Disturbance refugia within mosaics of forest fire, drought, and insect outbreaks

Meg A Krawchuk1*, Garrett W Meigs1†, Jennifer M Cartwright2, Jonathan D Coop3, Raymond Davis4, Andrés Holz5, Crystal Kolden6, and Arjan JH Meddens7

Disturbance refugia – locations that experience less severe or frequent disturbances than the surrounding landscape – provide a framework to highlight not only where and why these biological legacies persist as adjacent areas change but also the value of those legacies in sustaining biodiversity. Recent studies of disturbance refugia in forest ecosystems have focused primarily on fire, with a growing recognition of important applications to land management. Given the wide range of disturbance processes in forests, developing a broader understanding of disturbance refugia is important for scientists and land managers, particularly in the context of anthropogenic climate change. We illustrate the framework of disturbance refugia through the individual and interactive effects of three prominent forest disturbance agents: fire, drought, and insect outbreaks. We provide examples of disturbance refugia and related applications to natural resource management in western North America, demonstrate methods for characterizing refugia, identify research priorities, and discuss why a more comprehensive definition of disturbance refugia is relevant to conservation globally.

Front Ecol Environ 2020; 18(5):235–244, doi:10.1002/fee.2190

Natural disturbances drive change and shape landscapes, thereby supporting local and regional biodiversity in forested ecosystems. By creating heterogeneity in ecosystem attributes (e.g., soils and vegetation), these disturbances contribute to landscape-scale patterns and processes, including interactions between the local environment and species in the metacommunity (Turner 2010). Although disturbances can be beneficial to the maintenance of biodiversity in an ecosystem, those that exceed the historical range of variability can have adverse short- and long-term consequences (Landres et al. 1999). Ongoing global environmental change, including anthropogenic climate change, is raising concerns about the loss of forests and their biodiversity, and the role that natural and anthropogenic disturbances play in such losses (Millar and Stephenson 2015). Amid these concerns is a growing recognition of the importance of refugia, and especially disturbance refugia, as critical buffers to rapid ecosystem change (Morelli et al. 2020).

Refugia science is a subdiscipline that bridges diverse perspectives of biodiversity conservation, and refugia can be defined in multiple ways. They are considered “habitats that components of biodiversity retreat to, persist in, and can potentially expand from under changing environmental conditions” (Keppel et al. 2012), and climate-change refugia are “areas relatively buffered from contemporary climate change over time that enable persistence” (Morelli et al. 2016). Here, following the language used in Krawchuk et al. (2016) and Meddens et al. (2018a) to describe fire refugia, we define “disturbance refugia” as locations that are disturbed less severely or less frequently than other areas within the surrounding landscape. Our broad definition includes all disturbance types and their effects (both individual and interacting) within one comprehensive framework to facilitate their comparison and synthesis, but here we focus on three prominent disturbance types: fire, drought, and insect outbreaks. Although the term “disturbance refugia” has been used in the past (e.g., Lindenmayer and Franklin 2002), as interest in refugia concepts continues...
to grow in scientific and conservation communities in the context of climate change (Keppel et al. 2015; see also the papers in this Special Issue), it is important to advance our understanding of disturbance refugia, to learn how to detect and quantify them, and to assess their value in sustaining species and mediating trajectories of environmental change in forest ecosystems.

Disturbance refugia in forest ecosystems are important contributors to climate-change adaptation through their role as legacies that change more slowly than their disturbed surroundings. As such, they provide holdouts and stepping-stones for species and processes associated with refugia structure and function (for definitions of selected specialist terminology, see WebPanel 1 in Morelli et al. [2020]). In turn, disturbance refugia contribute to post-disturbance recovery and support the persistence of species as they adapt to landscape change (e.g., seed sources, habitat, and genetic variability). The overlap of disturbance refugia with climate-change refugia at micro and macro scales may provide critical sites within landscapes for organisms to adapt and move in response to global environmental change. Climate-change refugia and disturbance refugia are inevitably linked by common biophysical processes in some though not all situations, and collectively contribute to heterogeneous patterns of change (Morelli et al. 2020).

We synthesize recent research addressing forest fire, drought, insect outbreaks, and their drivers and interactions to illustrate a disturbance refugia framework. We build on the established idea that disturbance events generate mosaics of severity and focus deliberately on the low end of these disturbance-severity gradients in forests. Existing research on disturbance refugia in forests has predominantly focused on fire refugia (Meddens et al. 2018a), with more limited attention paid to hydrologic and drought-event refugia (McLaughlin et al. 2017), and has only recently looked at biotic disturbances like insect outbreaks (Cartwright 2018). Accordingly, in this review, we examine multiple agents of disturbance and their interactions, describe state-of-the-art methods to detect disturbance refugia, illustrate examples of disturbance refugia and related applications to land management based on our experiences in western North American forests, and explain why general principles of disturbance refugia are pertinent to conservation globally.

