sierra Nevada Bighorn Sheep Recovery Program does seasonal population surveys and uses GPS collars to monitor habitat use and survival of 200+ individuals (CDFW 2020), which may provide insights about refugia use and utility. An established rapid assessment method has been used for pika in this ecoregion, although it is not a systematic transect/plot method and may be subject to false negatives (Millar & Westfall 2010). Rosy-finch populations are not currently captured in breeding bird surveys, although Gray-crowned Rosy-finch is monitored as part of National Park Service Inventory and Monitoring efforts (Steel et al. 2012), and updated occupancy and distribution data are expected to be available in 2021. Mountain and Sierra Nevada yellow-legged frogs are monitored annually during the summer months to track population trajectories as well as disease outbreaks and recoveries (Knapp et al. 2016, Rothstein et al. 2020).

# DISCUSSION

This review has illuminated a path toward climate change refugia conservation at an ecoregion scale in the Sierra Nevada, demonstrating six priority resources arranged within the framework of the Climate Change Refugia Conservation Cycle. These refugia priorities have been both informed and constrained by the perspectives of coauthors and workshop participants. Accordingly, this work should be considered an early roadmap toward climate change refugia conservation in the Sierra Nevada. Like any roadmap, to remain current and maintain utility, this one can be updated through time to refine or expand priorities, include additional perspectives, incorporate new knowledge and research, and adapt to new goals in a changing climate.

Refugial status is merely one indicator that may be incorporated into decision-making around choosing sites for management or conservation action. Additionally, in an ecoregion approach to refugia conservation, priority resources may not be mutually exclusive. An ecoregion approach that iteratively considers climate vulnerabilities as well as interactions between priorities presents the opportunity for dynamic, network-based management of climate change refugia that act as “slow lanes” within the Sierra Nevada (Morelli et al. 2020). Process-based refugia (e.g., snow, fire) overlap with and support all of the ecosystem-based refugia discussed here, and some refugia types may be co-located (e.g., **Figure 4**). For example, snow refugia may overlap directly with alpine refugia, or fire refugia may be prioritized for management based on their capacity to conserve old growth forest refugia. Some priority resources may directly conflict; in an integrated prioritization process, managers may facilitate transitions of one type of vegetative refugia community to another -- such as allowing a meadow refugium to transition to forest if the meadow is not expected to persist without prohibitively intensive management. Not all refugial priorities will present straightforward alliances or conflicts, and temporal management scales are also important to consider, as areas predicted to be refugial in mid-century may no longer function as refugia by the end of the century. For example, managers may grapple with fire refugia management decisions that either benefit or conflict with management decisions for old growth forest refugia, given the potential temporal conflicts and co-benefits of fire and old growth forest density (e.g., Hanson & Odion 2016, DellaSalla et al. 2017).

