Vegetation refugia can inform climate-adaptive land management under global warming

James H Thorne1*, Melanie Gogol-Prokurat2, Sandra Hill2, Dana Walsh3, Ryan M Boynton1, and Hyeyeong Choe4

Natural resource managers need information about the risks associated with climate change to provide guidance on where to implement various management practices on natural lands. The spatial variation of projected impacts within a vegetation type can be used to target climate-adaptive management actions because different locations will be exposed to different levels of climatic stress. Vegetation refugia are areas that retain non-stressful climate conditions under future climates. Consensus vegetation refugia – areas retaining suitable climates under both wetter and drier future projections – represent only 14.6% of California’s natural vegetation. One state and one federal government agency have incorporated vegetation refugia maps into conservation planning for 522 vertebrate species and for post-wildfire reforestation. Monitoring how vegetation responds to management actions at sites within vegetation refugia can improve the conservation of plants subjected to a changing climate.

Land managers increasingly must develop and apply climate-adaptive management actions for the natural resources under their administration. One major issue they face is where and how to manage for persistence of existing resources, and where managing for transition might be more effective (Millar and Stephenson 2015). Recent ecological research about climate change has largely focused on its spatially dynamic components: that is, the velocity of climate change (Loarie et al. 2009); where analogous climate conditions might be found (Dobrowski and Parks 2016; Choe et al. 2017); and where species ranges, defined by climatically suitable conditions, may shift through time (Elith and Leathwick 2009). These types of projections can predict large latitudinal shifts (Dobrowski and Parks 2016), and can be a factor in considerations of landscape connectivity (Keeley et al. 2018). However, resource managers often must address more localized challenges, and they need information that provides context for a portfolio of climate-change adaptation strategies and actions, for lands they manage at local to watershed-scale extents. Such information can be used in adaptive management, in which iterative alterations to management approaches can be made based on the results of ongoing efforts. This iterative process can be guided by models that portray spatial variation of climate exposure on the landscape, and the outputs of which can be analogous to place-based risk assessments used in other disciplines, such as urban development planning (Brody et al. 2007). These types of models can help to identify climate refugia: locations that are expected to be buffered from climate change such that they remain suitable for extant species or groups of co-occurring dominant plant species (hereafter, “vegetation types”). Identification of refugia locations may present landscape managers with opportunities to continue to manage for existing habitats rather than for change (Morelli et al. 2016), and opens up the possibility of applying different land management treatments across the landscape based on anticipated impacts of climate change, particularly if this can be done with regular communication between resource managers, scientists, and stakeholders (Enquist et al. 2017).

We used a climate exposure analysis for 96% of lands primarily dominated by natural vegetation in California (340,350 km²) to identify possible vegetation refugia, which we defined as areas within the current extent of a vegetation type where future climate conditions are similar to those that this type of vegetation frequently occupies at present. We also defined consensus vegetation refugia as areas that remain climatically suitable for existing vegetation under the two climate-change

---

1Department of Environmental Science and Policy, University of California–Davis, Davis, CA *(jthorne@ucdavis.edu); 2California Department of Fish and Wildlife, Sacramento, CA; 3Eldorado National Forest, US Department of Agriculture Forest Service, Georgetown, CA; 4Kangwon National University, Chuncheon, South Korea

© 2020 The Authors. Frontiers in Ecology and the Environment published by Wiley Periodicals LLC on behalf of the Ecological Society of America.
projections used in this study (ie hotter and drier versus warmer and wetter conditions).

We used a California State Department of Forestry and Fire Protection satellite-imagery–derived land-cover map (FRAP 2016; WebFigure 1) containing 43 vegetation types that make up the natural vegetation of the state (as opposed to human land uses such as agriculture and urban), and classified the frequency with which each type occupies a range of current climate conditions. The use of satellite-derived vegetation maps in defining climate classifications offers the benefit of a large number of samples to define a vegetation type’s climate space, and also permits the mapping of distinct levels of future climate stress within its extent. To date, the approach has been applied to the forest types of the southwestern US (Thorne et al. 2018), to California’s natural vegetation types (Thorne et al. 2017), to the temperate forests of East Asia (Choe and Thorne 2019), and to a study of two axes of natural vegetation types (wet-to-dry tropical forests and chaparral-to-oak-to-pine/oak forests) in Oaxaca, Mexico (Williams et al. 2018).