### The disturbance refugia framework

Disturbance refugia are one component of the complex mosaics produced by disturbances in forest ecosystems (Figure 1). These refugia contain information and material legacies (Johnstone et al. 2016) that persist through the filter of disturbance. Legacies vary among disturbance types, regimes, and associated environmental gradients (Figure 2). For example, in subalpine or boreal forests of North America where relatively infrequent, high-severity fire is typical under historical and contemporary regimes, fire refugia could be thought of as islands where forest canopy persists in a matrix dominated by tree mortality, in a manner consistent with the principles of island biogeography. In these ecosystems, landscape-scale biodiversity is maintained by the forest community inside fire refugia at one end of the disturbance gradient, complemented by early successional “pre-forest” communities (Swanson et al. 2011) outside of fire refugia, with species well adapted to, or even requiring, high-severity fire and the successional
trajectories in between. In this simplified scenario, fire refugia are locations of persistent canopy through one fire event, but they can take on many different forms and be characterized across multiple spatial and temporal scales (Meddens et al. 2018a). Disturbance refugia can be viewed at spatial scales spanning from genetic loci and individual organisms, to species, to forest stands and landscapes. These refugia can be characterized in terms of persistence through one versus multiple disturbance events, as truly undisturbed areas versus those affected at low severity (lower than surroundings), and as stochastic features of forests versus more predictable ones (Figure 3), all of which are elements of a formal classification of disturbance refugia. When disturbance effects are more fine-grained, diffuse, or variable, such as in systems dominated by non-stand-replacing fire or disturbances like drought or insect outbreaks, the before-mentioned “islands” analogy is less effective at characterizing disturbance refugia. Differences in disturbance regimes, species composition, and evolutionary adaptations will translate into different ecological patterns, scales, and roles of disturbance refugia expressed along biophysical gradients and among forest ecosystems globally. To help inform the science and management of disturbance refugia, we present emerging research questions (WebTable 1) that are aimed at a broader understanding of these features in forest ecosystems in the context of climate change.

The potential ecological functions of disturbance refugia are diverse, as documented in the scholarly literature and inferred from ecological theory. Disturbance refugia can provide reservoirs of plant genetic diversity (Xu et al. 2018), seed sources for regeneration of surrounding disturbed areas (Haire and McGarigal 2010), critical resources for wildlife during and after disturbances (Robinson et al. 2013), diverse forest structure and composition (Meigs and Krawchuk 2018), microclimatic buffering of sub-canopy climate (Davis et al. 2019), and values to Indigenous cultures (Long et al. 2018). Identifying any particular disturbance refugium and its associated ecological roles can be clarified by asking, “a refugium from what?” (eg from stand-replacing fire) and “a refugium for what?” (eg for a mature forest obligate). For example, in seminal work on forest fire refugia, Camp et al. (1997) specifically sought to identify historical fire refugia as habitat for the northern spotted owl (Strix occidentalis caurina). Although most studies of disturbance refugia have focused on wildfire, we emphasize that the functions of refugia are likely similar in the context of drought or insects, as well as hurricanes, floods, windstorms, pathogens, invasive species, avalanches, landslides, forest harvest, and other agents of forest disturbance. Below, we illustrate the refugia framework for three distinct disturbance types – fire, drought, and insect outbreaks – and their potential interactions.

Fire refugia

Wildfire is an abrupt agent of forest change, and fire regimes – along with other factors of the biophysical template (geology, topography, climate, biota) – are a fundamental determinant of landscape pattern for many forest ecosystems. Fire refugia form across multiple spatiotemporal scales and support the maintenance of biota, ecological functions, and ecosystem services through single or multiple fire events (Meddens et al. 2018a). Fire refugia include areas that seldom burn (ie frequency refugia: forests with low frequency of fire events either at local scales, or even across an entire ecosystem) and refugial locations within a fire event (ie severity refugia) that represent unburned and/or low-severity areas. Refugia occurrence and probability are predictable for some fire refugia (ie through local and landscape topography, fuels, and vegetation traits), whereas others are largely stochastic, driven by fire behavior, weather, and fire suppression (Figure 3). Furthermore, the occurrence of fire refugia appears to vary depending on weather conditions (Krawchuk et al. 2016; Collins et al. 2019), so that more extreme winds, heat, and/
or drought degrade the protection from fire conferred by topographic position, context, or forest structure.

