Fire Refugia: What Are They, and Why Do They Matter for Global Change?

ARJAN J.H. MEDDENS, CRYSTAL A. KOLDEN, JAMES A. LUTZ, ALISTAIR M. S. SMITH, C. ALINA CANSLER, JOHN T. ABATZOGLOU, GARRETT W. MEIGS, WILLIAM M. DOWNING, AND MEG A. KRAWCHUK

Fire refugia are landscape elements that remain unburned or minimally affected by fire, thereby supporting postfire ecosystem function, biodiversity, and resilience to disturbances. Although fire refugia have been studied across continents, scales, and affected taxa, they have not been characterized systematically over space and time, which is crucial for understanding their role in facilitating resilience in the context of global change. We identify four dichotomies that delineate an overarching conceptual framework of fire refugia: unburned versus lower severity, species-specific versus landscape-process characteristics, predictable versus stochastic, and ephemeral versus persistent. We outline the principal concepts underlying the ecological function of fire refugia and describe both the role of fire refugia and uncertainties regarding their persistence under global change. An improved understanding of fire refugia is crucial to conservation given the role that humans play in shaping disturbance regimes across landscapes.

Keywords: biogeography, wildfires, refuge, resilience, landscape ecology

Fire is a global disturbance process that interacts with landscape pattern to create mosaics of ecosystem effects, including patches that remain both unburned and only minimally affected by low-intensity burning. These patches are increasingly of interest to ecologists and are often referred to as fire refugia (Kolden et al. 2012, Robinson et al. 2013, Krawchuk et al. 2016). In the broader ecological literature, refugia are components of ecosystems in which biodiversity can retreat to, persist in, and potentially expand from as environmental conditions change (Keppel et al. 2015). Refugia were originally defined in the context of large-scale processes on evolutionary time scales; continental glaciation and the subsequent isolation of unique habitat types resulted in speciation within refugia (Haffer 1969) and subsequent migrations from refugia (Petit et al. 2003, Brubaker et al. 2005). Refugia created by contemporary ecological phenomena have been the subject of recent studies (Dobrowski 2011, Keppel et al. 2012, Krawchuk et al. 2016, Morelli et al. 2016), reflecting interest in refugia formation and function at smaller spatial and shorter temporal scales, especially in relation to observed and projected climate change. Climate-change refugia have been defined as “areas relatively buffered from contemporary climate change that allow for habitat stability and species persistence over time” (Morelli et al. 2016). However, climate refugia identified for conservation and management purposes require that these areas also be buffered from severe disturbance events if they are to function as holdouts within a changing environment. Accordingly, fire refugia are a necessary complement to climate change refugia in fire-prone landscapes.

The term *fire refugia* has various definitions (e.g., Gill 1975, Camp et al. 1997, Mackey et al. 2002, Krawchuk et al. 2016), all of which focus on the idea of locations disturbed less frequently or less severely by wildfire relative to the surrounding vegetation matrix. Fire refugia provide habitat for individuals or populations in which they can survive fire, in which they can persist in the postfire environment, and from which they can disperse into the higher-severity burned landscape (Robinson et al. 2013). In this way, fire refugia can function similarly to islands in a biogeographic context, particularly in severely burned areas, recognizing that the matrix of burned areas still provides some habitat to many taxa. Mosaics of fire effects spanning the full range of burn severity—including refugial patches—influence succession, ecosystem processes, and the distribution of biological legacies (Franklin et al. 2000, Turner 2010, Johnstone et al. 2016). Locations in which biota survive fire have been shown to strongly influence postfire recovery and ecosystem dynamics (e.g., Haire and McGarigal 2010, Robinson et al. 2013, Stevens-Rumann et al. 2017). Uniquely, however, fire refugia

BioScience XX: 1–11. Published by Oxford University Press on behalf of American Institute of Biological Sciences 2018.
doi:10.1093/biosci/biy103

are not purely ecological or biophysical phenomena; they are also a socioecological construct—for example, because of human manipulation of vegetative fuels and fire suppression activities that can both facilitate and impede their formation. As patterns of fire refugia are increasingly affected by human activity, understanding their form and function is becoming a priority for conservation, management, and policy. Recognition and identification of fire refugia, including their spatial configuration, their physical location within the surrounding burned matrix, and their composition and structure will become increasingly important for effective conservation and land management under the nexus of altered land use, shifting land cover, and anthropogenic climate change, which we hereafter refer to as *global change*.

Given the growing interest in and number of publications on the form, function, and conservation value of contemporary fire refugia (Kolden et al. 2015a), our objective is to synthesize the existing literature and characterize the current thinking about fire refugia in forested ecosystems in the context of global change. By defining and identifying different aspects of fire refugia, we provide a clearer architecture for these important landscape elements, as a crucial step forward in refugia-based science and management. We address three overarching questions: First, what are fire refugia? That is, what are the commonalities and differences in the ways fire refugia have been defined in the scientific literature? Second, what theoretical frameworks underlie the ecological function of fire refugia? Third, how can fire refugia support ecosystem resilience under global change? We expand considerably on prior efforts by Robinson and colleagues (2013) by including flora and by focusing on refugia as microecosystems rather than as habitat only for a specific faunal species of interest. In addition, we characterize the temporal dynamism of refugia by addressing drivers of formation and persistence. Finally, we address global change and the role of refugia in ecosystem resilience. By clearly defining and identifying different aspects of fire refugia, we gain insight into whether they will persist or whether there are given thresholds that might lead to losses in fire refugia in a time of accelerating global change. To support our synthesis, we conducted a comprehensive literature search using standard scientific search engines (e.g., Web of Science, Academic Search Premier) and searched for all known terms used for fire refugia (e.g., *skips*, *unburned islands*, *refuges*) in sources published as of June of 2018. We then compiled these to identify common themes and determine which key research best highlighted the facets of these common themes (supplemental tables S1 and S2). We acknowledge that some studies that fall within broader definitions of fire refugia and more tangential research may be omitted from these tables.

What are fire refugia?

Fire refugia are defined and characterized variably in the literature. Other terms used to describe them include *unburned islands*, *habitat refugia*, *remnants*, *residual vegetation*, *fire shadows*, *skips*, *stringers*, *refuges*, *islands*, *biological legacies*, and *late-successional forest* (tables S1 and S2). Studies of fire refugia have been concentrated primarily in the boreal and temperate forests of western North America and the shrublands and forests of eastern Australia, with additional studies in Europe, South America, and Africa (tables S1 and S2). There is some ambiguity in the literature regarding the distinction between *refugia* and *refuges*, which we suggest is more of a language clarification than a formally defined difference. Although there are reasons to consider refugia and refuges differently, we recognize that both are focused on the same core idea—areas that are buffered from pressures or changes experienced by adjacent areas. From Camp and colleagues (1997), one of the early seminal works on fire refugia, and to be consistent with the authors' more recent contributions in this field, we use *refugia* in the present article rather than *refuges*. On the basis of the existing literature, we identify four taxonomic dichotomies that delineate a conceptual framework for characterizing fire refugia: unburned versus lower severity, species-specific versus landscape-process characteristics, predictable versus stochastic formation, and ephemeral versus persistent. We describe each of these in a global change context.

Unburned versus lower severity refugia In some studies, fire refugia are defined specifically as unburned areas within fire perimeters (Meddens et al. 2016, Swan et al. 2016), whereas in others, the definitions include low-severity fire patches within the burned area (Krawchuk et al. 2016). Many researchers, however, do not explicitly define whether fire refugia are unburned, low severity, or a mixture of the two (e.g., Camp et al. 1997, Schwilk and Keeley 2006). The widespread use of Landsat-based change detection methods to generate maps of burn severity and identify fire refugia has led some researchers to describe relatively large areas as unburned (Roman-Cuesta et al. 2009, Wood et al. 2011, Kolden et al. 2012, Kolden et al. 2015a, Meddens et al. 2016) but has also yielded a growing recognition that it is difficult in some ecosystems to accurately differentiate between unburned islands and low-severity patches from such spectral reflectance-based remote-sensing data sets (van Wagtendonk and Lutz 2007, Kolden et al. 2015b). This difficulty stems from the variability of subcanopy surface conditions within a pixel when the imagery values primarily reflect conditions associated with an unaffected overstory canopy (Cansler and McKenzie 2014). Furthermore, the delineation of refugia from spectral data without additional ground observations does not provide information on the prefire composition and structure of the fire refugia (Meigs and Krawchuk 2018) or their potential ecological functions.

