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

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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.

Natural disturbances drive change and shape landscapes, thereby supporting local and regional biodiversity in forested ecosystems. By creating heterogeneity in ecosystem attributes (eg 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 (eg Lindenmayer and Franklin 2002), as interest in refugia concepts continues

In a nutshell:

- Areas that are disturbed less severely or less frequently than the surrounding landscape can be described as disturbance refugia
- Disturbance refugia can occur at many scales of space and time
- Forest disturbances often overlap, generating complex positive and negative relationships, or even feedbacks, that influence the structure and function of refugia
- We present a comprehensive definition of disturbance refugia, which recognizes multiple types of disturbances in forests under a single term, as a framework to assist in forest ecosystem research and management in the context of climate change
- It is important for scientists and resource managers to identify refugia and to understand why they occur, how they persist, and their value in sustaining biodiversity

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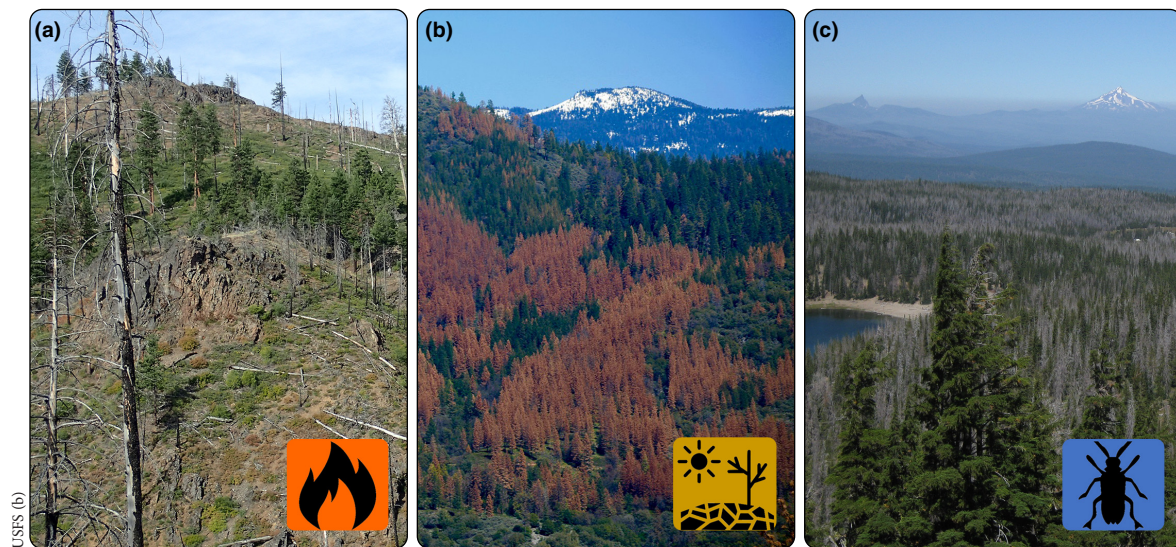
Figure 1. Examples of disturbance refugia in forests of western North America: (a) fire refugia in the Mill Creek Wilderness area, in Oregon, 15 years post-fire; (b) a combination of drought and insect outbreak refugia in California's Sierra National Forest during peak tree mortality; (c) insect outbreak refugia in the Cascade Range of Oregon, 10 years after a mountain pine beetle (*Dendroctonus ponderosae*) outbreak. The most prominent feature of disturbance refugia in forests is persistent live canopy – green "islands" – embedded within a mosaic of more severe effects. Some refugia are relatively concentrated in their spatial pattern (eg in [a] and [b]), whereas others are more diffuse (eg in [c]).