Wildfire activity is increasing under anthropogenic climate change (Abatzoglou and Williams 2016), and projected increases in the likelihood of large fires through the 21st century (Barbero et al. 2015) will have important implications for the distribution and function of fire refugia. Although climate-change–induced trends in wildfire refugia occurrence have not surfaced in recent records (Meddens et al. 2018b), observed relationships among climate metrics, weather, and refugia patterns suggest a reduction in fire refugia in future climates (Kolden et al. 2015; Krawchuk et al. 2016). Projected continuing anthropogenic alteration of fire regimes via climate change and associated drought and vegetation dynamics, coupled with the effects of fire suppression and other anthropogenic activities, suggest that the formation, composition, and stability of fire refugia will change (and likely diminish), potentially altering their capacity to support the resilience of forest ecosystems.

**Drought refugia**

Drought refugia are locations where species are relatively buffered from physiological stress and mortality induced by drought events (ie anomalously dry periods relative to long-term average climatology). Drought refugia can occur where soil moisture is locally elevated (ie hydrologic refugia) or as a result of spatial variation in forest structure and drought-tolerance characteristics (Cartwright 2018). Localized inputs to soil moisture include shallow or discharging groundwater or concentrated surface runoff in areas where topographic features converge (Figure 3; Mackey et al. 2012). Groundwater buffering of soil moisture occurs across a range of scales, from small and isolated springs (Davis et al. 2013) to entire river deltas (Reynolds et al. 2016). Soil moisture losses from evapotranspiration may be lower in areas of topographic shading and wind sheltering, and soil water-holding capacity based on soil particle size, organic matter, and bulk density may also help maintain hydrologic refugia (Cartwright 2018). In addition to these landscape-scale physical processes, drought resistance in forests can arise from physiological traits (Figure 2) that vary among individuals, populations, and species. In California, for example, Malone et al. (2016) found that drought event resistance was strongest in vegetation with the highest baseline water-use efficiency, suggesting adaptation to chronic water limitation.

Increasing drought-induced tree mortality has the potential to push forests past ecological tipping points, resulting in extreme transformations (eg conversion of forests to shrublands or grasslands) and loss of ecosystem services (Millar and Stephenson 2015). Because future drought events will likely be more intense, longer lasting, and more geographically widespread due to climate change (Allen et al. 2010), forest management can benefit from identifying and conserving drought refugia.

**Insect outbreak refugia**

In contrast to fire and drought events, forest insect outbreaks are biotic disturbances and are generally host-specific, impacting certain taxonomic groups and/or size classes of trees (Figure 2). Various insect species (eg bark beetles, defoliators, bud and shoot insects) affect tree physiology differently by feeding on foliage, cambium, sap, or reproductive organs. Outbreak effects range from local reductions in tree health to widespread tree mortality (Pureswaran et al. 2018). By characterizing outbreak refugia as the low end of the outbreak severity gradient (or lack of outbreak), we bring together the range of mechanisms and conditions associated with various insect agents, from forests with diverse tree species compositions, environmental contexts, and associated outbreak dynamics.

Although few studies have explicitly identified refugia from insect outbreaks, the stand and landscape characteristics driving observed spatial patterns in outbreak severity are supported by a robust literature for well-studied forest pests (eg mountain pine beetle [Dendroctonus ponderosae]; Raffa et al. 2008). This existing knowledge can inform hypotheses about spatiotemporal patterns of outbreak refugia (eg see Table 1 in Cartwright [2018]). Similar to the distribution of fire and drought refugia, the distribution of outbreak refugia could be driven by landscape physical characteristics, forest stand characteristics, and population demographics of host tree
species, as well as vigor and genetic traits of individuals con-
ferring insect resistance (Figure 3; Cartwright 2018). For ex-
ample, we might hypothesize that refugia from mountain
pine beetle could occur in areas with cooler temperatures (eg
from topographic shading) that protect trees from water
stress; in areas with lower host density, allowing for greater
wind disruption of beetle pheromone communication and
more vigorous tree growth and chemical defenses; and in
areas with fewer large-diameter host trees or among trees
with greater investment in insect-resistance strategies, such as
resin ducts.