A definition of fire refugia that includes areas that experienced underburns, surface fire, or low fire severity, in addition to areas that were truly unburned, reflects a broader and more inclusive perspective of refugia that supports the preponderance of taxa and fire effects of interest for conservation and management concerns. For example, in a forested ecosystem, a stand of trees in which the surface has

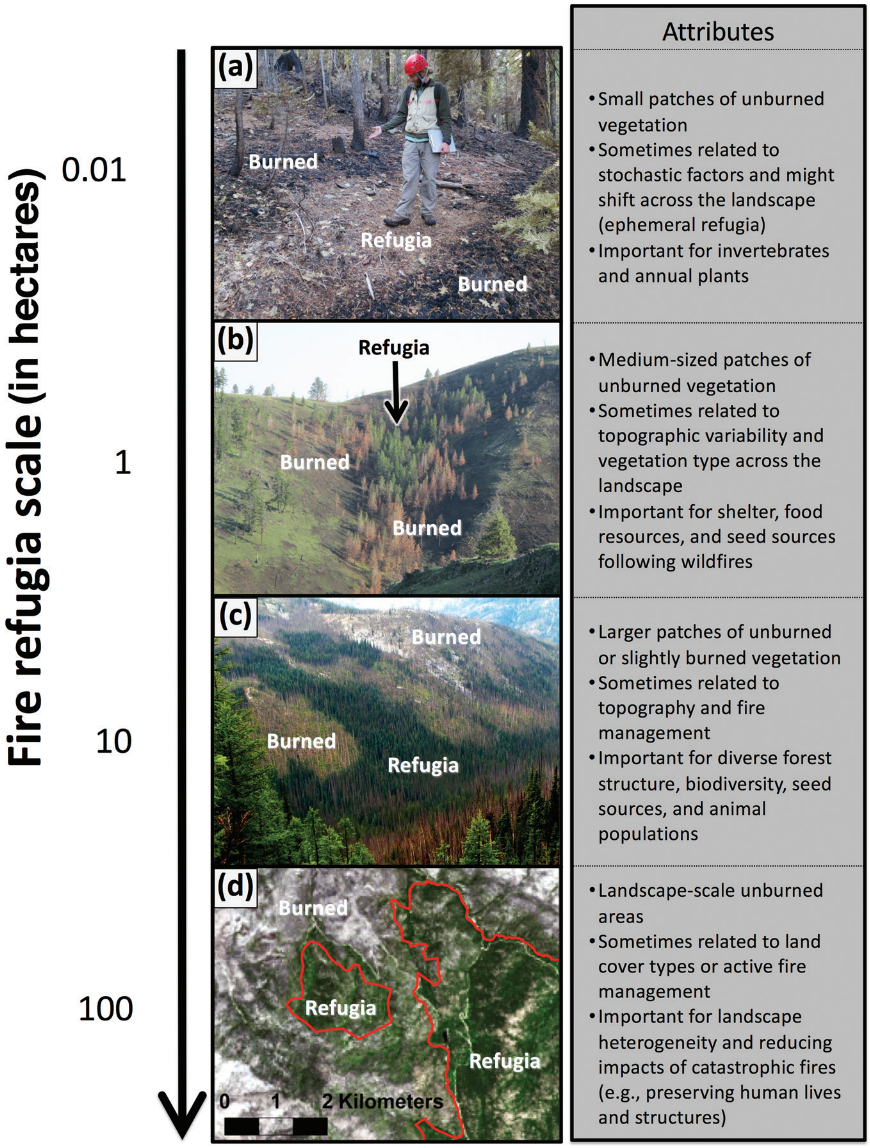

Figure 1. Examples of different spatial scales of fire refugia: (a) small patch of unburned forest floor from the Rim Fire in California (2013), (b) unburned overstory ponderosa pine (Pinus ponderosa) stand from the Big Cougar Fire in Idaho (2014), (c) larger unburned island within forested areas from the Butte Creek fire in Washington (1994), and (d) natural color Landsat scene subset from the Carlton Complex fire in Washington (2014).

moved through the understory, leaving the canopy intact when the surrounding area burned at a high severity would be considered a fire refugium. The overstory trees in this fire refugium were resistant to fire, persisted as legacies on the landscape, and will function as seed source for forest reestablishment. Surface fire in fire refugia may, in fact, increase the chances of the overstory community persisting through subsequent events—for example, as "fire-tended" old growth forest fire refugia. In comparison, a nearby stand may have received no fire, and this unburned area is also a fire refugium but with different compositional and structural attributes. Researchers and managers interested in specific ecosystem components, such as rare, fire-intolerant species, understory vegetation, surface fuels, or belowground processes would likely define refugia more restrictively (tables S1 and S2). The inclusive definition of fire refugia, with recognition of the distinctions between unburned and low-severity fire refugia, is crucial in integrating the role of refugia across broad regions and fire ecologies.

Species-specific refugia versus landscape process Studies of fire refugia generally fall into two broad research perspectives (Lindenmayer 2009): fire refugia specific to a species or group of species (table S1) and fire refugia as the product of landscape-scale processes (table S2).

A species-oriented perspective is focused on how taxa (or their habitat) respond to direct exposure to combustion and fire-induced habitat change; this perspective is covered in depth by Robinson and colleagues (2013). Existing species-oriented fire refugia research includes studies of butterfly populations, invertebrates, bryophytes, birds, small mammals, and vegetation (table S1). These studies stem from the need to understand specific mechanisms of survival, connectivity, dispersal, and the persistence of species and populations during and after wildfires, particularly when a species is threatened or endangered. Species-specific refugia can refer to single plants (requiring refugia of only a few square meters) that remain unburned and shelter invertebrates (e.g., Brennan et al. 2011) or larger areas (tens to hundreds of square meters) that remain unburned and promote persistence of plant species and vertebrates that rely on these structural elements as habitat (e.g., Banks et al. 2012; figure 1). Species-specific refugia may also involve larger unburned or lightly burned patches or collections of patches that maintain a single species across the larger landscape (e.g., *Pinus sabinana* in Schwilk and Keeley 2006). To meet regulatory mandates to preserve such species under global change, however, habitat requirements must be embedded in more comprehensive landscape processes that facilitate specific ecosystem functions, particularly when multiple management objectives must be met.

Landscape-process fire refugia have primarily been characterized as landscape patches that did not burn or that burned less severely or frequently than adjacent areas did, irrespective of species composition (cf. Berry et al. 2015b). In contrast to a species-specific approach, research focused on landscape-process refugia is generally intended to quantify and characterize patterns of fire refugia across a range of spatiotemporal scales and to associate refugial formation with environmental factors (Lindenmayer 2009; table S2, figure 1). This approach is often embedded within broader landscape ecology theory or remote-sensing queries and analyses (e.g., Kolden et al. 2012, Kane et al. 2015, Meigs and Krawchuk 2018), but landscape-process studies also include modeling (Wimberly and Kennedy 2008) or quantification of forest stand structure and composition from field observations (Camp et al. 1997). In contrast to species-centric perspectives, landscape-process studies often lack quantifiable mechanistic links to the fine-scale ecological processes that are important for understanding ecological function of fire refugia. However, landscape-process studies (table S2) can inform efforts focused on ecosystem process, particularly those interested in trends and patterns of reforestation and plant regeneration under global change (e.g., Stevens et al. 2017). Similarly, landscape-process studies may inform species-specific management objectives by identifying changes in patch metrics of crucial habitat, such as the optimal patch-size distributions of shade for ectotherms (e.g., Sears et al. 2016).