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 (eg 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-standreplacing 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 har-
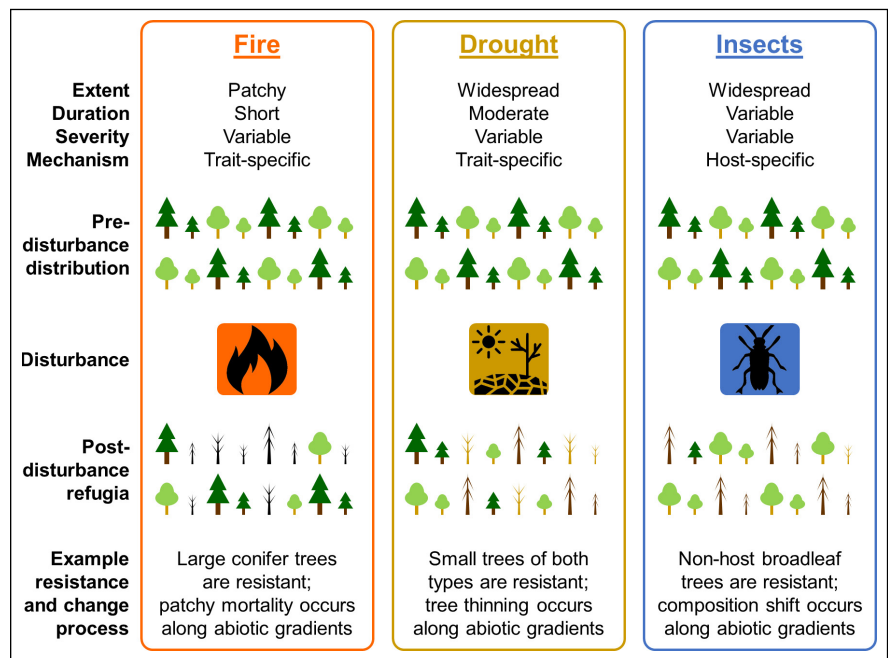

Figure 2. Implications of three forest disturbance types for disturbance refugia. Each disturbance has unique attributes that can influence disturbance mosaics, here illustrated as spatial patterns of tree mortality and survival, the latter representing disturbance refugia. In this example, each of the three forests has the same pre-disturbance distribution, tree sizes indicate mature and young trees, and tree shapes represent generic conifer and broadleaf trees. Note that each forest shows 50% tree survival, but disturbance effects and responses can vary widely among events and across spatiotemporal scales; as such, these examples represent just a few of many possible outcomes.

vest, 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/
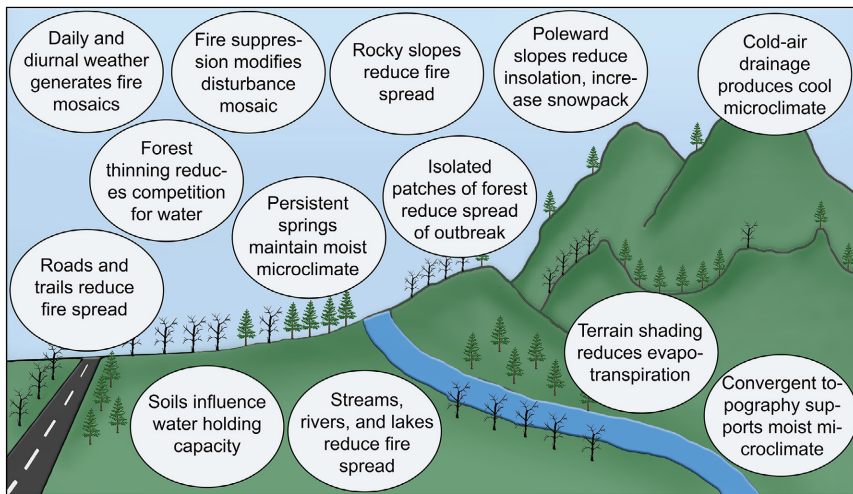
Figure 3. Examples of processes and landscape features contributing to fire, drought, and insect outbreak refugia. Enduring topographic and soil features confer predictability to where disturbance refugia are more likely to occur in a landscape. These can be naturally formed topographic elements or human constructs (eg roads). Land management activities like forest thinning alter forest structure in ways that can contribute to disturbance refugia. More dynamic, meteorological features can also contribute to refugia formation, particularly fire refugia, resulting in more stochastic patterns on the landscape. All of these features, interacting in complex ways, contribute to patterns of disturbance refugia on the landscape.