Disturbance refugia and overlapping disturbances
Forest ecosystem dynamics include multiple types of dis-
turbances, whose co-occurrence and interaction can enhance
or erode refugia functionality. The capacity for disturbance
refugia to retain species and structure and promote recovery
of their surroundings through successive disturbances
depends on disturbance regime (eg type, extent, severity,
frequency), sequence of occurrence, interactions and/or feed-
backs, life-history characteristics of affected forest species,
and post-disturbance climate conditions.

Prior studies of disturbance interactions demonstrate a
wide range of both negative (stabilizing) and positive (ampli-
fying) feedbacks. Negative feedbacks occur when one disturb-
ance enhances resistance of refugia to subsequent events,
or even provides a template for future refugia formation. For
example, repeated low- and moderate-severity fires can reg-
ulate fuel structure, promoting tree survival during subse-
quent fire events (Walker et al. 2018), and low-severity fire
can induce resin duct production in trees, which provides
resistance against subsequent bark beetle attacks (Hood
et al. 2015). Conversely, stand-replacing fire can generate
patches of younger trees that will be less affected by subse-
quent bark beetle-induced mortality (Bebi et al. 2003).
However, positive feedbacks among drought, insects, and
fire may become more prevalent given climate-change pro-
jections. Drought enhances wildfire activity (Abatzoglou
and Williams 2016), increases fire-induced tree mortality
(van Mantgem et al. 2013), increases vulnerability to insects
(Raffa et al. 2008), and reduces post-disturbance tree seed-
ling establishment (Stevens-Rumann et al. 2018). In addi-
tion, insect-caused mortality of mature trees could reduce
the capacity of fire refugia to serve as seed sources for post-
fire tree regeneration (Harvey et al. 2014). Where such posi-
tive feedbacks occur, we anticipate reduced refugia
abundance (Figure 4), impaired refugia function, and slower
forest recovery, with potential for transformation to alter-
nate forest or non-forest states.

Figure 4. Overlapping disturbances may reduce the capacity of the landscape to support refugia and diminish their short-term functioning. In subalpine
forests of the San Juan Mountains of southern Colorado, mature Engelmann spruce (Picea engelmannii; aqua in upper left) trees were killed by the spruce
beetle (Dendroctonus rufipennis; orange in upper right) across large portions of the landscape. Subsequently, much of this area burned during the 44,000
ha West Fork Complex Fire in 2013 (bottom left), resulting in markedly lower spruce cover (blue in lower right). Burn severity within the fire perimeter
ranged from low (blue; refugia) to high (red-orange). Note that the burn severity legend in this panel matches that in Figure 5a. As such, locations and
smaller size classes that were less affected by beetles were subsequently removed by fire, and unburned fire refugia lacked the large seed-bearing
spruce trees that would promote population recovery. Data for pre-disturbance Engelmann spruce cover from FSVeget Spatial (www.fs.fed.us/nrm), bark
beetle damage from US Forest Service aerial detection surveys (www.fs.usda.gov/detail/r2/forest-grasslandhealth), Landsat-derived burn severity from
Monitoring Trends in Burn Severity (www.mtbs.gov), and post-disturbance spruce cover based on Savage et al. (2017).

Front Ecol Environ doi:10.1002/fee.2190
Synthesizing the underlying causes of disturbance refugia and testing generalized spatial hypotheses about why and where refugia from different disturbances co-occur are important next steps in refugia science. For example, based on our understanding of drivers of fire, drought, and outbreak refugia, a subset of these locations may share a common relationship with cooler and/or moister spatiotemporal environments via terrain effects on climate (Dobrowski 2011), and associated plant ecophysiology. Specifically, tree water balance can influence (1) live-fuel moisture that affects fire behavior and severity, (2) physiological water balance that affects drought response, and (3) water-based sap production that affects defense capacity to insect outbreaks. Identifying and testing these types of cross-cutting linkages is an important benefit of bringing multiple agents together under the framework of disturbance refugia. However, given the broad range of processes that generate heterogeneity in forest ecosystems, identifying single unifying drivers of the full suite of disturbance refugia in forest ecosystems (e.g., from hurricanes to harvest) will be a difficult task.

Detection, evaluation, and prediction of disturbance refugia

Numerous methods have been established for the detection, evaluation, and prediction of disturbance refugia. Long-term micro/macrorefugia have been identified using fossil evidence (Magri et al. 2006) and examined via dendrochronology (Holz et al. 2018), which facilitate the reconstruction of past climate-change-vegetation relationships over longer time scales. These approaches can capture enduring refugia through multiple or interacting disturbance events (e.g., wildfire following insect outbreaks). In contrast, field-based studies (Camp et al. 1997), remote sensing (Meddens et al. 2018b), and simulation modeling (Wimberly and Kennedy 2008) can be used to detect and quantify spatially explicit locations of contemporary disturbance refugia (Figure 5). Overall, the integration of multiple techniques for refugia characterization will provide an effective means to investigate disturbance refugia and their origins, as well as their capacity to deliver ecosystem services and sustain biodiversity.

