

Validating climate-change refugia: empirical bottom-up approaches to support management actions

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Efforts to conserve biodiversity increasingly focus on identifying climate-change refugia – areas relatively buffered from contemporary climate change over time that enable species persistence. Identification of refugia typically includes modeling the distribution of a species' current habitat and then extrapolating that distribution given projected changes in temperature and precipitation, or by mapping topographic features that buffer species from regional climate extremes. However, the function of those hypothesized refugia must be validated (or challenged) with independent data not used in the initial identification of the refugia. Although doing so would facilitate the incorporation of climate-change refugia into conservation and management decision making, a synthesis of validation methods is currently lacking. We reviewed the literature and defined four methods to test refugia predictions. We propose that such bottom-up approaches can lead to improved protected-area designations and on-the-ground management actions to reduce influences from non-climate stressors within potential refugia.

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A healthy tension exists in climate-change research between developing concepts and insights with broad implications and providing information that can be applied to specific locations by conservation practitioners (eg Cook *et al.*

2013; Meadow *et al.* 2015). Models and broader theory regarding the spatial patterns of biodiversity can convey important insights into how those patterns might affect species' survival in a changing environment (Thuiller *et al.* 2008; Franklin *et al.* 2017). However, conservation practitioners urgently need additional direction on what they can do on the ground to stem, or at least slow, climate-change-related biodiversity loss. While broader implications are typically analyzed at large scales, meeting the needs of conservation practitioners requires data at finer scales, with clearly delineated boundaries to confirm and refine understanding of processes implied by larger-scale analyses (Hannah *et al.* 2014; Keppel and Wardell-Johnson 2015).

Climate-change refugia are areas relatively buffered from contemporary climate change that enable the persistence of valued physical, ecological, and sociocultural resources (Keppel *et al.* 2015; Morelli *et al.* 2016). An initial step to managing refugia for climate adaptation is identifying where they exist. This initial identification represents a spatial hypothesis constructed through various methods. Examples include comparing the current distribution of suitable habitat for a particular species with the modeled distribution of that habitat, given climate-change projections (Maher *et al.* 2017; Sweet *et al.* 2019), and mapping topographic features that buffer species from regional climate extremes (McCullough *et al.* 2016; Schwantes *et al.* 2018). However, these methods merely establish a spatial hypothesis of where climate buffering may occur, which is not an end in itself but rather a starting point toward ensuring that natural lands managers can identify, protect, and manage climate-change refugia. Morelli *et al.* (2016) illustrated the sequence of necessary tasks through the development of

In a nutshell:

- Modeling the occurrence of climate-change refugia helps to generate predictions regarding locations of climate-change refugia – areas buffered from contemporary climate change
- Validating predicted occurrences of such refugia is a critical yet often overlooked step needed to identify climate-change refugia targets for conservation and natural lands management
- On-the-ground measures of species richness, endemic species persistence, genetic diversity, and reproduction can provide independent means to validate climate-change refugia
- We highlight how scientists and managers can collaborate to mobilize on-the-ground efforts to protect and conserve refugia

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the “climate-change refugia conservation cycle” (CCRCC; Figure 1). A key, but often neglected, component of this cycle is the need to “validate” refugia (that is, to independently verify the location and function of hypothesized refugia) before management actions can be refined and acted upon. Our focus here is to elevate that “validation step” from a concept that is often overlooked to an essential task that can translate into adaptive and more effective responses to protect biodiversity and high-value species.