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 conferring insect resistance (Figure 3; Cartwright 2018). For example, 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 disturbances, 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 feedbacks, 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 (amplifying) feedbacks. Negative feedbacks occur when one disturbance 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 regulate fuel structure, promoting tree survival during subsequent 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 subsequent bark beetle-induced mortality (Bebi *et al*. 2003). However, positive feedbacks among drought, insects, and fire may become more prevalent given climate-change projections. 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 seedling establishment (Stevens-Rumann *et al*. 2018). In addition, 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 positive feedbacks occur, we anticipate reduced refugia abundance (Figure 4), impaired refugia function, and slower forest recovery, with potential for transformation to alternate forest or non-forest states.
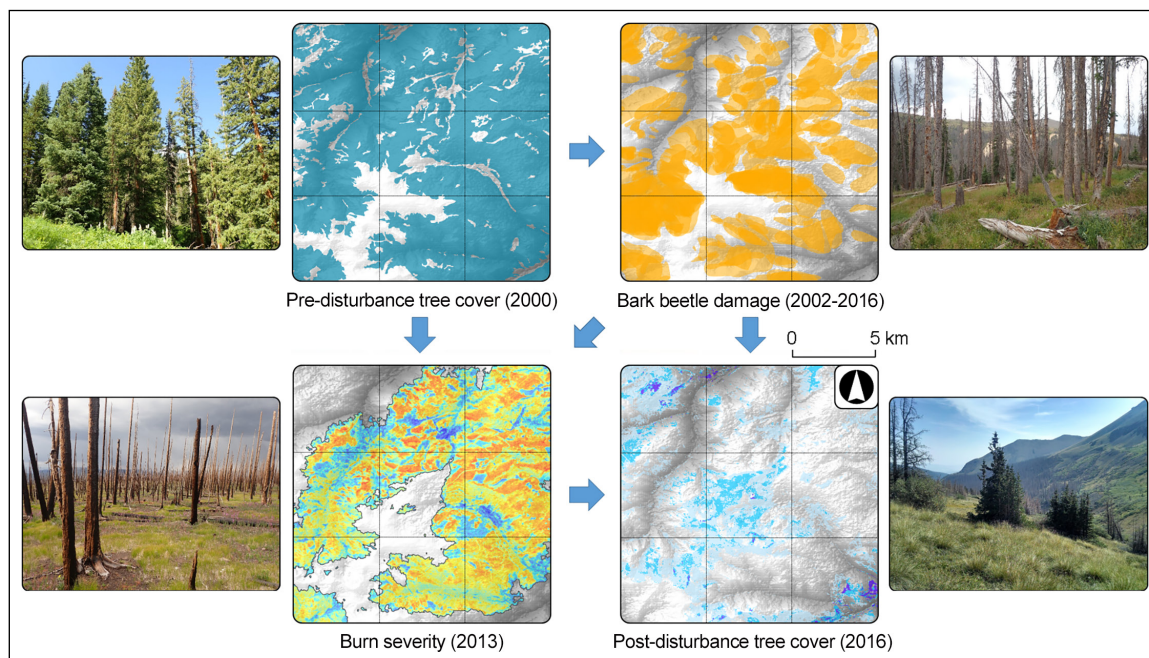