Predictable versus stochastic refugia formation For any given fire event, fire refugia are formed through fire behavior driven by the three factors of the fire behavior triangle: topography, fuels, and weather. These three factors control fireline intensity and direction of spread. A change in any factor can deprive a fire of available fuel, creating refugia. Water features, riparian areas, roads, and clearings are some of the most obvious contributors to stopping or slowing fire spread, thereby providing a degree of predictability to the occurrence of fire refugia in the vicinity. Topography and edaphic factors, including surface soil characteristics, are enduring features that are more stable than fuels or weather, and they influence the predictability of where fire refugia occur (Camp et al. 1997, Perera and Buse 2014, Krawchuk et al. 2016). Specifically, permanent topoedaphic features, such as rock outcrops, ridges, or scree slopes, can function as firebreaks that protect adjacent vegetated areas, because they are unburnable, and they may also serve as refugia for species that can inhabit these environments. At the same time, fire refugia are more likely to occur in valley bottoms, local concavities, draws, or gullies (Bradstock et al. 2010, Leonard et al. 2014, Krawchuk et al. 2016), potentially as a function of cold air pooling (Wilkin et al. 2016), and through increased soil and fuel moisture (Romme and Knight 1981, Coop and Givnish 2007). Slope, aspect, and elevation also can play a role, such that cooler and moister sites burn less frequently and support late-successional, fire-resistant individuals and populations (Camp et al. 1997, Wood et al. 2011). Under more extreme dry and hot weather conditions, however, these facets may lose their protective characteristics and burn more severely because of high fuel accumulation (Beaty and Taylor 2001, Krawchuk et al. 2016).

By contrast, fire refugia formation can also be driven by stochastic factors. Sudden wind shifts, fire-generated behavior (e.g., fire whirls and self-generating weather), and changes in weather are all frequent causes of fire refugia formation as an advancing flaming front skips over an area. This is particularly characteristic of fire refugia formed in discontinuous fuels or landscapes with benign terrain (Krawchuk et al. 2016), in which fire spread depends strongly on wind, and therefore, fire refugia formation is similarly related to wind patterns. Importantly, human actions related to fuel management and fire suppression can be more challenging to predict consistently. People build fire breaks and containment lines around resources at risk, intentionally making those resource areas into fire refugia. At the same time, humans unintentionally create refugia through activities that alter fuel continuity (e.g., off-highway vehicle trails, resource extraction activities such as logging or drilling, and clearing of surface fuels through firewood gathering), facilitating changes in fire behavior. Part of the current challenge in distinguishing predictable from stochastic refugia formation is that much of the science currently depends on imperfect post hoc reconstruction of fire events, with the most predictable refugia being those that have persisted through multiple wildfires.

Ephemeral versus persistent fire refugia Over multiple fire-return intervals, fire refugia that last through only a single fire event are defined in the present article as *ephemeral*, whereas refugia that survive through multiple fires are defined as *persistent* refugia. Generally, persistent refugia are formed through relatively predictable processes, and ephemeral refugia are formed through stochastic factors, but this is not always the case. For example, some ephemeral refugia may be predictable if they remain unburned under more benign or moderate conditions (e.g., a meadow above a certain threshold of soil moisture) but may burn at other times (e.g., the same meadow in an extreme drought year); such refugia would be predictable, because the conditions prescribing their formation are known, but they would not necessarily persist through multiple fires (Perera and Buse 2014, Berry et al. 2015a, Krawchuk et al. 2016). Although ephemeral refugia remain only through individual fire events, the aggregate population of these refugia over landscapes and regions may be important in supporting the persistence of refugia-associated species over longer timeframes and under global change.

By contrast, persistent fire refugia are those that remained intact through multiple fire events (including reburns; Prichard et al. 2017), and this persistence suggests that they are more likely to be predictably associated with stable

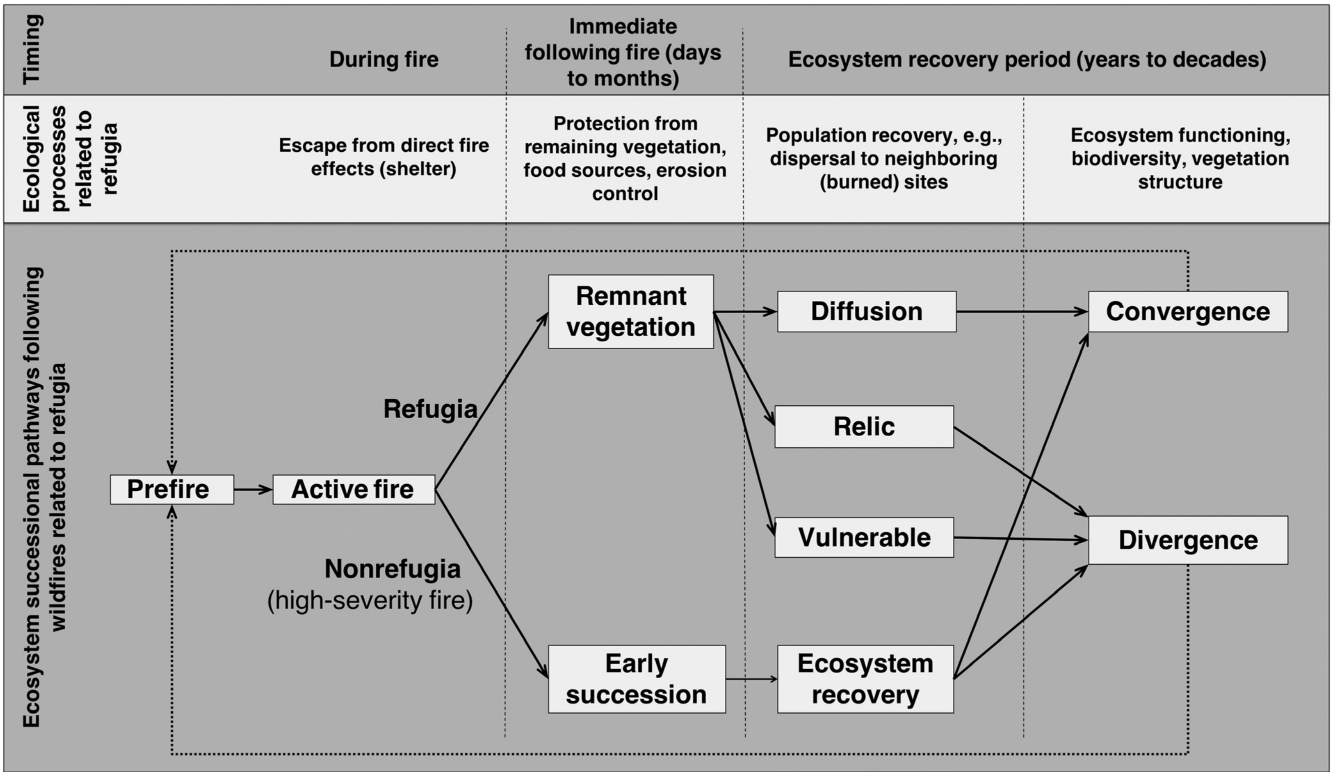

Figure 2. Successional pathways of refugia and nonrefugia following fires in relation to the broader ecosystem. During and immediately after fire, refugia provide shelter or food resources, whereas over longer time periods fire refugia facilitate ecosystem recovery by providing seed sources and increasing biodiversity. The burned area can recover to similar vegetation as the preburn condition, leading to convergence of refugia and the surrounding matrix maintaining prefire ecosystem function. However, if the surrounding matrix transitions to a different ecological state, the refugia become a relic or are left vulnerable to subsequent disturbance, leading to a divergence from prefire ecosystem function.

landscape features (Clarke 2002). Fire-resistant conditions may also occur through self-reinforcing fire–vegetation feedback loops that are either natural (e.g., Wood et al. 2011) or human induced through repeated intentional burning, such as annual indigenous burning to protect key resources (Kimmerer and Lake 2001). Ephemeral and persistent fire refugia can provide similar ecological functions (e.g., as seed sources; Weisberg et al. 2008). However, persistent refugia are more likely to provide unique structures and functions associated with late-successional ecosystems (e.g., diverse structural conditions; Camp et al. 1997, Kolden et al. 2015a), older individuals (e.g., large-diameter trees; Lutz et al. 2013, Lutz et al. 2018), or landscape context (e.g., position or configuration; Russell-Smith and Bowman 1992). Persistent fire refugia may also be more vulnerable to losses associated with anthropogenic climate change and changing fire regimes (Kolden et al. 2017), because the climatic conditions that previously sustained persistent refugia may give way to conditions that support and facilitate fire spread into a previously persistent patch. This novel introduction or reintroduction of fire would have considerable implications for ecosystems that have been dependent on such refugia.