Validating the occurrence and function of climate-change refugia requires identifying appropriate response variables and approaches. Such variables differ from those used to create the spatial hypothesis for the existence of climate-change refugia; they are independent, empirical data that corroborate or challenge the utility of those refugia. We conducted a review of the scholarly literature to identify the key concepts, approaches, and future directions for the science of refugia validation. We found that existing empirical approaches for validating refugia fall into four categories: (1) metrics of biodiversity and endemism, (2) characterization of fine-scale genetic diversity, (3) physiological trait–environment matches, and (4) population structure/demography responses to current levels of climate change (Figure 2). Approaches 1–3 allow for the detection of the “ghosts of climate-change past”, which enabled the function of, and species persistence within, prior refugia; moreover, these approaches also allow for analyses of species’ reproduction and survivorship responses to current patterns of climate change, and as such provide an important test of continued refugia function. Approach 4 assesses demographic responses to current levels of climate change. For all approaches, validation is achieved when there is congruence between the spatial extent of these independent data and the potential refugia identified through analyses of spatially explicit abiotic and biotic conditions (Figure 2). When scientists and managers work together to complete this important validation step, it can catalyze on-the-ground efforts to protect and conserve refugia.

■ Approach 1: biodiversity response variables

High species richness and endemism within a defined region is evidence that an area has functioned as a refugium during past episodes of environmental change and may indicate future refugia function (Harrison and Noss 2017). Here, we postulate that, as compared to non-refugial habitats, refugia increase local diversity and endemism through (1) reduced extinction rates and (2) increased opportunity for speciation due to area-specific patterns of insularity, dispersal barriers, and ecological opportunities. Therefore, mapping the spatial extents of beta diversity, species richness, or endemism “hotspots” offers an impartial way to validate hypothesized climate-change refugia identified through other means (eg species distribution modeling or climate velocity approaches). For example, Mokany *et al.* (2017) used empirically

determined paleoendemism scores (derived from pollen records) to validate modeled projections of refugia based on climate and species distributions. Such multistep approaches to identify and validate refugia are rare, due in part to the scarcity of available data from surveys (Sequeira *et al.* 2018), but are valuable for building the confidence needed to prioritize management action.

Stable climates result from slow-to-change geographic (eg coastal areas, low latitude regions) and topographic (eg montane environments) characteristics, as well as from emergent ecosystem processes (eg canopy buffering of understories; Davis *et al.* 2019) that are relatively persistent through time (Jansson 2003; Harrison and Noss 2017; Sandel *et al.* 2017). However, because contemporary climate change has no perfect analog, past performance as refugia does not necessarily guarantee that these areas will function as such in the future (Malcolm *et al.* 2006; Mokany *et al.* 2017; Sandel *et al.* 2017). Indeed, in areas of high endemism, species losses could be substantial if climate-change velocities and amplitudes are considerably greater than that which occurred during past climate shifts (Malcolm *et al.* 2006; Sandel *et al.* 2011, 2017; Mokany *et al.* 2017). Nevertheless, elevated rates of extinction may be the exception more than the rule (Harrison and Noss 2017), which underscores the value of relying on biodiversity and endemism (as opposed to extinction) to validate refugia function, as well as using metrics such as response variables to monitor future conditions under an adaptive management approach.