Several emerging methods show promise for future investigations of spatial structure and function of disturbance refugia over time. These new tools contribute to the development of future research questions for disturbance refugia science (WebTable 1). For instance, refugia typically have been described at landscape scales using Landsat imagery with a pixel resolution of 900 m² (Figure 5a). Disturbance refugia can occur at much finer scales (e.g., a single large tree persisting through multiple disturbances might have important ecological or cultural value; Lindenmayer and Laurence 2017), but fine-scale detection requires high spatial resolution satellite data (e.g., WorldView), aerial photography (Figure 5b), or very high-resolution data (e.g., obtained via drone-based lidar and structure-from-motion photogrammetry) that reveal forest structure. Multi-temporal lidar techniques with data collection before and after disturbance have the potential to provide precise information on the structure and composition of refugia, with an opportunity for major improvements in the detection of fire effects (Figure 5c;
Disturbance refugia enable forest persistence

Hoe et al. (2018). Similarly, high-fidelity imaging spectroscopy can reveal canopy water content for individual trees, exposing pockets of hydrologic and drought refugia within landscapes (Asner et al. 2016). Dynamic landscape simulation modeling that explicitly accounts for terrain, vegetation, climate, and multiple disturbances could help to disentangle multiple determinants of forest formation and persistence, especially in the context of ongoing climate change. Finally, research that investigates landscape genetics of different plant species may shed light on the influence of disturbance mosaics and refugia on population dynamics and gene flow (Moran et al. 2017).

Management to promote disturbance refugia

Amid changing forests, natural resource managers remain responsible for achieving multiple objectives, including conserving important species, habitats, and ecosystem goods and services. Two case studies (Panels 1 and 2) illustrate the potential for disturbance refugia to support management actions for the conservation of vulnerable forests and the species they harbor; fire refugia and conservation in late-successional forests in the northwestern US are discussed in Panel 1, while early application of fire refugia science by managers and conservation practitioners in the southwestern US is highlighted in Panel 2.

Land managers have implemented strategies to increase forest resistance and/or resilience to disturbance, some of which also sustain disturbance refugia. For example, managers can facilitate fire refugia through fire suppression and exclusion but also through broader forest restoration practices such as implementing prescribed fires, thinning trees, and allowing some wildfires to burn to achieve resource benefits. Practices that ameliorate water stress to plant communities may help to create and sustain various refugia from
multiple disturbances, including fire, drought, and insect outbreaks. In addition, measures to conserve drought refugia may include protecting aquifers from groundwater extraction, contamination, and salinization (e.g., Davis et al., 2013), along with efforts to enhance drought resistance (e.g., propagation of trees with desired physiological traits; Millar and Stephenson, 2015). Assessing the effectiveness of such practices to protect or promote refugia is an emerging research need (WebTable 1) as well as a necessary component of adaptive forest management. Collaborative efforts between researchers and practitioners can encourage the development of important scientific questions and new management tools to identify and prioritize refugia based on value and vulnerability.

### Global applications

Despite focusing on three natural disturbances prevalent in western North American conifer forests, our proposed disturbance refugia framework is relevant to other forest ecosystems and a broader array of disturbance agents worldwide. Disturbances are key features in temperate and tropical broadleaf forests, savannas, boreal–taiga, and other ecosystems (both treed and non-treed). Recent global-scale research on forest disturbances emphasizes the widespread nature of fire (Krawchuk et al., 2009), drought (Allen et al., 2010), and insect outbreaks (van Lierop et al., 2015), as well as forest harvest, land conversion, and other disturbance agents (Hansen et al., 2013). Fire refugia are increasingly recognized globally, including in forests in South America (Landesmann and Morales, 2018), Australia (Wood et al., 2011), Africa (Adie et al., 2017), and Europe (Zackrisson, 1977). The widespread investigation of these concepts and growing interest in applications to forest management and conservation science (e.g., Panels 1 and 2) highlight the importance of developing a broader understanding and management capacity for disturbance refugia around the world.