We discuss uses of vegetation refugia maps and show how they are being applied by two government agencies – California Department of Fish and Wildlife (CDFW) and the US Forest Service – that manage natural resources for their planning and land management activities. In the first example, an agency that manages wildlife is using the maps to identify areas of lower climate vulnerability for the habitat of vertebrate species. The second example highlights the use of vegetation refugia maps as ancillary information for forest restoration after a large wildfire.

Methods

To combine the vegetation map from FRAP (2016) with current and future climates, we extracted 100,000 randomly selected grid cells from the vegetation map’s 4.8 million 270-m × 270-m grid cells and applied a principal components analysis (PCA) to nine climate variables associated with each location, to reduce the dimensionality of the climate data to two axes (WebPanels 1 and 2; WebTable 1). The 100,000 scores from the first two axes of the PCA were partitioned into each vegetation type, to represent the range of climates occurring within each type’s extent. We then used a kernel density estimator to classify the frequency distribution of current time period (mean of 1981–2010) and future (mean of 2070–2099) climatic conditions found in the grid cells of each vegetation type (WebFigure 2; Thorne et al. 2016, 2017). We classified the climate frequency distribution for each vegetation type in the current time period as follows: the central 80% of its distribution was considered to be climatically non-stressful, the following 15% of the distribution had uncertain levels of stress, and the marginal 5% of the distribution was considered to be climatically stressful (WebFigure 3). For each of the 43 vegetation types, we used the climate conditions identified in the central 80% of its current climate distribution to define the conditions for its vegetation refugia in the future, and then applied this classification to all of the grid cells of that particular vegetation type. We then analyzed changes in climatic conditions within each vegetation type for two global climate models (GCMs), CNRM-CM5 (Centre National de Recherches Météorologiques–Climate Model version 5; Voldoire et al. [2013]; a warmer and wetter future) and MIROC-ESM (Model for Interdisciplinary Research on Climate–Earth System Model; Watanabe et al. [2011]; a hotter and drier future), for the representative concentration pathway 8.5 (RCP8.5) emissions scenario (ie the "business as usual" pathway). These climate futures bracket conditions by +28.7% or –24.3% mean annual precipitation and by +3.1 to +3.8°C mean warming, respectively, for California for 2070–2099 (WebPanel 1).

For each climate future, we assessed which areas within the extents of the 43 vegetation types will qualify as vegetation refugia by the end of the century. We combined the maps and spatially intersected the vegetation refugia predicted under the two GCMs; doing so reduced the overall extent of areas predicted to remain suitable but also reduced uncertainty for field operations by identifying consensus vegetative refugia (areas predicted to remain climatically suitable for extant vegetation within an explicit range of bounding conditions).

Results

Of the 340,350 km² included in our analysis, 49,877 km² (14.6%) was identified as consensus vegetation refugia. An additional 31,535 km² remained within the 80% frequency cutoff under CNRM-CM5 (ie the warmer and wetter future) and 56,919 km² remained under MIROC-ESM (ie the hotter and drier future) (Figure 1). Large areas where adjoining vegetation types occur within consensus refugia included the northwest Klamath Mountains, the northern Sierra Nevada, and California’s Central Coast Ranges.

Eleven of the 43 vegetation types had over 20% of their extent within climate refugia, with the largest being the middle-elevation montane chaparral (57.2% of its range), Klamath mixed conifer (56.8%), and Douglas fir (Pseudotsuga menziesii) forests (26.6%) (WebTable 2). In contrast, nine of the 43 vegetation types had no extent and eight have less than 1% remaining within consensus vegetation refugia (WebTable 2). Moreover, the ranges of certain iconic vegetation types were poorly represented within the consensus refugia, including coast redwood (Sequoia sempervirens) forests (0.4% of its range), coast live oak (Quercus agrifolia) woodlands (3.8%), and red fir (Abies magnifica) forests (2.3%). Three forest types – Klamath mixed conifer, Sierra mixed conifer, and Douglas fir forests – occupied consensus vegetation refugia across large
Recognizing vegetation refugia in the Central Coast Ranges, a highly plant-diverse region (Thorne et al. 2009; Burge et al. 2016), the Klamath Mountains and Central Coast areas identified as consensus vegetation refugia were also identified as potential climate-change refugia by Michalak et al. (2020) because of their low climate exposure, high environmental diversity, and accessibility of suitable future climatic conditions.