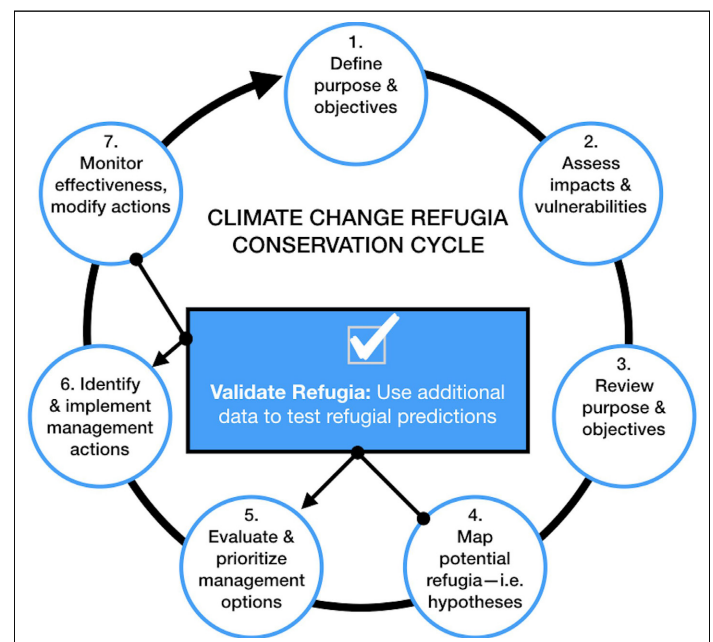


Figure 1. The “climate-change refugia conservation cycle” (CCRCC), adapted from Figure 3 in Morelli *et al.* (2016), to illustrate the central role of validating climate-change refugia. Validation using empirical approaches is a necessary step for advancing beyond spatial hypotheses (step 4) and for providing managers with the confidence to evaluate specific management actions (step 5). It is also a key element to include in ongoing monitoring to foster an adaptive management approach (steps 6 and 7). Used under CC0 1.0 Universal (creativecommons.org/publicdomain/zero/1.0).

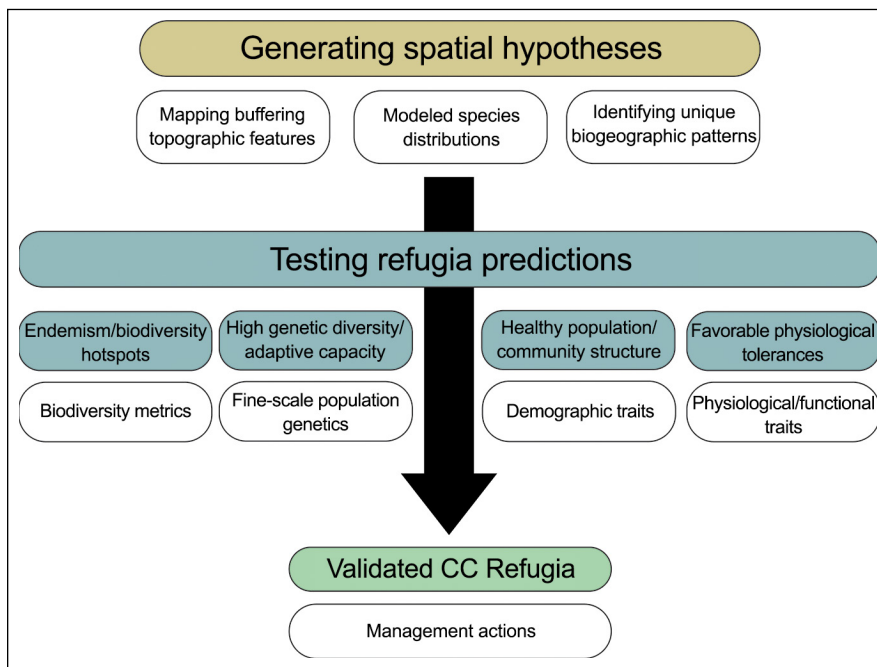


Figure 2. A conceptual framework for validating climate-change refugia. Generating spatial hypotheses through modeling is followed by further investigation into the features of the hypothesized refugia, which can be validated through different empirical approaches. Validated refugia are then passed on to the next steps of the CCRCC, where management actions are identified and prioritized.

The presence of a high degree of species diversity and endemism could serve as an initial identification of a climate-change refugium or a subsequent validation step, depending on the nature of the study; paleobotanical studies, for instance, have long inferred stable climates from patterns of endemism (Stebbins and Major 1965). Research on current climate change necessitates modern approaches that involve identification of future distributions of stable climates or low climate velocity over large, complex landscapes using sophisticated computer modeling. More empirical and natural-history-based approaches are not well suited to questions at this scale but are ideal for validating and focusing these approaches at scales more useful to natural lands managers and other decision makers.

■ Approach 2: genetic diversity

Greater adaptive capacity underlies a species' ability to weather novel conditions (Williams *et al.* 2008). Although adaptive capacity is the product of multiple factors (eg phenotypic plasticity, life-history and behavioral traits, dispersal ability), a fundamental element of the capacity to adapt to new conditions is genetic diversity (Frankham *et al.* 2002). However, this elementary unit of biodiversity is rarely quantified in studies that examine species responses to climate change due to the lack of an explicit framework for analyzing climate-related threats and adaptive responses (Williams *et al.* 2008; Yannic *et al.* 2014).