The ecological functions of fire refugia

The ecological functions of fire refugia depend on the reproductive age, mobility, and fire sensitivity of the biota within them; the contrast between refugia and the surrounding burned matrix; and the postfire successional trajectories of nearby burned areas. The differential ecological functions of fire refugia also change over time after a fire (Robinson et al. 2013, Perera and Buse 2014). For instance, refugia can shelter and protect fauna during an active wildfire, function as remnant habitat immediately postfire, or support population reestablishment in the years to decades following fire (figure 2). In this way, refugia variably function as islands in a biogeographic context or as patches in a landscape matrix.

During the fire Areas within the fire perimeter that provide shelter or protection from fire effects are key to maintaining populations and seed sources. Biota with limited or no mobility and limited resistance to fire effects (e.g., butterflies, snails, annual plants, and fire-intolerant woody plants) will be locally extirpated from the ecosystem without shelter from combustion and radiant heat (Hylander and Johnson 2010, Hylander 2011). Refugia generally comprise these unburned areas or slightly burned areas in which fire energy does not reach a lethal dose (Hylander and Johnson 2010, Gongalsky et al. 2012, Smith et al. 2017). More mobile taxa, such as ungulates and birds, may use refugia to evade flames (Henriques et al. 2000, Lindenmayer et al. 2009, Banks et al. 2011), but they could be more vulnerable to the immediate and longer-term postfire effects on the landscape (Banks et al. 2012).

Immediate postfire Remnant vegetation following fire provides functional habitat and other crucial ecological functions days to months after fire. Refugia can supply food resources (Schwilk and Keeley 1998, Henriques et al. 2000) that are otherwise consumed by fire in the surrounding landscape, provide cover or protection from predators, or reduce influences from exposure to abiotic stressors (e.g., wind and solar radiation). Competition within refugia may increase from before to after a fire, because of decreases in available resources in the surrounding burned landscape (Banks et al. 2012). In addition, these refugia can function as buffers against erosion and landslides that can occur following fires (Shakesby and Doerr 2006), mediating detrimental habitat loss.

Recovery period Depending on the severity of the surrounding burned area, refugia can function as biogeographic islands during the early recovery period. They increase habitat variability on the landscape, providing patches with later successional species interspersed within an early successional landscape (e.g., Swanson et al. 2010), thereby increasing beta diversity within a given fire perimeter. Fire refugia also can function as long-term, postfire habitat from which species can expand to neighboring areas, effectively functioning as a seed source (e.g., diffusion; figure 2; Schwilk and Keeley 2006, Stevens-Rumann et al. 2017). Environmental conditions (e.g., climate) and the recovery trajectory of the surrounding vegetation determine whether refugia merge with recovering vegetation and ultimately maintain prefire ecosystem function (convergence), or the surrounding vegetation recovers differently from how fire refugia do, resulting in a change of ecosystem function (e.g., divergence; figure 2). Relic refugia may persist in the postfire landscape, but if the structure or composition of surrounding vegetation transitions to a new state, refugia may no longer support prefire ecosystem function; Lindenmayer and colleagues (2011) described these as *landscape traps*. For example, anthropogenic climate change may be facilitating type conversion of forest to shrublands in some regions by inhibiting seedling regeneration (Stevens-Rumann et al. 2017), and relic forest refugia unable to regenerate the forest around them may be vulnerable to further disturbances, such as cases in which a new surrounding vegetation matrix has a higher vegetative fuel load or shorter fire return interval than the prior matrix (figure 2; Kolden et al. 2017), potentially leading to total loss of forest habitat for that site.

Fire refugia and global change

Climate change has increased both fire potential and realized fire activity in many parts of the world (Jolly et al. 2015, Abatzoglou and Williams 2016). The greatest recent increases have been observed in boreal forests and tundra (Andela et al. 2017), consistent with observations of the most rapid rates of climate change in high latitudes (IPCC 2013). In the western United States, increased fire extent in recent decades (Westerling 2016) has been attributed to myriad factors, including past fire suppression, land use and land cover changes, and increased ignitions by humans (Balch et al. 2017), as well as anthropogenic climate change (Abatzoglou and Williams 2016). Climate change is projected to continue to increase the potential for large, destructive fires across the United States (Barbero et al. 2015) and globally (Bowman et al. 2017), albeit with heterogeneous impacts to realized fire activity across the broader region (Kitzberger et al. 2017).

This considerable increase in fire has prompted questions of whether fires are also increasing in severity and completeness of combustion, which should hypothetically reduce the occurrence and extent of fire refugia. To date, there is mixed evidence that fires are burning more severely over the contemporary record, outside of a few isolated subregions (e.g., Picotte et al. 2016, Abatzoglou et al. 2017), and climatic conditions do not appear to be a strong driver of burn severity (Birch et al. 2015, Abatzoglou et al. 2017). Some studies focused on high-severity fire have shown increases in high-severity patch interior (Cansler and McKenzie 2014, Stevens et al. 2017), implying that small scale refugia—such as individual trees that serve as a seed source—may be becoming rarer in some landscapes, but higher-resolution data are needed to confirm the loss of these small-scale refugia. Studies focused solely on fire refugia have shown no trends toward reduced or altered patterns of refugia, suggesting that fires are burning neither more completely nor more severely (Kolden et al. 2012, Kolden et al. 2015a, Meddens et al. 2018). Nor are there clear or strong relationships between climate and patterns and proportions of fire refugia across regions (Kolden et al. 2012, Kolden et al. 2015a, Meddens et al. 2018). Instead, local-level topography seems to be a strong driver of refugia patterns, athough importantly, the capacity for terrain features to support refugia appears to diminish under more extreme daily fire weather conditions (Roman-Cuesta et al. 2009, Krawchuk et al. 2016).

The fire refugia studies described in the preceding paragraph defined fire refugia on the basis of landscape process rather than the species-specific definition, so it is unknown whether these trends are applicable to refugia for specific species of interest. Species-specific or biodiversity-focused approaches for fire refugia may show global change trends that are not evident when a landscape-process approach is used. For example, in the boreal forest of North America, climate change and increased fire activity are already thought to be facilitating the loss of continuous permafrost that is required for the regeneration of black spruce (*Picea*