Although refugia may most easily be coded into a variable with only two states (refugia and non-refugia), in reality scientists and managers will be required to conceptualize landscapes comprising gradients of continuously varying types and qualities of refugia, particularly as climate and disturbance regimes continue to change. Considering a broad palette of disturbance refugia together, as proposed in our disturbance refugia framework, is integral to the ongoing synthesis of climate-change refugia. Continued scientific research to inform management of disturbance refugia is required to advance our framework further, with priorities ranging from the investigation of ecosystem values provided by microclimate buffering from disturbance refugia to understanding the costs and benefits of integrating these refugia into land management practices (WebTable 1).

Disturbance refugia will play an increasingly important role in the capacity of climate-change refugia to support species persistence. If one of the goals in identifying climate-change refugia is to maintain in situ populations of species in locations buffered from changing climate, then identifying disturbance refugia – locations within that range that are also most likely to persist through disturbances or recover from them – would result in high-quality, multifaceted refugia. In this era of rapid environmental change, disturbance refugia within mosaics of fire, drought, insect outbreaks, and other agents will shape patterns of persistence of forest biodiversity and ecosystem function globally.

---

Panel 2. Conifer forest refugia in the Jemez Mountains, New Mexico

The Jemez Mountains are a small mountain range at the southern tip of the Rocky Mountains in New Mexico. Over the past quarter century, extensive forest losses have occurred, particularly across the drier, eastern portion of the range. Ecosystem type conversion to non-forest has been driven by multiple interacting factors, including hotter droughts, insect outbreaks, and unusually severe wildfire events, including re-burn of prior high-severity burned patches. Within the 60,000 ha of the 2011 Las Conchas burn, >75% of the landscape is now in a non-forested state, with a mean distance to a fire refugium (defined as a live tree seed source) of 274 m (JDC unpublished data).

The East Jemez Landscape Futures (EJLF) collaborative group convened land managers, researchers, and stakeholders representing over 20 government agencies, non-governmental organizations, and Pueblos to assess priorities and opportunities for research, management, and coordination across these altered landscapes (Stortz et al., 2017). Conifer forest refugia, as essential seed sources for forest landscape recovery, were identified as one of three key landscape management foci. The EJLF also recommended a range of vital management actions for refugia. The identification and protection of ponderosa pine (Pinus ponderosa) refugia from future stand-replacing fire, via thinning or prescribed fire, is a high priority. Another recommended management activity is designing and implementing reforestation efforts that re-establish appropriate levels of forest connectivity between these isolated tree islands. Refugia are currently being used for ponderosa pine seed collection efforts, with seedlings being planted by US National Park Service personnel as part of an assisted dispersal study. EJLF stakeholders are also incorporating disturbance refugia for other species beyond ponderosa pine in reforestation efforts. Cottonwood (Populus spp) stands that survived fire and post-fire debris flows are being targeted for seed collection and pole cuttings, while seeds from refugia of culturally important species like Douglas-fir (Pseudotsuga menziesii) are being collected from refugia for reforestation efforts that could support traditional use in the future. These initiatives highlight just a few of the important roles that disturbance refugia may play in the management of rapidly changing landscapes.
Disturbance refugia enable forest persistence

Acknowledgements

Publication of this Special Issue was funded by the US Department of the Interior (DOI) National, Northeast, and Northwest Climate Adaptation Science Centers. This manuscript was supported through grants to MAK (US Department of Agriculture [USDA], US Forest Service [USFS] Joint Venture Agreement [JVA] 16-JV-11221639-101, US Geological Survey Cooperative Agreement G18AC00242), JDC (USDA USFS JVA 16-JV-11221639-107), AH (National Science Foundation awards 1738104 and 1832483), and AJHM (Joint Fire Science Program, Cooperative Agreement L16AC00202, USDA USFS Western Wildland Environmental Threat Assessment Center award 18-CR-11221633-109, and USDA USFS Special Technology Development Program award 18-JV-11221633-195). Thanks to the DOI Northwest Climate Adaptation Science Center for their support of research on drought and fire refugia. Special thanks to A Ramirez for helpful discussions on drought. We acknowledge C Dunn, C Meigs, and C Miwa for assistance with imagery and graphics for Figure 5, and T Eaves, who aided in the development of Figure 3. Thanks to C Miller at Aldo Leopold Wilderness Research Institute for thoughtful comments that improved the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

References

Abatzoglou JT and Williams AP. 2016. Impact of anthropogenic climate change on wildfire across western US forests. *P Natl Acad Sci USA* 113: 11770–75.

Adie H, Kotze DJ and Lawes MJ. 2017. Small fire refugia in the grassy matrix and the persistence of Afrotemperate forest in the Drakensberg Mountains. *Sci Rep-UK* 7: 6549.