The accumulation of genetic diversity can be a characteristic product of species occupying stable refugia (Hampe and Petit 2005; Morelli *et al.* 2017; Fonseca *et al.* 2019). Past disturbances can influence genetic patterns through both selection-driven and neutral (ie random) processes, leading to current patterns of genetic diversity that reflect the “ghost of past disturbances” (Gugger *et al.* 2013; Davies *et al.* 2016). For example, Yannic *et al.* (2014) used a creative “phylogeographic” approach that combined spatial analysis and genetic diversity data from caribou (*Rangifer tarandus*) populations to determine that climatically stable regions have historically maintained high genetic diversity and would be likely to do so under future climate change.

Genetic diversity-based approaches, while often focused on individual species, may prove valuable in identifying and validating areas that function as refugia for other taxa as well. For example, Vandergast *et al.* (2008) and Wood *et al.* (2013) identified “hotspots” of genetic diversity across southern California via analyses of a broad array of reptile, amphibian, mammal, and plant species. These hotspots were concordant with climate-change refugia that were later modeled and then validated for Joshua trees (*Yucca brevifolia*), a species not included in those previous analyses (Sweet *et al.* 2019).

Maintaining genetic diversity can serve as a safeguard against the negative impacts of climate change. Incorporating genetic diversity into climate adaptation conservation schemes, including protecting refugia, is an important step toward reducing the loss of species due to climate change. As with Approach 1, the scale at which genetic traits can be reliably determined makes them ill-suited for identifying refugia across large landscapes; however, such traits are excellent indicators of past refugia function for key species and also provide valuable information on how those taxa may adapt to future climate change. In addition, genetic traits are highly useful for understanding the adaptive capacity of species of conservation concern, and can provide insights for managers to improve management options for these important biological resources (Panel 1; Figure 3).

■ Approach 3: physiological ecology

An organism's response to climate change is a function of its ecological, physiological, and genetic traits, combined with that organism's exposure to environmental stressors (Williams *et al.* 2008). Fundamentally, species inhabiting refugia exhibit favorable trait–environment matches that are sufficient to allow for survival, growth, and reproduction in situ through episodes of environmental change. These external and internal factors

Panel 1. Using genetic traits to validate refugia clarifies conservation opportunities for whitebark pine

Whitebark pine (*Pinus albicaulis*) is a foundational species that regulates snowmelt and runoff in upper subalpine and alpine ecosystems, and fosters biodiversity as a nurse plant and a food source for numerous wildlife species (Degrassi *et al.* 2019). Approximately 48% of the 2.6 million ha that make up this species' range occurs in existing protected locations (ie designated or proposed wilderness and roadless areas; Scott *et al.* 2001). The characteristics of existing protected areas provide consistently cooler, wetter habitats, and therefore are potential climate-change refugia. However, a warming climate is not the only threat to this species. Due to the combined impacts of white pine blister rust (*Cronartium ribicola*) and mountain pine beetle (*Dendroctonus ponderosae*) infestations, as well as altered fire regimes, whitebark pine associations are now among the most endangered of all North American forest types. These accumulated threats have led to whitebark pine candidacy for federal listing under the US Endangered Species Act (FWS 2016). To conserve this important species, managers need to know where to target efforts to mitigate these threats.