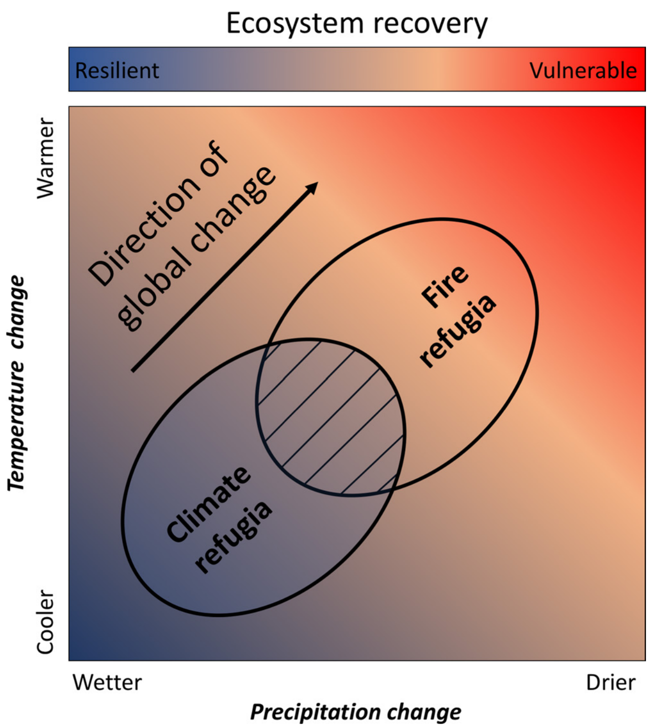

Figure 3. Conceptual effect of global change on ecosystem recovery in relation to climate and fire refugia, adapted from Allen and colleagues (2010). The ovals indicate the fire refugia and climate refugia that exist under current and persist under future conditions. Because of topographic connections to both fire and climate refugia, there is likely a partial overlap between the two refugia types (hatched area) across the landscape. Climatic impacts on fire refugia are expected to shift more rapidly as opposed to climate refugia, because climate refugia are more buffered from these global changes. Identifying the geospatial overlap between fire refugia and climate refugia is an important research need.

mariana). This ecosystem is transitioning to white spruce– and deciduous-dominated conditions, leaving fire refugia vulnerable to extirpation by subsequent fire (Johnstone et al. 2016). Similarly, the invasive spread of exotic annual grasses into the arid and semiarid regions of North America and Australia has induced more frequent fire, facilitating a type conversion to annual grassland. Shrub-steppe fire refugia that serve as crucial habitat for species of concern are vulnerable to loss in subsequent fire, completing the type conversion by removing the regeneration seed source (D'Antonio and Vitousek 1992, Rossiter et al. 2003).

Although changing fire regimes may influence the distribution and quantity of fire refugia, fire is a naturally occurring, dynamic agent of ecosystem change in most seasonally dry ecoregions. As anthropogenic changes continue to alter ecosystems, there is renewed focus on refugia as key components of ecosystem resilience that will buffer some of the more immediate negative impacts of climate change (Keppel and Wardell-Johnson 2012, Taylor et al. 2014). For example, climate and land use changes increase the vulnerability of ecosystem services (Smith et al. 2014), whereas fire refugia can mitigate the negative effects of altered disturbance regimes by providing places in which species that are not adapted to new disturbance regimes can persist, migrate through, or adapt in place (Dobrowski 2011). In addition, plant seedling establishment and persistence are related to the availability of seed sources but also to climatic conditions. Juveniles tend to occupy a cooler and wetter niche (Dobrowski et al. 2015), so refugia such as old-growth forest that foster locally moderated microclimate conditions by providing shade (Frey et al. 2016, Lutz et al. 2018) may improve their establishment success on adjacent sites, particularly as increased summer drought may negatively affect ecosystem recovery (Harvey et al. 2016, Stevens-Rumann et al. 2017).

Given projections of warmer and sometimes drier conditions in the future, colocation of fire refugia and climate refugia will become more important for effective function of fire refugia (Wilkin et al. 2016). When these refugia are not colocated, ecosystem recovery potential might be severely hampered, because recovering species are pushed out of their historic climatic envelope (figure 3). Therefore, the spatial arrangement of fire refugia may play a key role in how landscape heterogeneity buffers ecosystems from anthropogenic climate change. This buffering role is especially important where colocated refugia support or facilitate recovery of the predisturbance ecosystem function, whereas fire refugia that do not overlap with climate refugia are more vulnerable to being compromised (figure 3). For example, because drought refugia are more resistant to the extremes of interannual climatic variability, it is hypothesized that such locations will continue to be buffered as the climate changes (McLaughlin et al. 2017), thereby harboring remnant populations of sensitive species prioritized by conservation adaptation and mitigation solutions (Morelli et al. 2016). However, this hypothesis depends on climate feedback loops not reducing the resilience of refugia through increased ecological disturbances, such as wildfire, bark beetles, and drought.

Research needs and management implications

There is a crucial need to prioritize fire refugia for conservation and management under global change. The fire refugia taxonomic dichotomies presented in the present article provide a framework to consider conservation values and potential trends in fire refugia characteristics. Understanding the distribution, abundance, composition, and function of fire refugia may help in prioritizing land management activities on the basis of the concepts of resistance and resilience to fire and of the vulnerability to further disturbances. This prioritization will likely require a comprehensive understanding of both the spatial and the temporal predictors of refugia, integrated with conservation needs and policy limitations.

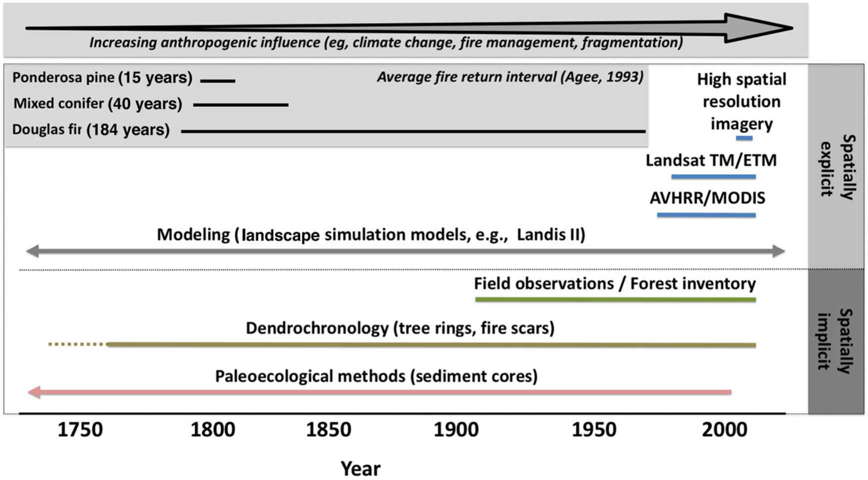

Figure 4. Examples of approximate timescales at which different methods or instruments can contribute to understanding of wildland fire and the occurrence of fire refugia. Average fire return intervals for three different ecosystems across the western United States are given with the bars representing the time period across the time axis.

Because the patterns of fire refugia can be affected by human activity and because the management of fire refugia has considerable implications for conservation and policy, there is a need for research integrating different spatial and temporal methodologies to improve understanding of the ecological function of fire refugia (figure 4, table 1). Integration of field and remote-sensing data into both statistical and simulation modeling frameworks has been proposed to facilitate dynamic species distribution modeling under global change (Franklin et al. 2016), and such integration also holds great potential to enhance the understanding of fire refugia by scaling across space and time (e.g., O'Connor et al. 2016). For example, consider a study identifying the minimum areal extent and canopy cover for refugia required by a specific species as habitat in the field. This estimate could then be extended geospatially by predicting the number of refugia that meet the criteria from remote sensing and modeled into the future from downscaled global climate model outputs and landscape-scale ecosystem simulations. Linking species-specific and landscape-process approaches could also help identify criteria for land managers wishing to conserve species and habitats in fire-prone landscapes. The challenge is that such approaches require large calibration areas to link across scales (Lutz 2015).

Because fire activity is projected to increase under future climate scenarios, fire refugia will likely be important to preserving ecosystem resiliency for a variety of taxa (tables S1 and S2). Therefore, future management actions should focus on identifying, maintaining, or promoting fire refugia within landscapes holistically. For example, the actual locations of ephemeral fire refugia may be less important than their aggregate area and their spatial configuration. On the other hand, understanding the location and environmental determinants of predictable, persistent, and semipersistent fire refugia may be vital for increasing the resilience of both natural and human-occupied landscapes (Smith et al. 2016).