Figure 4. Overlapping disturbances may reduce the capacity of the landscape to support refugia and diminish their short-term functioning. In subalpine forests of the San Juan Mountains of southern Colorado, mature Engelmann spruce (*Picea engelmannii*; aqua in upper left) trees were killed by the spruce 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 FSVeg 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).
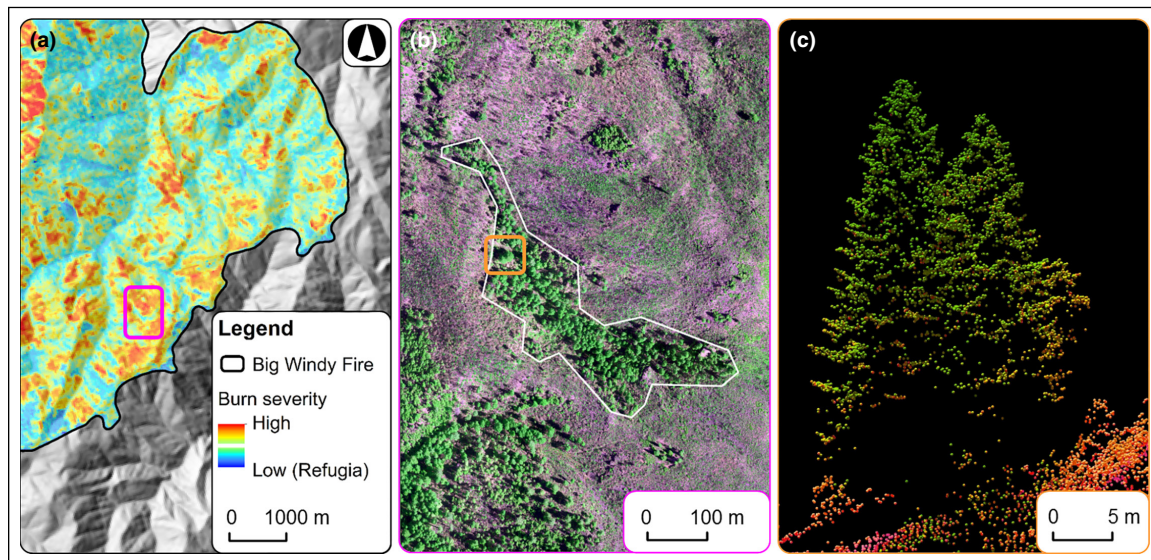
Figure 5. Illustration of several spatially explicit methods for detecting and analyzing disturbance refugia. (a) Landscape-scale patterns of burn severity across a portion of the Big Windy Complex Fire (Oregon) in 2013. Patterns of potential fire refugia (blue–green areas) are generally captured with moderate spatial resolution satellite data (eg 30-m grain Landsat RdNBR index based on imagery 1-year pre- and post-fire). (b) High-resolution digital orthophotography of a small subset of the Big Windy Fire 2 years following fire (corresponding to the rectangular fuchsia inset in panel [a]), illustrating the ability to delineate fire refugia using visible and infrared imagery. (c) Cross-section of high-resolution lidar data capturing remnant tree height and structure within the refugium (corresponding to the rectangular orange inset in panel [b]). Landsat data from Monitoring Trends in Burn Severity (www.mtbs.gov); digital orthophotography and lidar imagery from the Oregon LiDAR Consortium (www.oregongeology.org/lidar).

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 (eg 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 (eg 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 m^2 (Figure 5a). Disturbance refugia can occur at much finer scales (eg 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 (eg WorldView), aerial photography (Figure 5b), or very high-resolution data (eg 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;