Successful conservation of whitebark pine hinges on identifying the locations of populations that possess favorable adaptive traits and high genetic diversity. To this end, scientists and managers at the US Forest Service and the University of Idaho have co-developed new, interdisciplinary methods for combining empirical measures of traits and genetic diversity with spatial analysis and climate suitability models, in an effort to identify and validate genetically robust macrorefugia for whitebark pine. The foundation of this approach is a link between studies of adaptive trait variation (such as blister rust resistance, drought avoidance, and later winter cold hardiness) in common garden experiments (Morgenstern 1996; Mahalovich *et al.* 2006, 2016) and mapping of genetic diversity markers (Mahalovich and Hipkins 2011) to determine functional genetic diversity. This bottom-up approach is then combined with soil suitability data and modeled outputs from extreme climate-change scenarios (eg RCP 8.5, usually referred to as “business as usual”, a future with limited mitigation effort and high population growth; Huntley and Webb 2012) to identify areas that not only are suitable in terms of abiotic conditions but also include populations that possess the biotic traits needed for adaptation and resilience to climate change.

The interdisciplinary nature of the approach allowed for simultaneous identification and validation of whitebark pine refugia that are most likely to be robust to climate change. The outcome of these analyses was that only a small portion of protected (and formerly hypothesized) refugia

were likely to still protect the genetic diversity of this species as the effects of climate change intensify (Figure 3). These findings clarify the conservation and management needs and opportunities that exist for this species.

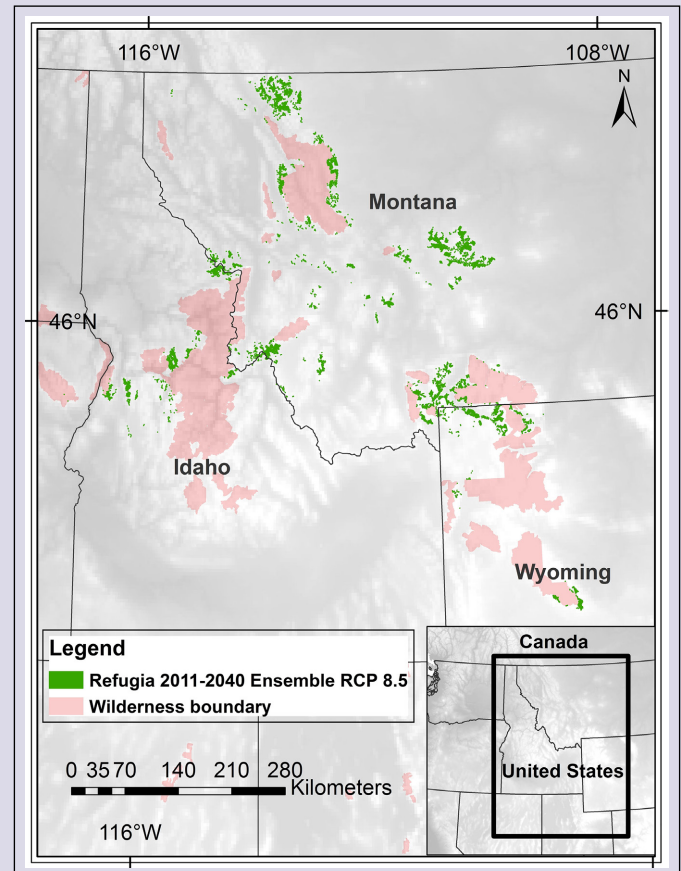


Figure 3. Distribution of mid-century genetic macrorefugia for whitebark pine (*Pinus albicaulis*) under Representative Concentration Pathway (RCP) 8.5 and protected area boundaries in the western US. The trait-based analyses of genetic macrorefugia were conducted in the Blue Ridge Parkway, Shoshone National Forest, Wyoming. Base map generated from the US Geological Survey (USGS) National Elevation Dataset (NED; <http://ned.usgs.gov>). Used under CC-BY-3.0 (creativecommons.org/licenses/by/3.0/).

are related to both how exposed and how sensitive an organism is to the changes taking place (Williams *et al.* 2008). However, studies identifying refugia have focused primarily on characterizing the exposure component, by estimating the level to which species experience regional climatic change and local, microhabitat buffering. Therefore, quantifying the sensitivity component has been largely underutilized as a means to validate the function and occurrence of climate-change refugia; doing so may complement, and provide greater confidence in results obtained from, exposure-based techniques.