Management actions specifically designed to support the formation and conservation of fire refugia generally do not yet exist or have not been tested for efficacy. However, one management strategy that would have clear positive outcomes for conserving fire refugia could be reducing the use of backfires and burnouts (or "blackout burning") as wildfire suppression tactics where feasible. During large fire events, firefighters routinely use firing operations to consume available fuel ahead of an advancing fire front; as the flaming front passes or reaches containment lines, they subsequently burn out any remnant green vegetation (i.e., fire refugia) to reduce the potential for flare-ups and ember-ignited spot fires across the containment line. Although this operation tactic is highly effective for protecting crucial infrastructure and resources, it may not be necessary to achieve containment on fires that are remote or being managed to meet natural resource objectives. One strategy for addressing the potential loss of fire refugia from this practice is to embed fire refugia in national and global conservation plans through entities such as The Nature Conservancy and Conservation International, which work with regional and local partners to identify the best management practices and policies to support ecological conservation.

Targeted suppression efforts can be used strategically to protect sensitive refugia. For example, giant sequoia (*Sequoiadendron giganteum*) groves that historically burned at low severity prior to modern fire suppression have specifically been protected through preventative prescribed fire, silvicultural treatment, and subsequent enhanced suppression efforts in several recent fires in Yosemite and Sequoia and Kings Canyon National Parks in California. To date, fire refugia are generally not considered "at risk," or areas worth protecting during fire suppression activities. Identifying ecologically valuable fire refugia or locations on the landscape in which significant proportions of fire refugia are desired in the postfire mosaic would allow fire managers to integrate the conservation or formation of fire refugia into their preplanning, strategy and tactics (e.g., Dunn et al. 2017).

Conclusions

Fire refugia are crucial for the maintenance of biodiversity and ecosystem resilience under global change (Keppel and Wardell-Johnson 2012) but may also be at risk because of feedback loops of a changing climate, land management, and fire management practices. Projected increases in fire

Table 1. Future key research needs and their associated management and applications questions for fire refugia.

Topic	Key research need	Key management and applications questions
Historic natural variability	Historical range of refugia abundance, size, and complexity across ecotypes[a,b,c,d,e,f]	How do we facilitate refugia through ecosystem restoration tactics (e.g., prescribed fire)?
Refugia characteristics	Ranked importance of refugia characteristics by key species[b,e]	How do we integrate metrics of refugia (e.g., distribution, abundance, physical complexity) into ecosystem function management goals?
Landscape pattern	Refugial connectivity across landscapes; species-specific needs for network size and connectivity[e,g,h,i,j,k,l,m,n,o,p,q]	How do we create refugial connectivity on the landscape through forest and fire management activities?
Biophysical determinants	Relationships between refugia longevity and biophysical factors (persistent, predictable, stochastic)[e,r,s,t,u,v,w]	How and where can we establish biophysical barriers to create, enhance, or preserve fire refugia on the landscape?
Fire behavior	Models of fire behavior that accurately project refugial formation[d,e,x]	Under what conditions can we actively pursue protection or facilitation of fire refugia?
Climate change	Climate change impacts on refugial trajectories, patterns, function, and characteristics[y,z]	How do we identify and protect crucial fire refugia as seed sources and biodiversity hot spots?
Successional pathways	Probabilities of different successional pathways for refugia[e,w,aa,bb,cc]	How do we protect the ecological integrity of fire refugia years to decades after a fire?

Note: Literature that in some way or form contributes to or highlights the need for (a) research, (b) management, or (c) applications, related to fire refugia: [a]Meddens et al. 2016, [b]Meddens et al. 2018, [c]Kolden et al. 2012, [d]Krawchuk et al. 2016, [e]Perera and Buse 2014, [f]Robinson et al. 2013, [g]Banks et al. 2012, [h]Banks et al. 2011, [i]Berry et al. 2015b, [j]Brennan et al. 2011, [k]Gongalsky et al. 2012, [l]Henriques et al. 2000, [m]Hylander 2011, [n]Hylander and Johnson 2010, [o]Lindenmayer et al. 2009, [p]Schwilk and Keeley 1998, [q]Swan et al. 2016, [r]Berry et al. 2015a, [s]Clarke 2002, [t]Leonard et al. 2014, [u]Roman-Cuesta et al. 2009, [v]Wilkin et al. 2016, [w]Schwilk and Keeley 2006, [x]Wimberly and Kennedy 2008, [y]Abatzoglou et al. 2017, [z]Kolden et al. 2015*a*, [aa]Camp et al. 1997, [bb]Harvey et al. 2016, [cc]Kolden et al. 2017.

season duration and fuel aridity in response to anthropogenic climate change alongside invasion of exotic annual grasses are expected to increase future fire activity across both moist and arid ecosystems, which, in turn, will increase the importance of fire refugia. The ecological functions of refugia—locations in which biodiversity can retreat to during and immediately after fire, and persist in and expand from following fire—will continue to be important for overall ecosystem resilience. The four dichotomies in our fire refugia taxonomy clarify the full spectrum of fire refugia characteristics while facilitating their identification and classification. This holistic approach to thinking about fire refugia, which includes both landscape-process and species-specific perspectives, can help contextualize future research that investigates the formation, function, or conservation of fire refugia, and can also be incorporated by land managers into fire management strategies from local to global scales.

Supplemental material

Supplemental data are available at *BIOSCI* online.

Acknowledgments

This work was partially supported by the Joint Fire Science Program (JFSP, cooperative agreement no. L16AC00202), the National Science Foundation under grant no. DMS-1520873, the College of Natural Resources, the NASA Idaho Space Grant Consortium, and the Department of the Interior Northwest Climate Science Center (NW CSC) through cooperative agreement no. G14AP00177 from the US Geological Survey (USGS). Its contents are solely the responsibility of the authors and do not necessarily represent the views of NSF, NW CSC, or USGS. The views and conclusions contained in this document are those of the authors and should not be interpreted as representing the opinions or policies of the US government. Mention of trade names or commercial products does not constitute their endorsement by the US government. This manuscript is submitted for publication with the understanding that the US government is authorized to reproduce and distribute reprints for governmental purposes. Tyler Bleeker and Jeffrey Hicke provided helpful comments on early drafts of this manuscript. We thank three anonymous reviewers for their helpful comments.

References cited

Abatzoglou JT, Kolden CA, Williams AP, Lutz JA, Smith AM. 2017. Climatic influences on interannual variability in regional burn severity across western US forests. International Journal of Wildland Fire 26: 269–275.

Abatzoglou JT, Williams AP. 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences 113: 11770–11775.

Agee JK. 1993. Fire ecology of Pacific Northwest forests. Island Press.

Allen CD, et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259: 660–684.

Andela N, Morton D, Giglio L, Chen Y, van der Werf G, Kasibhatla P, DeFries R, Collatz G, Hantson S, Kloster S. 2017. A human-driven decline in global burned area. Science 356: 1356–1362.

Balch JK, Bradley BA, Abatzoglou JT, Nagy RC, Fusco EJ, Mahood AL. 2017. Human-started wildfires expand the fire niche across the United States. Proceedings of the National Academy of Sciences 114: 2946–2951.

Banks SC, Blyton MDJ, Blair D, McBurney L, Lindenmayer DB. 2012. Adaptive responses and disruptive effects: How major wildfire influences kinship-based social interactions in a forest marsupial. Molecular Ecology 21: 673–684.

Banks SC, Dujardin M, McBurney L, Blair D, Barker M, Lindenmayer DB. 2011. Starting points for small mammal population recovery after wildfire: Recolonisation or residual populations? OIKOS 120: 26–37.

Barbero R, Abatzoglou JT, Larkin NK, Kolden CA, Stocks B. 2015. Climate change presents increased potential for very large fires in the contiguous United States. International Journal of Wildland Fire 24: 892–899.

Beaty RM, Taylor AH. 2001. Spatial and temporal variation of fire regimes in a mixed conifer forest landscape, Southern Cascades, California, USA. Journal of Biogeography 28: 955–966.

Berry LE, Driscoll DA, Stein JA, Blanchard W, Banks SC, Bradstock RA, Lindenmayer DB. 2015a. Identifying the location of fire refuges in wet forest ecosystems. Ecological Applications 25: 2337–2348.