Allen CD, Macalady AK, Chenchouni H, et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecol Manag* 259: 660–84.

Asner GP, Brodrick PG, Anderson CB, et al. 2016. Progressive forest canopy water loss during the 2012–2015 California drought. *P Natl Acad Sci USA* 113: E249–55.

Barbero R, Abatzoglou J, Larkin N, et al. 2015. Climate change presents increased potential for very large fires in the contiguous United States. *Int J Wildland Fire* 24: 892–99.

Bebi P, Kulakowski D, and Veblen TT. 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. *Ecology* 84: 362–71.

Camp A, Oliver C, Hessburg P, et al. 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. *Forest Ecol Manag* 95: 63–77.

Cartwright J. 2018. Landscape topoecological features create refugia from drought and insect disturbance in a lodgepole and whitebark pine forest. *Forests* 9: 715.

Collins L, Bennett AF, Leonard SJW, and Penman TD. 2019. Wildfire refugia in forests: severe fire weather and drought mute the influence of topography and fuel age. *Glob Change Biol* 25: 3829–43.

Davis J, Pavlova A, Thompson R, et al. 2013. Evolutionary refugia and ecological refuges: key concepts for conserving Australian arid zone freshwater biodiversity under climate change. *Glob Change Biol* 19: 1970–84.

Davis KT, Dobrowski SZ, Holden ZA, et al. 2019. Microclimatic buffering in forests of the future: the role of local water balance. *Ecography* 42: 1–11.

Dobrowski SZ. 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Glob Change Biol* 17: 1022–35.

FEMAT (Forest Ecosystem Management Assessment Team). 1993. Forest ecosystem management: an ecological, economic, and social assessment. Portland, OR: FEMAT.

Haire SL and McGarigal K. 2010. Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (*Pinus ponderosa*) in New Mexico and Arizona, USA. *Landscape Ecol* 25: 1055–69.

Hansen MC, Potapov PV, Moore R, et al. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342: 850–53.

Harvey BJ, Donato DC, Romme WH, et al. 2014. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. *Ecol Appl* 24: 1608–25.

Hoe MS, Dunn CJ, and Temesgen H. 2018. Multitemporal lidar improves estimates of fire severity in forested landscapes. *Int J Wildland Fire* 27: 581–94.

Holz A, Hart SJ, Williamson GJ, et al. 2018. Radial growth response to climate change along the latitudinal range of the world’s southernmost conifer in southern South America. *J Biogeogr* 45: 1140–52.

Hood S, Sala A, Heyerdahl EK, et al. 2015. Low-severity fire increases tree defense against bark beetle attacks. *Ecology* 96: 1846–55.

Johnstone JF, Allen CD, Franklin JF, et al. 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Front Ecol Environ* 14: 369–78.

Keppel G, Mokany K, Wardell-Johnson GW, et al. 2015. The capacity of refugia for conservation planning under climate change. *Front Ecol Environ* 13: 106–12.

Keppel G, Van Niel KP, Wardell-Johnson GW, et al. 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecol Biogeogr* 21: 393–404.

Kolden CA, Abatzoglou JT, Lutz JA, et al. 2015. Climate contributors to forest mosaics: ecological persistence following wildfire. *Northwest Sci* 89: 219–38.

Krawchuk MA, Haire SL, Coop J, et al. 2016. Topographic and fire weather controls of fire refugia in forested ecosystems of northwestern North America. *Ecosphere* 7: e01632.

Krawchuk MA, Moritz MA, Parisien M-A, et al. 2009. Global pyrogeography: the current and future distribution of wildfire. *PLoS ONE* 4: e5102.

Landesmann JB and Morales JM. 2018. The importance of fire refugia in the recolonization of a fire-sensitive conifer in northern Patagonia. *Plant Ecol* 219: 455–66.

Landres PB, Morgan P, and Swanson FJ. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecol Appl* 9: 1179–88.

Lindenmayer DB and Franklin JF. 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. Washington, DC: Island Press.
Lindenmayer DB and Laurence WF. 2017. The ecology, distribution, conservation and management of large old trees. *Biol Rev* **92**: 1434–58.

Long J, Lake FK, Lynn K, et al. 2018. Tribal ecocultural resources and engagement. In: Spies TA, Stine PA, Gravenmier R, et al. (Eds). Synthesis of science to inform land management within the Northwest Forest Plan area. Portland, OR: US Department of Agriculture.

Mackey B, Berry S, Hugh S, et al. 2012. Ecosystem greenspots: identifying potential drought, fire, and climate-change micro-refugia. *Ecol Appl* **22**: 1852–64.