For most organisms (especially those inhabiting refugia; Harrison and Noss 2017), there is little information on their specific physiological tolerances that might confer resistance or resilience to climate change (Williams *et al.* 2008). Species occupying stable climate conditions could develop narrow physiological tolerances that make them more sensitive to future climate instability (Jansson 2003), which could in theory reduce the effectiveness of localized buffering provided by refugial habitats (Harrison and Noss 2017). However, the low extinction rates that have characterized past climate refugia

(Harrison and Noss 2017), combined with the fact that many physiological tolerance limits are phylogenetically constrained (Chown *et al.* 2002; Ackerly 2003; Blomberg *et al.* 2003), suggest that organisms occupying refugia are not more sensitive to climate change. Comparative studies of key physiological traits (eg thermal tolerance, drought tolerance, disease resistance) of organisms within and outside refugia could confirm whether those areas will function as hypothesized.

Measuring drought-related physiological traits of woody plants in refugia versus non-refugia habitats provides an important means of comparing their climate-related mortality risk in the 21st century (Anderegg and HilleRisLambers 2016; Choat *et al.* 2018). For example, Ramirez *et al.* (2020) compared the drought-related physiological traits of chaparral shrubs inhabiting dry interior (continental) sites to those within climatically stable nearshore island habitats, which are believed to serve as regional climate refugia (Axelrod 1967). Despite their exposure to a stable maritime climate, the island-based plants' physiological tolerances indicated resistance to drought conditions in excess of those typically experienced on the study island. Notably, this favorable trait pattern corresponded to reduced impacts to island vegetation during recent droughts, which have been exacerbated by climate change. Studies like this underscore the value of using empirical approaches not only to validate past refugia function but also to improve understanding and predictions of species responses to future conditions, which is precisely the kind of information needed to operationalize climate-change refugia for management and conservation (Morelli *et al.* 2016).

■ Approach 4: demography

Demographic patterns that are indicative of long-term, viable populations may also provide a tool for validating modeled estimations of climate-change refugia. As the surrounding climate becomes increasingly less suitable, populations within refugia would be expected to have higher successful recruitment rates than populations outside such areas. An example of this phenomenon comes from Joshua trees of California's Mojave Desert (Sweet *et al.* 2019). Plot-based surveys revealed that young Joshua trees were more numerous in areas within and nearest to modeled climate-change refugia than in areas outside of modeled refugia. If recent drought events in the region, exacerbated by climate change (2000–2004 and 2012–2016; Williams *et al.* 2015), are an analog for future conditions, then patterns of recruitment and survivorship in refugia locations during these early 21st-century droughts indicate that these populations will be sustained. By examining patterns of pollination and viable seed set in Joshua trees in these same areas, Harrower and Gilbert (2018) corroborated the model-based hypotheses of Joshua tree refugia (Sweet *et al.* 2019), as well as providing important information that managers of these lands could put into practice (Panel 2; Figures 4 and 5). Populations located in

climate-change refugia should also exhibit higher occupancy and survival rates as measured through standard, field-based assessments. For example, Maher *et al.* (2017) created a map of likely refugial meadows in California's Sierra Nevada mountain range based on a century of modeled climate change. These hypothesized refugia were then validated via population data collected on Belding's ground squirrel (*Urocitellus beldingi*), an easily detectable climate-sensitive species. Belding's ground squirrels, which were extirpated from nearly half of their historical California range over the past century (Morelli *et al.* 2012), had higher occupancy and lower extinction rates in meadows that were mapped as refugia by Morelli *et al.* (2017). Validating refugial meadows then allowed them to be prioritized for restoration and other management actions (Maher *et al.* 2017).