Berry LE, Lindenmayer DB, Driscoll DA. 2015b. Large unburnt areas, not small unburnt patches, are needed to conserve avian diversity in fire-prone landscapes. Journal of Applied Ecology 52: 486–495.

Birch DS, Morgan P, Kolden CA, Abatzoglou JT, Dillon GK, Hudak AT, Smith A. 2015. Vegetation, topography and daily weather influenced burn severity in central Idaho and western Montana forests. Ecosphere 6: 1–23.

Bowman DM, Williamson GJ, Abatzoglou JT, Kolden CA, Cochrane MA, Smith AM. 2017. Human exposure and sensitivity to globally extreme wildfire events. Nature ecology and evolution 1: 0058.

Bradstock RA, Hammill KA, Collins L, Price O. 2010. Effects of weather, fuel and terrain on fire severity in topographically diverse landscapes of south-eastern Australia. Landscape Ecology 25: 607–619.

Brennan KEC, Moir ML, Wittkuhn RS. 2011. Fire refugia: The mechanism governing animal survivorship within a highly flammable plant. Austral Ecology 36: 131–141.

Brubaker LB, Anderson PM, Edwards ME, Lozhkin AV. 2005. Beringia as a glacial refugium for boreal trees and shrubs: new perspectives from mapped pollen data. Journal of Biogeography 32: 833–848.

Camp A, Oliver C, Hessburg P, Everett R. 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. Forest Ecology and Management 95: 63–77.

Cansler CA, McKenzie D. 2014. Climate, fire size, and biophysical setting control fire severity and spatial pattern in the northern Cascade Range, USA. Ecological Applications 24: 1037–1056.

Clarke PJ. 2002. Habitat islands in fire-prone vegetation: do landscape features influence community composition? Journal of Biogeography 29: 677–684.

Coop JD, Givnish TJ. 2007. Gradient analysis of reversed treelines and grasslands of the Valles Caldera, New Mexico. Journal of Vegetation Science 18: 43–54.

D'Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23: 63–87.

Dobrowski SZ. 2011. A climatic basis for microrefugia: the influence of terrain on climate. Global Change Biology 17: 1022–1035.

Dobrowski SZ, Swanson AK, Abatzoglou JT, Holden ZA, Safford HD, Schwartz MK, Gavin DG. 2015. Forest structure and species traits mediate projected recruitment declines in western US tree species. Global Ecology and Biogeography 24: 917–927.

Dunn CJ, Calkin DE, Thompson MP. 2017. Towards enhanced risk management: planning, decision making and monitoring of US wildfire response. International Journal of Wildland Fire 26: 551–556.

Franklin J, Serra-Diaz JM, Syphard AD, Regan HM. 2016. Global change and terrestrial plant community dynamics. Proceedings of the National Academy of Sciences 113: 3725–3734.

Franklin JF, Lindenmayer DB, MacMahon JA, McKee A, Magnuson J, Perry DA, Waide R, Foster D. 2000. Threads of continuity: ecosystem disturbance, recovery, and the theory of biological legacies. Conservation Biology in Practice 1: 8–17.

Frey SJ, Hadley AS, Johnson SL, Schulze M, Jones JA, Betts MG. 2016. Spatial models reveal the microclimatic buffering capacity of old-growth forests. Science advances 2: e1501392.

Gill AM. 1975. Fire and the Australian flora: a review. Australian Forestry 38: 4–25.

Gongalsky KB, Malmstrom A, Zaitsev AS, Shakhab SV, Bengtsson J, Persson T. 2012. Do burned areas recover from inside? An experiment with soil fauna in a heterogeneous landscape. Applied Soil Ecology 59: 73–86.

Haffer J. 1969. Speciation in Amazonian forest birds. Science 165: 131–137.

Haire SL, McGarigal K. 2010. Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (*Pinus ponderosa*) in New Mexico and Arizona, USA. Landscape Ecology 25: 1055–1069.

Harvey BJ, Donato DC, Turner MG. 2016. High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Global Ecology and Biogeography 25: 655–669.

Henriques RPB, Bizerril MXA, Palma ART. 2000. Changes in small mammal populations after fire in a patch of unburned cerrado in Central Brazil. Mammalia 64: 173–185.

Hylander K. 2011. The response of land snail assemblages below aspens to forest fire and clear-cutting in Fennoscandian boreal forests. Forest Ecology and Management 261: 1811–1819.

Hylander K, Johnson S. 2010. In situ survival of forest bryophytes in small-scale refugia after an intense forest fire. Journal of Vegetation Science 21: 1099–1109.

IPCC. 2013. Climate Change 2013: The physical science basis. Working Group 1 (WG1) Contribution to the Intergovernmental Panel on Climate Change (IPCC) Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V and Midgley PM (eds.). 5th Assessment Report (AR5). Cambridge, United Kingdom and New York, NY 1535 pp. Cambridge, UK and New York, New York, USA.

Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC, Meentemeyer RK, Metz MR, Perry GL. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14: 369–378.

Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DM. 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. Nature Communications 6:7537: e1–e11.

Kane VR, Lutz JA, Cansler CA, Povak NA, Churchill DJ, Smith DF, Kane JT, North MP. 2015. Water balance and topography predict fire and forest structure patterns. Forest Ecology and Management 338: 1–13.

Keppel G, Mokany K, Wardell-Johnson GW, Phillips BL, Welbergen JA, Reside AE. 2015. The capacity of refugia for conservation planning under climate change. Frontiers in Ecology and the Environment 13: 106–112.

Keppel G, Van Niel KP, Wardell-Johnson GW, Yates CJ, Byrne M, Mucina L, Schut AG, Hopper SD, Franklin SE. 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. Global Ecology and Biogeography 21: 393–404.

Keppel G, Wardell-Johnson GW. 2012. Refugia: keys to climate change management. Global Change Biology 18: 2389–2391.

Kimmerer RW, Lake FK. 2001. The role of indigenous burning in land management. Journal of Forestry 99: 36–41.

Kitzberger T, Falk DA, Westerling AL, Swetnam TW. 2017. Direct and indirect climate controls predict heterogeneous early mid 21st century wildfire burned area across western and boreal North America. PLOS ONE 12 (art. e0188486).

Kolden CA, Abatzoglou JT, Lutz JA, Cansler CA, Kane JT, van Wagtendonk JW, Key CH. 2015a. Climate contributors to forest mosaics: ecological persistance following wildfire. Northwest Science 89: 219–238.

Kolden CA, Abatzoglou JT, Smith AMS. 2015b. Limitations and utilisation of Monitoring Trends in Burn Severity products for assessing wildfire severity in the USA. International Journal of Wildland Fire 24: 1023–1028.

Kolden CA, Bleeker TM, Smith A, Poulos HM, Camp AE. 2017. Fire effects on historical wildfire refugia in contemporary wildfires. Forests 8: 400.

Kolden CA, Lutz JA, Key CH, Kane JT, van Wagtendonk JW. 2012. Mapped versus actual burned area within wildfire perimeters: characterizing the unburned. Forest Ecology and Management 286: 38–47.

Krawchuk MA, Haire SL, Coop J, Parisien MA, Whitman E, Chong G, Miller C. 2016. Topographic and fire weather controls of fire refugia in forested ecosystems of northwestern North America. Ecosphere 7: 1–18.

Leonard SWJ, Bennett AF, Clarke MF. 2014. Determinants of the occurrence of unburnt forest patches: Potential biotic refuges within a large, intense wildfire in south-eastern Australia. Forest Ecology and Management 314: 85–93.

Lindenmayer DB. 2009. Large-scale landscape experiments: lessons from Tumut. Cambridge University Press.

Lindenmayer DB, Hobbs RJ, Likens GE, Krebs CJ, Banks SC. 2011. Newly discovered landscape traps produce regime shifts in wet forests. Proceedings of the National Academy of Sciences 108: 15887–15891.