Magri D, Vendramin GG, Comps B, et al. 2006. A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytol* **171**: 199–221.

Malone SL, Tulbure MG, Pérez-Luque AJ, et al. 2016. Drought resistance across California ecosystems: evaluating changes in carbon dynamics using satellite imagery. *Ecosphere* **7**: e01561.

McLaughlin BC, Ackerly DD, Klos PZ, et al. 2017. Hydrological refugia, plants, and climate change. *Glob Change Biol* **23**: 2941–61.

Meddens AJH, Kolden CA, Lutz JA, et al. 2018a. Fire refugia: what are they, and why do they matter for global change? *BioScience* **68**: 944–54.

Meddens AJH, Kolden CA, Lutz JA, et al. 2018b. Spatiotemporal patterns of unburned areas within fire perimeters in the northwestern United States from 1984 to 2014. *Ecosphere* **9**: e02029.

Meigs GW and Krawchuk MA. 2018. Composition and structure of forest fire refugia: what are the ecosystem legacies across burned landscapes? *Fronts* **9**: 243.

Millar CI and Stephenson NL. 2015. Temperate forest health in an era of emerging megadisturbance. *Science* **349**: 823–26.

Moran E, Lauder J, Musser C, et al. 2017. The genetics of drought tolerance in conifers. *New Phytol* **216**: 1034–48.

Morelli TL, Barrows CW, Ramirez AR, et al. 2020. Climate-change refugia: biodiversity in the slow lane. *Front Ecol Environ* **18**: 228–34.

Morelli TL, Daly C, Dobrowski SZ, et al. 2016. Managing climate change refugia for climate adaptation. *PLos ONE* **11**: 1–7.

Pureswaran DS, Roques A, and Battisti A. 2018. Forest insects and climate change. *Curr Forest Rep* **4**: 35.

Raffa KF, Aukema BH, Bentz BJ, et al. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience* **58**: 501–17.

Reynolds SC, Marston CG, Hassani H, et al. 2016. Environmental hydro-refugia demonstrated by vegetation vigour in the Okavango Delta, Botswana. *Sci Rep-UK* **6**: 35951.

Robinson NM, Leonard SW, Ritchie EG, et al. 2013. Refuges for fauna in fire-prone landscapes: their ecological function and importance. *J Appl Ecol* **50**: 1321–29.

Savage SL, Lawrence RL, and Squires JR. 2017. Mapping post-disturbance forest landscape composition with Landsat satellite imagery. *Forest Ecol Manag* **399**: 9–23.

Stevens-Rumann CS, Kemp KB, Higuera PE, et al. 2018. Evidence for declining forest resilience to wildfires under climate change. *Ecol Lett* **21**: 243–52.

Stortz SD, Haflter C, and Kimball C. 2017. East Jemez Landscape Futures needs assessment and recommendations: identifying cross-boundary opportunities for management in altered landscapes. Flagstaff, AZ: Northern Arizona University.

Swanson ME, Franklin JF,Beschta RL, et al. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Front Ecol Environ* **9**: 117–25.

Turner MG. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* **91**: 2833–49.

van Lierop P, Lindquist E, Sathyapala S, et al. 2015. Global forest area disturbance from fire, insect pests, diseases and severe weather events. *Forest Ecol Manag* **352**: 78–88.

van Mantgem PJ, Nesmith JC, Keifer M, et al. 2013. Climatic stress increases forest fire severity across the Western United States. *Ecol Lett* **16**: 1151–56.

Walker RB, Coop JD, Parks SA, et al. 2018. Fire regimes approaching historic norms reduce wildfire-facilitated conversion from forest to non-forest. *Ecosphere* **9**: e02182.

Wimberly MC and Kennedy RS. 2008. Spatially explicit modeling of mixed-severity fire regimes and landscape dynamics. *Forest Ecol Manag* **254**: 511–23.

Wood SW, Murphy BP, and Bowman DMJS. 2011. Firescape ecology: how topography determines the contrasting distribution of fire and rain forest in the south-west of the Tasmanian Wilderness World Heritage Area. *J Biogeogr* **38**: 1807–20.

Xu H, Tremblay F, and Bergeron Y. 2018. Importance of landscape features and fire refuges on genetic diversity of *Thuya occidentalis* L, in boreal forest dominated landscapes. *Conserv Genet* **19**: 1231–41.

Zackrisson O. 1977. Influence of forest fires on the north Swedish boreal forest. *Oikos* **29**: 22–32.

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.2190/suppinfo