A final example comes from recent work on high-elevation conifer populations used to validate purported indicators of montane climate refugia. Millar *et al.* (2018, 2019) analyzed current and long-term spatial distributions and ages of limber pine (*Pinus flexilis*), the dominant subalpine tree species of the Great Basin, and assessed these against climate reconstructions based on various proxies. They reconstructed 4000 years of limber pine occurrence in the western Great Basin and found that, despite climate variability, no differences in occupancy at upper and lower elevations were identified; except for populations on north aspect slopes, all other populations were extirpated over time. By demonstrating that low-elevation ravines, riparian corridors, and north aspects did indeed provide long-term climate refugia, Millar *et al.* (2018, 2019) established these features as priority management areas for limber pine in this part of the Great Basin.

■ Conclusions

The existence of climate-change refugia justifies cautious optimism that there are locations and populations that are relatively buffered from projected climate change. The first steps toward leveraging these areas for species and habitat conservation would be to identify where refugia occur and what species would benefit from them. By supplementing spatial hypotheses generated by modeling and mapping with independent empirical analyses that test and validate predictions concerning refugia, we offer an active, research-based means for resource managers to protect populations within those refugia. In this study, we reviewed four evolving approaches that go beyond identification of climate-change refugia and allow for validation of their hypothesized function. In each case, we identified response variables specific to species of conservation concern, suggested a validation approach, and emphasized protection and active management of these refugia. The examples of diversity-based, demographic, physiological, and genetics-based approaches described here illustrate the research that is necessary to advance and

Panel 2. Validating climate-change refugia for Joshua trees leads to improved management

Joshua Tree National Park (JTNP), which straddles the Mojave and Colorado deserts in southern California, may be especially vulnerable to climate change (Gonzalez *et al.* 2018). At a spatial scale that encompassed most of the Mojave Desert, Cole *et al.* (2011) predicted the widespread extinction of the iconic Joshua tree (*Yucca brevifolia*) across much of its current range as a result of climate change, including areas within JTNP. Barrows and Murphy-Mariscal (2012) and Sweet *et al.* (2019) then used finer spatial-scale analyses to identify climate-change refugia within JTNP that could maintain Joshua tree populations under all climate futures except for that predicted by a high emissions scenario. These divergent future outcomes highlighted the need for independent data to evaluate the existence of predicted refugia, and to devise informed strategies to apply limited public resources to effectively manage climate-change refugia. Sweet *et al.* (2019) provided that validation by employing a demographic analysis of seedling recruitment patterns across the park (ie Approach 4).

Joshua trees are imperiled not only by hotter and drier climates but also by invasive, fire-prone annual grasses, whose growth is promoted by nitrogen-laden smog blown in from the Los Angeles basin to the west (Rao *et al.* 2010). Grass-infested areas have altered the park's historical fire regimes, with fires becoming more frequent and larger, as well as having higher burn severities (Brooks and Matchett 2006). Approximately one-quarter to one-half of the mapped Joshua tree refugia in JTNP has already burned (Figure 4); Joshua trees generally do not recover following fire (DeFalco *et al.* 2010). Regardless of the temperature buffering capacity of identified climate refugia, Joshua trees and much of the associated Mojave Desert vegetation are also at risk from invasive grass-catalyzed wildfires.

Using the validated climate-change refugia as justification, in 2017 and 2018, JTNP managers obtained funding to identify and implement cost-effective methods to reduce annual grass fuels, and then, with mapped and validated Joshua tree refugia in hand, prioritized treatments to control these invasive grasses. Manual removal of grasses and fuel material along existing roads enhanced their function as firebreaks and improved

access routes for safer fire suppression among fire crews (Figure 5). In addition to acting as fire planning and prevention tools, this information is also being applied within a resource advisor context; that is, resource advisors can access this information to guide fire suppression and mitigate or prevent damage from suppression tactics within these areas. While it is daunting for land managers to tackle climate change directly, it is possible to prioritize management actions in identified (and validated) climate refugia to protect the species therein and thus provide the best opportunity to sustain populations into the future.