Some elevation and latitudinal patterns were evident. The two oak-dominated vegetation types at lower elevations—blue oak (Quercus douglasii) woodlands and blue oak–foothill pine (Pinus sabriniana) woodlands—had lower representation in consensus vegetation refugia than the two oak-dominated vegetation types at higher elevations: namely, mixed hardwood and montane hardwood conifer (Figure 2; WebTable 2). Similarly, lower-elevation mixed chaparral had proportionally less area in consensus vegetation refugia (33.2%) than higher-elevation montane chaparral. Moreover, the hotter and drier (MIROC-ESM) model identified (non-consensus) refugia closer to the coast of the Pacific Ocean (red in Figure 1), whereas the warmer and wetter (CNRM-CM5) model identified (non-consensus) refugia (blue in Figure 1) along the more-easterly inner Coast Ranges and at higher elevations in the Sierra Nevada.

Incorporating vegetation refugia maps into land management

**Vertebrate species conservation by the CDFW**

The CDFW analyzed the extent to which climate exposure could impact the habitat of 522 vertebrate species in California (Gogol-Prokurat and Hill 2019), based on (1) climate exposure results obtained from the current study and from Thorne et al. (2017) and (2) output from the California Wildlife Habitat Relationships model (CDFW 2014), which describes vegetation types that represent habitats commonly used by each of these species. This model relies on the FRAP (2016) vegetation map (that is, the same land-cover map used in the current study) to generate distribution maps of potentially suitable habitat for these species. Assessing the consensus vegetation refugia within each species’ suitable habitats identifies those parts of each species’ range that are most likely to persist under future climate conditions, such as for the California towhee (Melozone crissalis; Figure 3).

The distribution and persistence of suitable habitat under future climates will play an integral role in shaping the future distributions of species. The refugia locations identified in the present study are being used in conjunction with data on how species’ ranges may shift over time (WebPanel 3) and assessments of species’ sensitivity and adaptive capacity (WebPanel 1) to inform CDFW evaluations of the vulnerability of the 522 vertebrate species. The results provide crucial information for vertebrate species conservation and climate adaptation planning by helping to identify areas where conservation efforts are most likely to be successful under future climate conditions. The vegetation refugia maps are being integrated with other conservation-relevant information in CDFW’s Areas of Conservation Emphasis tool (www.wildlife.ca.gov/Data/Analysis/Ace) to provide spatially explicit guidance to the agency’s efforts to manage vertebrate biodiversity, implement the California State Wildlife Action Plan (www.wildlife.ca.gov/SWAP/Final) and its Biodiversity Initiative (https://wildlife.ca.gov/Science-Institute/Biodiversity), and provide context for conservation and restoration decision making.

**Reforestation of a wildfire area by the US Forest Service**

In California, wildfire size and severity are increasing (Steel et al. 2018), wildfires are occurring at higher elevations (Schwartz et al. 2015), and fire risk is expected to grow under future warming (Westerling 2018). These conditions necessitate new strategies for land managers tasked with post-fire restoration...
Figure 2. (a) At lower elevations, the southern Sierra Nevada currently contains two vegetation types dominated by blue oak (*Quercus douglasii*). These woodlands adjoin two upper-elevation forest types that contain black oak (*Quercus kelloggii*). (b) Consensus vegetation refugia are projected to be found only along the upper elevations of montane hardwood forests, suggesting an upslope retreat for that vegetation type; in contrast, no climatically suitable areas remain for the blue oak woodlands within their current extent in this area. The white area shows the current extent of all oak types mentioned, while the gray area currently is occupied by other natural vegetation types.

Figure 3. Finding habitat that remains climatically suitable for (a) the California towhee (*Melozone crissalis*), which uses several vegetation types, including (b) various oak woodlands, and urban areas as habitat. (c) We examined vegetation comprising suitable habitats for the towhee in its range to identify the areas that remain climatically suitable for this species under the two GCMs analyzed. We expect that the consensus vegetation refugia from the two GCMs (in green) will be the most likely areas to remain suitable for the towhee as the climate changes.
Identifying vegetation refugia

CLIMATE-CHANGE REFUGIA

For example, California’s 2014 King Fire burned 259 km² of the Eldorado National Forest, the staff of which are now engaged in reforestation. Planning reforestation for such a large area requires consideration of many factors, including slope steepness and position, burn severity, access via dirt roads, previous forest composition, the ability to protect reforestation investments given future fire potential, and the possible effects of future climate change (Figure 4). Post-fire reforestation planning following the King Fire included identifying locations within the fire perimeter that were at lower climatic risk for replanting species of trees that grew there previously. Within this burn area, the wetter and drier future projections indicated the presence of non-consensus (non-overlapping) vegetation refugia but only a minimal degree of consensus (overlapping) vegetation refugia.