Panel 1. Fire refugia and old forest conservation in the US Pacific Northwest

In the US Pacific Northwest, recent large forest fires have sparked concerns about forest loss and increasing interest in fire refugia, particularly in old-growth forests of the Northwest Forest Plan region (Figure 6). The historical context of the Plan is important for understanding the application of disturbance ecology within the region, and how disturbance refugia (ie locations with higher probabilities of persisting as old-growth forest through contemporary fire) fit into future forest planning. The analysis that led to the Northwest Forest Plan (FEMAT 1993) divided the management region, which is based on the US range of the northern spotted owl (*Strix occidentalis caurina*, a species listed as "threatened" under the US Federal Endangered Species Act), into two broad geographic areas with "dramatic differences" in wildfire activity. The likelihood of large wildfires was identified as higher in the "dry provinces" to the east and south, whereas the likelihood of maintaining contiguous, closed-canopy, late-successional forests (the preferred nesting habitat of the northern spotted owl) was considered higher in the "moist provinces" to the west and north. Although the Northwest Forest Plan recognized these differences, it was limited by uncertainty in predicting fire frequency, extent, and severity at finer geographic scales. Subsequently, land managers and scientists began considering finer geographic scales and topographic influences on biotic and abiotic processes, including research on fire refugia in one landscape of the Plan's region – the Swauk Late Successional Reserve (Camp *et al.* 1997). In 2018, a broader research program was initiated to understand the predictability of contemporary fire refugia within late-successional, old-growth forests across the

region, and to identify locations with the greatest potential for long-term late-successional forest sustainability (http://firerefugia.forestry.oregonstate.edu). Federal forest and resource management plan revisions provide key opportunities to evaluate and integrate this type of new scientific information on fire refugia into planning revisions aimed at conserving old forests and the habitats therein.
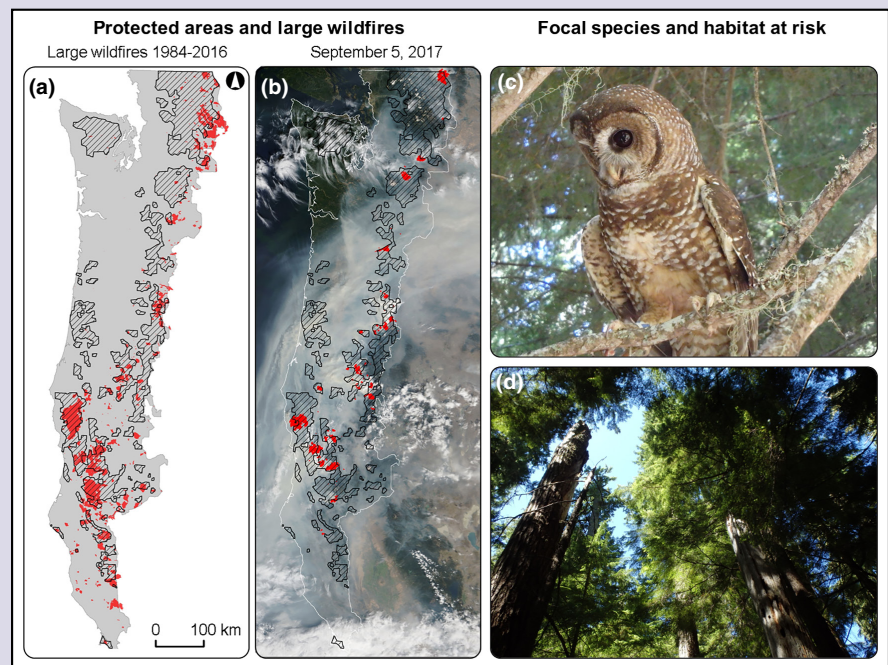

Figure 6. (a and b) Recent large wildfire activity (red polygons) affecting late-successional reserves (cross-hatched polygons) within the Northwest Forest Plan (gray background in [a]) in the US Pacific Northwest (portions of Washington State, Oregon, and California). (a) Fire perimeters from 1984 to 2016. (b) Active 2017 wildfires and smoke (MODIS satellite imagery). (c) Northern spotted owl (*Strix occidentalis caurina*); (d) typical northern spotted owl nesting and roosting habitat in late-successional conifer forest.

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

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 restoration 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.

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 (eg Davis *et al.* 2013), along with efforts to enhance drought resistance (eg 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 (eg 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.

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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