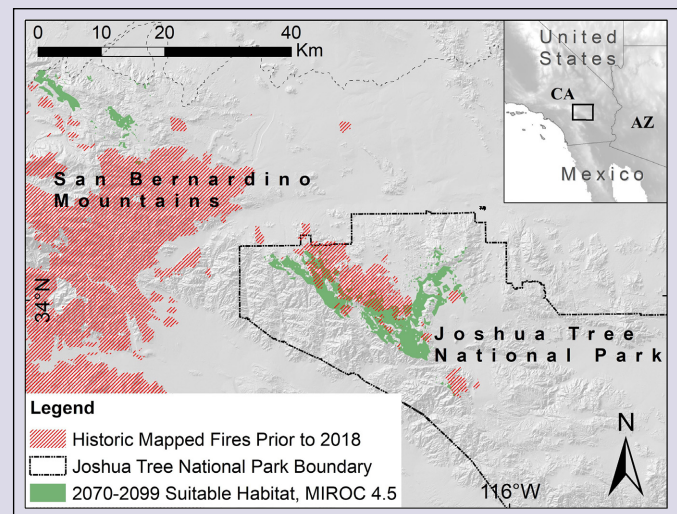


Figure 4. Distribution of modeled end-of-century Joshua tree (*Yucca brevifolia*) refugia under Model for Interdisciplinary Research on Climate (MIROC) RCP 4.5 (green), and overlap with mapped historical fires (red cross-hatching) within Joshua Tree National Park, adapted from Figure 2 in Sweet *et al.* (2019). Data from National Park Service/Joshua Tree National Park and CalFire Fire Resource Assessment Program (as of 2019; <https://frap.fire.ca.gov>); basemaps generated from USGS NED (<http://ned.usgs.gov>).

connect applied climate science to on-the-ground management in the 21st century.

Partnerships between scientists and managers can increase the capacity required to generate these types of data at the scales that are appropriate to management. Identifying and then validating climate-change refugia highlights an emerging need to step up landscape-level land management to maintain habitat for species facing the multiple threats posed by development, invasive species, and altered disturbance regimes. Management actions (eg restoration initiatives, protected-area designations) often represent substantial investments, and managers typically have many other priorities to consider besides refugia (eg regulatory requirements, public perceptions). As such, there is a high “burden of proof” needed for managers to justify expending resources on protecting climate-change refugia to their respec-

tive agencies and to the public. Once refugia are validated, land managers can then assess what, if any, additional threats exist, and take action to mitigate for and reduce those threats. Our hope is that the validation and application of this knowledge to management will provide a framework for future climate-change refugia research and management.

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Figure 5. (a) Joshua trees on fire; (b) aftermath of that same fire; (c) field crews creating fuel breaks to protect Joshua tree refugia; (d) fuel break to lessen the risk of fires spreading.

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Changing color can have health benefits

The Chinese giant salamander (*Andrias davidianus*) – one of the world's largest and most ancient amphibian species, having existed for more than 350 million years – is often described as a living fossil. Nowadays, it is classified as Critically Endangered by the IUCN Red List, since its populations have declined dramatically owing to habitat degradation and unsustainable exploitation.

An interesting phenomenon observed among giant salamanders is their changing skin color. When the larvae live in caves, their body color is light, but when they are outside the caves, they exhibit a dark coloration. Here, we show a light individual (from inside an underground cave in Zhangjiajie Forest Park, in Hunan Province, China) and two dark individuals (from outside the cave) side-by-side.

Skin pigment change is a well-known phenomenon in many animals. For example, chameleons change skin color as a defense mechanism so that they can blend unobtrusively into the background to avoid predation. However, the giant salamander is not using this as camouflage or to escape predators. We believe it is an adaptive strategy for living in different ambient light levels, since dark skin pigment acts as an antioxidant, and has anti-ultraviolet-light and antimicrobial properties. Understanding this phenomenon could enrich our knowledge of the giant salamanders' responses to changing light levels, given their unique evolutionary position in the transition from aquatic to terrestrial vertebrates.

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