Of the Eldorado National Forest lands that were completely deforested by the King Fire, so far only about 10% of the area has been reforested and less than half of that area is currently scheduled for reforestation over the next several years. Reforestation guidelines from the US Forest Service for California specify that seeds from within the same seed zone be used when replanting a given area (Buck et al. 1970). However, to date, planting efforts to move seedlings not only from their parent trees to higher elevations but also from other areas, primarily from south to north, have occurred only to a limited extent, due in part to seedling availability; these actions are meant to better align the area’s existing tree species with future climate conditions. For planned reforestation plantings, evaluation of the suitability of planting pre-fire tree species given future climate conditions has generally considered the vulnerability of pre-fire vegetation under a single future climate and time. This has allowed for some prioritization of planting at sites where current forest types are more likely to persist and has limited planting in areas that are likely to be more vulnerable to loss. At a subset of sites identified as highly vulnerable to climate change, planting of pre-fire vegetation was allowed to proceed for reasons other than to maintain long-term species persistence, an acknowledgment that reforestation benefits at these locations may be relatively short term. A more thorough evaluation of climate exposure and predicted locations of refugia could better inform species-specific planting decisions with respect to site selection, planting densities, and seed sources. At present, it is difficult to isolate the influence of climate change on the early survival of planted seedlings from other factors, such as handling of seedlings, timing of planting, local competition for resources, annual weather patterns, and seed sources. To make inferences about the impacts of factors (both related and unrelated to climate change) on seedling survival, resource managers will be required to monitor trees over the long term.

Discussion

Place-based hypotheses

Place-based and spatially dynamic models provide complementary views of the impacts of climate change. For a vegetation type at a specific location, the arrival or departure of species is potentially connected with species’ range shifts, which are frequently modeled using a biogeographic framework (eg Choe et al. 2017). This species turnover may be initially exhibited as changes in the relative abundance of species, such as observed increases in the prevalence of oaks as compared to pines in California (McIntyre et al. 2015). Such transitions may continue until a different vegetation type occupies the site, particularly if a disturbance event removes the dominant species (Goforth and Minnich 2008;
Davis et al. 2019). Nevertheless, many land managers use existing vegetation as the spatial framework for their planning and operations; are increasingly challenged to invest limited resources either to retain current vegetation or to manage for transition (Millar and Stephenson 2015); and often want to retain existing vegetation for such benefits as habitat for animals, ecosystem processes, and cultural values.

Maps of vegetation refugia can also be used to determine locations where existing vegetation could be retained. This place-based approach permits testing spatial hypotheses by being explicit about the threshold assumptions of what constitutes suitable or less stressful climate conditions. For example, after a wildfire, scientists and managers can identify areas where planting the dominant plant species that previously occupied the site could result in successful establishment, and areas where those plantings are expected to fail. If “real-world” survival follows those modeled spatial patterns, then the assumption of an 80% suitability threshold for vegetation refugia may be accurate. If the planting fails, however, perhaps the suitability threshold is actually lower, and only sites retaining a more narrow range of original conditions (eg 50%) are suitable. Conversely, if planted areas that are expected to fail in actuality do well, perhaps either the vegetation can tolerate a wider range of climates, or site conditions are buffering climate conditions to a greater extent than hypothesized when the marginal 5% of current climate conditions is considered stressful (Thorne et al. 2017). In this manner, managers and researchers can jointly design and monitor hypothesis-driven experiments (Hallett et al. 2017) that are embedded in adaptive land management. All land management actions (or inaction) are experiments under climate change. Testing spatial hypotheses through this climate-exposure approach facilitates understanding of how sites interact with climate change as the results of management actions are monitored.

**Focusing landscape management activities**

Large expanses of vegetation refugia may be candidates for scaled-up land management for climate resilience. However, while consensus vegetation refugia can define areas most likely to retain standing vegetation, active management of those areas may still be needed due to the increasing frequency of climate-related disturbances, such as flooding, wildfire, pest and pathogen outbreaks, and invasive species (Morelli et al. 2016). Context to help land managers decide where to expend limited capacity to maximize ecosystem function and resilience across landscapes is therefore critical, and this requires multi-objective optimization modeling (Yoon et al. 2019), further experimentation, and the development of explicit frameworks of vegetation response to land management actions, which can lead to better understanding of the ecosystem and ecological processes at site-level scales. In some cases, the use of focal species models (eg dynamic demographic/dispersal models; Perez-Garcia et al. 2017) can help to identify underlying ecological processes and inform species-specific climate-adaptation plans. Assessment of the climate vulnerability of individual species, which is based on their sensitivity and adaptive capacity as well as their exposure to climate change, can also be informative for land management (WebPanels 1 and 3; Thorne et al. 2016). We suggest that land managers in California consider vegetation refugia as areas of potentially higher value through the end of the century because they have the potential to retain existing ecosystem and habitat functions (Morelli et al. 2016). The two examples presented above illustrate how vegetation refugia can be used to prioritize locations for preservation of the existing habitat of vertebrate species and to inform post-wildfire reforestation decisions about what species combinations to plant.