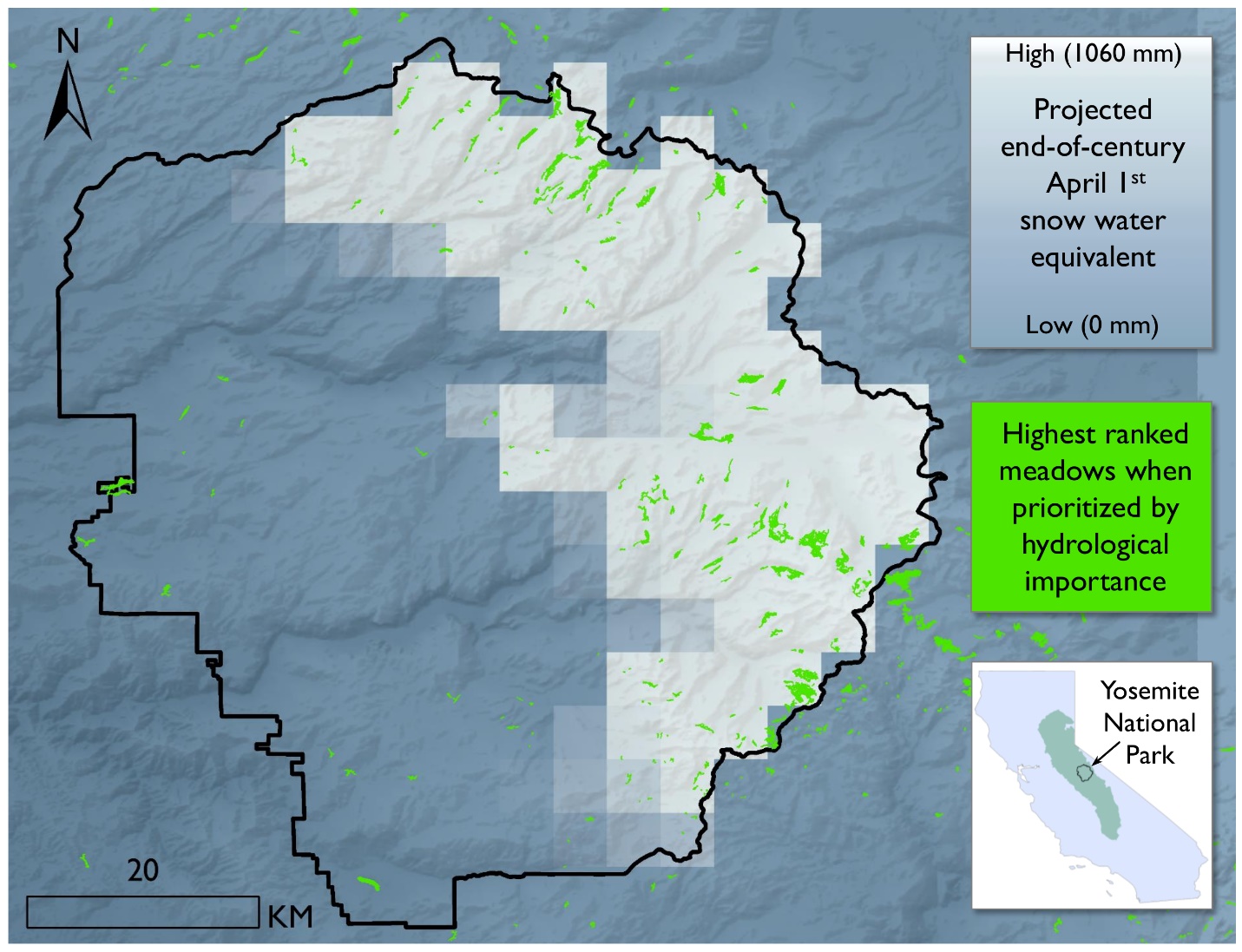


Figure 4. Illustration of potential intersecting climate change refugia priorities (meadows, snow, alpine) at Yosemite National Park. This example shows where meadows that rank highest by hydrological importance using the Sierra Meadows Prioritization Tool (Vernon 2019) overlap or do not overlap with potential snow refugia based on projected end-of-century April 1st snow water equivalent (Luce et al. 2014, Lute & Luce 2017). Underlying these data is the 10m Digital Elevation Model for Yosemite National Park (USGS 2007), a source which might contribute to alpine refugia identification efforts (such as refugia for whitebark pine, e.g., Moore et al. 2017).

Placing Sierra Nevada refugia conservation efforts into adaptive management frameworks can help account for current limitations by reducing system uncertainty under climate change and providing clear triggers for management action (Williams 2011). However, challenges remain. Though adaptive management is discussed in several priority management contexts (e.g., meadows: Vernon et al. 2019; Pacific fisher: Spencer et al. 2016, pika, whitebark pine: Kellermann et al. 2019), an integrated, dynamic, ecoregion network-based approach to refugia conservation faces both hurdles and opportunities in the form of diverse land tenure and differences in land management mandates, objectives, and capacity. The USDA Forest Service holds the majority of land in the Sierra Nevada, with the Bureau of Land Management, National Park Service, and other federal, state, tribal, and municipal entities also managing substantial areas. Agency mandates and funding cycles often incentivize managers to confront immediate, non-climate-specific threats (e.g., pests, invasive species), making it harder to prioritize projects that support the decadal-scale management required for climate change adaptation planning, although there are efforts to shift this trend (e.g., 2012 Forest Service Planning Rule; 77 FR 21162).

Varying management objectives mean that management capacity and approach may be different within each management unit. For instance, barriers to using prescribed fire to meet management objectives, along with the motivations for using fire as a management tool, differ in national forests vs. national parks (Doane et al. 2006, Quinn-Davidson et al. 2012), and social, economic, and regulatory hurdles constrain forest management options (Schwartz et al. 2020). Meanwhile, cattle grazing is prohibited in meadows within the national parks, but allowed on national forest land in the Sierra Nevada (Multiple Use Sustained Yield Act, P.L. 104–333). This diversity in management motivation and capacity likely compounds on private lands. Approximately ⅓ of land in the Sierra Nevada is privately owned, particularly at lower elevations (Millar 1996), and engagement with landowners through land trusts or conservation easements could be critical where identified refugia overlap with private lands. However, coordinated, region-scale planning can meet multiple objectives at large scales and promote greater resilience under climate change; existing cross-jurisdictional partnerships aim to address such challenges in the Sierra Nevada ecoregion (e.g., Tahoe-Central Sierra Initiative (TCSI): Manley et al. 2020).

This work reviews a pathway toward climate change adaptation planning in a region currently facing tangible threats from climate change. Future climate change refugia conservation in the Sierra Nevada might incorporate regional landscape connectivity work (Buttrick et al. 2015, McRae et al. 2015), considerations for increased human-wildlife conflict and zoonotic disease (e.g., Hammond et al. 2020, MacDonald et al. 2020), additional existing climate change refugia conservation approaches in the region (Buhler et al. 2019), and much more. Placing priorities and resources into an actionable framework provides ideas for near-term application, and is expected to stimulate additional collaboration to meet the challenges of climate change adaptation in the Sierra Nevada ecoregion. To help address pressing challenges posed by climate change, the management paradigm of climate change refugia conservation can be similarly pursued in other ecoregions, wherein marshaling existing resources within a climate adaptation framework can help translate science into conservation practice.

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