Lindenmayer DB, et al. 2009. What factors influence rapid post-fire site re-occupancy? A case study of the endangered Eastern Bristlebird in eastern Australia. International Journal of Wildland Fire 18: 84–95.

Lutz JA. 2015. The evolution of long-term data for forestry: large temperate research plots in an era of global change. Northwest Science 89: 255–269.

Lutz JA, Furniss TJ, Johnson DJ, Davies SJ, Allen D, Alonso A, Anderson-Teixeira KJ, Andrade A, Baltzer J, Becker KM. 2018. Global importance of large-diameter trees. Global Ecology and Biogeography 27: 849–864.

Lutz JA, Larson AJ, Freund JA, Swanson ME, Bible KJ. 2013. The importance of large-diameter trees to forest structural heterogeneity. PLOS ONE 8 (art. e82784).

Mackey B, Lindenmayer D, Gill M, McCarthy MJL. 2002. Wildfire, fire and future climate: a forest ecosystem analysis. CSIRO Publishing.

McLaughlin BC, Ackerly DD, Klos PZ, Natali J, Dawson TE, Thompson SE. 2017. Hydrologic refugia, plants, and climate change. Global Change Biology 23: 2941–2961.

Meddens AJ, Kolden CA, Lutz JA. 2016. Detecting unburned areas within wildfire perimeters using Landsat and ancillary data across the northwestern United States. Remote Sensing of Environment 186: 275–285.

Meddens AJ, Kolden CA, Lutz JA, Abatzoglou JT, Hudak AT. 2018. Spatial and temporal patterns of unburned areas within fire perimeters in the northwestern United States from 1984 to 2014. Ecoshpere 9: 1–16. doi: e02029.02010.01002/ecs02022.02029.

Meigs GW, Krawchuk MA. 2018. Composition and Structure of Forest Fire Refugia: What Are the Ecosystem Legacies across Burned Landscapes? Forests 9: 243.

Morelli TL, Daly C, Dobrowski SZ, Dulen DM, Ebersole JL, Jackson ST, Lundquist JD, Millar CI, Maher SP, Monahan WB. 2016. Managing climate change refugia for climate adaptation. PLOS ONE 11 (art. e0159909).

O'Connor CD, Thompson MP, Rodríguez y Silva F. 2016. Getting ahead of the wildfire problem: quantifying and mapping management challenges and opportunities. Geosciences 6: 35.

Perera A, Buse L. 2014. Ecology of wildfire residuals in boreal forests. John Wiley and Sons.

Petit RJ, et al. 2003. Glacial refugia: Hotspots but not melting pots of genetic diversity. Science 300: 1563–1565.

Picotte JJ, Peterson B, Meier G, Howard SM. 2016. 1984–2010 trends in fire burn severity and area for the conterminous US. International Journal of Wildland Fire 25: 413–420.

Prichard SJ, Stevens-Rumann CS, Hessburg PF. 2017. Tamm Review: shifting global fire regimes: Lessons from reburns and research needs. Forest Ecology and Management 396: 217–233.

Robinson NM, Leonard SWJ, Ritchie EG, Bassett M, Chia EK, Buckingham S, Gibb H, Bennett AF, Clarke MF. 2013. Refuges for fauna in fire-prone landscapes: their ecological function and importance. Journal of Applied Ecology 50: 1321–1329.

Roman-Cuesta RM, Gracia M, Retana J. 2009. Factors influencing the formation of unburned forest islands within the perimeter of a large forest fire. Forest Ecology and Management 258: 71–80.

Romme WH, Knight DH. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology 62: 319–326.

Rossiter NA, Setterfield SA, Douglas MM, Hutley LB. 2003. Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. Diversity and Distributions 9: 169–176.

Russell-Smith J, Bowman D. 1992. Conservation of monsoon rainforest isolates in the Northern Territory, Australia. Biological Conservation 59: 51–63.

Schwilk DW, Keeley JE. 1998. Rodent populations after a large wildfire in California chaparral and coastal sage scrub. The Southwestern Naturalist: 480–483.

Schwilk DW, Keeley JE. 2006. The role of fire refugia in the distribution of *Pinus sabiniana* (Pinaceae) in the southern Sierra Nevada. Madrono 53: 364–372.

Sears MW, Angilletta MJ, Schuler MS, Borchert J, Dilliplane KF, Stegman M, Rusch TW, Mitchell WA. 2016. Configureuration of the thermal landscape determines thermoregulatory performance of ectotherms. Proceedings of the National Academy of Sciences 113: 10595–10600.

Shakesby R, Doerr S. 2006. Wildfire as a hydrological and geomorphological agent. Earth-Science Reviews 74: 269–307.

Smith A, Kolden CA, Tinkham WT, Talhelm AF, Marshall JD, Hudak AT, Boschetti L, Falkowski MJ, Greenberg JA, Anderson JW. 2014. Remote sensing the vulnerability of vegetation in natural terrestrial ecosystems. Remote Sensing of Environment 154: 322–337.

Smith AM, et al. 2016. The science of firescapes: achieving fire-resilient communities. BioScience 66: 130–146.

Smith AM, Talhelm AF, Johnson DM, Sparks AM, Kolden CA, Yedinak KM, Apostol KG, Tinkham WT, Abatzoglou JT, Lutz JA. 2017. Effects of fire radiative energy density dose on Pinus contorta and Larix occidentalis seedling physiology and mortality. International Journal of Wildland Fire 26: 82–94.

Stevens JT, Collins BM, Miller JD, North MP, Stephens SL. 2017. Changing spatial patterns of stand-replacing fire in California conifer forests. Forest Ecology and Management 406: 28–36.

Stevens-Rumann CS, Kemp KB, Higuera PE, Harvey BJ, Rother MT, Donato DC, Morgan P, Veblen TT. 2017. Evidence for declining forest resilience to wildfires under climate change. Ecology Letters 21: 243–252.

Swan M, Galindez-Silva C, Christie F, York A, Di Stefano J. 2016. Contrasting responses of small mammals to fire and topographic refugia. Austral Ecology 41: 437–445.

Swanson ME, Franklin JF, Beschta RL, Crisafulli CM, DellaSala DA, Hutto RL, Lindenmayer DB, Swanson FJ. 2010. The forgotten stage of forest succession: Early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9: 117–125.

Taylor C, McCarthy MA, Lindenmayer DB. 2014. Nonlinear effects of stand age on fire severity. Conservation Letters 7: 355–370.

Turner MG. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91: 2833–2849.

van Wagtendonk JW, Lutz JA. 2007. Fire regime attributes of wildland fires in Yosemite National Park, USA. Fire Ecology 3: 34–52.

Weisberg PJ, Ko D, Py C, Bauer JM. 2008. Modeling fire and landform influences on the distribution of old-growth pinyon-juniper woodland. Landscape Ecology 23: 931–943.

Westerling AL. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Phil. Trans. R. Soc. B 371: 20150178.

Wilkin KM, Ackerly DD, Stephens SL. 2016. Climate change refugia, fire ecology and management. Forests 7: 77.

Wimberly MC, Kennedy RSH. 2008. Spatially explicit modeling of mixed-severity fire regimes and landscape dynamics. Forest Ecology and Management 254: 511–523.

Wood SW, Murphy BP, Bowman DM. 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. Journal of Biogeography 38: 1807–1820.

Arjan J.H. Meddens (ameddens@uidaho.edu), Crystal A. Kolden, and Alistair M. S. Smith are affiliated with the College of Natural Resources at the University of Idaho, in Moscow. James A. Lutz is affiliated with Utah State University's Wildland Resources Department, in Logan, Utah. C. Alina Cansler is affiliated with the Fire, Fuel, and Smoke Science Program, part of the USDA Forest Service, in Missoula, Montana. John T. Abatzoglou is affiliated with the Department of Geography at the University of Idaho, in Moscow. Garrett W. Meigs, William M. Downing, and Meg A. Krawchuk are affiliated with the Department of Forest Ecosystems and Society in the College of Forestry at Oregon State University, in Corvallis.