**Scale of refugia through time**

Because this method of defining vegetation refugia was developed to visualize variation in future climate stress across lands managed by resource managers, the spatial patterns produced are not tied to other types of refugia, such as those associated with landscape processes. Local elements such as areas within a wildfire that do not burn (Krawchuk et al. 2020) or landscape elements that persist across centuries even while the surrounding dominant vegetation continues to transition (Cartwright 2019) may be prioritized for conservation under climate change. Vegetation refugia identify spatial patterns of mean climate stress according to projected climate futures. The effects of climate change are expected to intensify and continue beyond 2100, and the locations we identify should therefore perhaps be considered as transient or stepping-stone refugia (Morelli et al. 2020). If, in the future, such places transition to new assemblages of plant species, then those locations may be better suited for that vegetation. If the existing species assemblages persist over even longer times, then these locations might be considered climate refugia in the long-term sense of the word. It is our task to identify such potential areas and consider what interventions, if any, would best promote such a future.

**Acknowledgements**

Publication of this Special Issue was funded by the US Department of the Interior National, Northeast, and Northwest Climate Adaptation Science Centers. Thanks to TL Morelli for comments.

**References**

Brody SD, Azhran S, Maghelal P, et al. 2007. The rising costs of floods: examining the impact of planning and development decisions on property damage in Florida. J Am Plann Assoc 73: 330–45.

Buck JM, Adams RS, Cone J, et al. 1970. California tree seed zones. San Francisco, CA: US Forest Service.
CLIMATE-CHANGE REFUGIA  287

Keeley ATH, Ackerly DD, Cameron DR, et al. 2018. New concepts, Hallett LM, Morelli TL, Gerber LR, et al. 2017. Navigating transla-
Gogol-Prokurat M and Hill S. 2019. Assessment of climate impacts to
Morelli TL, Barrows CW, Ramirez AR, et al. 2020. Climate-change refugia: biodiversity in the slow lane. Front Ecol Environ 18: 228–34.

Steel ZL, Koontz MJ, and Safford HD. 2018. The changing landscape of wildfire: burn pattern trends and implications for California’s yellow pine and mixed conifer forests. Landscape Ecol 33: 1159–76.

Thorne JH, Boynton RM, Holguin AJ, et al. 2016. A climate change vulnerability assessment for California’s vegetation: a macro-habitat scale for aggregated terrestrial vegetation types. Sacramento, CA: California Department of Fish and Wildlife.

Thorne JH, Choe H, Boynton RM, et al. 2017. The impact of climate change uncertainty on California’s vegetation and adaptation management. Ecosphere 8: e02021.

Thorne JH, Stine WP, Chambers J, et al. 2018. Climate change vulnerability assessment of forests in the Southwest US. Climatic Change 148: 387–402.

Voldoire A, Sanchez-Gomez E, Salas D, et al. 2013. The CNRM-CM5.1 global climate model: description and basic evaluation. Clim Dyn 40: 387–402.

Watanabe S, Hajima T, Sudo K, et al. 2011. MIROC-ESM 2010: model description and basic results of CMIP5-20c3m experiments. Geosci Model Dev 4: 845–72.

Westerling AL. 2018. Wildfire simulations for California’s Fourth Climate Change Assessment: projecting changes in extreme wildfire events with a warming climate. Sacramento, CA: California Energy Commission.

Williams JN, Rivera R, Choe H, et al. 2018. Climate risk on two vegetation axes – tropical wet-to-dry and temperate arid-to-moist forests. J Biogeogr 45: 2361–74.

Yoon EJ, Thorne JH, Lee DK, et al. 2019. Modeling land use adaptations to mitigate climate change impacts on disaster, rice yield, and species richness using multi-objective genetic algorithms. Environ Res Lett 14: 024001.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2208/supinfo