

Fire refugia: What are they and why do they matter for global change?

Journal:	<i>BioScience</i>
Manuscript ID	18-0038.R1
Manuscript Type:	Overview Article
Date Submitted by the Author:	n/a
Complete List of Authors:	<p>Meddens, Arjan; University of Idaho, Department of Natural Resources and Society Kolden, Crystal; University of Idaho, Forest, Rangeland, and Fire Sciences Lutz, James; Utah State University, Wildland Resources Smith, Alistair; University of Idaho, Forest, Rangeland, and Fire Sciences Cansler, C.; USDA Forest Service, Fire, Fuel, and Smoke Science Program Abatzoglou, John; University of Idaho, Department of Geography Meigs, Garrett; Oregon State University, Department of Forest Ecosystems and Society Downing, William; Oregon State University, Department of Forest Ecosystems and Society Krawchuk, Meg; Oregon State University, Department of Forest Ecosystems and Society</p>
Key words:	biogeography, wildfires, refuge, resilience, landscape ecology
Abstract:	<p>Fire refugia are landscape elements that remain unburned or minimally impacted by fire, thereby supporting post-fire 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 critical 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: 1) unburned versus lower severity; 2) species-specific versus landscape-process characteristics; 3) predictable versus stochastic; and 4) 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 critical to conservation given the role that humans play in shaping disturbance regimes across landscapes.</p>

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Draft Manuscript

Fire refugia: What are they and why do they matter for global change?

Arjan J.H. Meddens^{1§}, Crystal A. Kolden¹, James A. Lutz², Alistair M. S. Smith¹, C. Alina Cansler³, John T. Abatzoglou⁴, Garrett W. Meigs⁵, William M. Downing⁵, Meg A. Krawchuk⁵

¹ College of Natural Resources, University of Idaho, Moscow, ID, 83844, USA.

² Utah State University, Wildland Resources, Logan, UT, 84322-5230 USA.

³ Fire, Fuel, and Smoke Science Program, USDA Forest Service, Missoula, MT 59808, USA.

⁴ Department of Geography, University of Idaho, Moscow, ID 83844-3021, USA.

⁵ Department of Forest Ecosystems and Society, College of Forestry, Oregon State University, Corvallis, OR 97331, USA.

§ Corresponding author: ameddens@uidaho.edu

Revised manuscript submitted to *BioScience* on July 3rd, 2018

1 **Abstract**

2 Fire refugia are landscape elements that remain unburned or minimally impacted by fire,
3 thereby supporting post-fire ecosystem function, biodiversity, and resilience to disturbances.
4 Although fire refugia have been studied across continents, scales, and affected taxa, they have
5 not been characterized systematically over space and time, which is critical for understanding
6 their role in facilitating resilience in the context of global change. We identify four dichotomies
7 that delineate an overarching conceptual framework of fire refugia: 1) unburned versus lower
8 severity; 2) species-specific versus landscape-process characteristics; 3) predictable versus
9 stochastic; and 4) ephemeral versus persistent. We outline the principal concepts underlying the
10 ecological function of fire refugia and describe both the role of fire refugia and uncertainties
11 regarding their persistence under global change. An improved understanding of fire refugia is
12 critical to conservation given the role that humans play in shaping disturbance regimes across
13 landscapes.

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

15 **Introduction**

16 Fire is a global disturbance process that interacts with landscape pattern to create mosaics of
17 ecosystem effects, including patches that remain both unburned and only minimally affected by
18 low-intensity burning. These patches are increasingly of interest to ecologists and are often
19 referred to as fire refugia (Kolden et al. 2012, Krawchuk et al. 2016, Robinson et al. 2013). In the
20 broader ecological literature, refugia are components of ecosystems where biodiversity can
21 retreat to, persist in, and potentially expand from as environmental conditions change (Keppel et
22 al. 2015). Refugia were originally defined in the context of large-scale processes on evolutionary

1
2
3 23 time scales; continental glaciation and the subsequent isolation of unique habitat types resulted in
4
5 24 speciation within refugia (Haffer 1969) and subsequent migrations from refugia (Brubaker et al.
6
7
8 25 2005, Petit et al. 2003). Refugia created by contemporary ecological phenomena have been the
9
10 26 subject of recent studies (Dobrowski 2011, Keppel et al. 2012, Krawchuk et al. 2016, Morelli et
11
12 27 al. 2016), reflecting interest in refugia formation and function at smaller spatial and shorter
13
14 28 temporal scales, especially in relation to observed and projected climate change. Climate-change
15
16 29 refugia have been defined as ‘areas relatively buffered from contemporary climate change that
17
18 30 allow for habitat stability and species persistence over time’ (Morelli et al. 2016). However,
19
20 31 climate refugia identified for conservation and management purposes require that these areas
21
22 32 also be buffered from severe disturbance events if they are to function as hold-outs within a
23
24 33 changing environment. Accordingly, fire refugia are a necessary complement to climate change
25
26 34 refugia in fire-prone landscapes.

30
31 35 The concept of fire refugia has various definitions (e.g., Camp et al. 1997, Gill 1975,
32
33 36 Krawchuk et al. 2016, Mackey et al. 2002), all of which focus on the idea of locations disturbed
34
35 37 less frequently or less severely by wildfire relative to the surrounding vegetation matrix. Fire
36
37 38 refugia provide habitat for individuals or populations to survive fire, to persist in the post-fire
38
39 39 environment, and from which to disperse into the higher-severity burned landscape (Robinson et
40
41 40 al. 2013). In this way, fire refugia can function similarly to islands in a biogeographic context,
42
43 41 particularly in severely burned areas, recognizing that the matrix of burned areas still provides
44
45 42 some habitat to many taxa. Mosaics of fire effects spanning the full range of burn severity –
46
47 43 including refugial patches – influence succession, ecosystem processes, and the distribution of
48
49 44 biological legacies (Franklin et al. 2000, Johnstone et al. 2016, Turner 2010). Locations where
50
51 45 biota survive fire have been shown to strongly influence post-fire recovery and ecosystem
52
53
54
55
56
57
58
59
60

1
2
3 46 dynamics (e.g., Haire and McGarigal 2010, Robinson et al. 2013, Stevens-Rumann et al. 2017).
4
5 47 Uniquely, however, fire refugia are not purely ecological or biophysical phenomena, they are
6
7 48 also a social-ecological construct, for example due to human manipulation of vegetative fuels
8
9
10 49 and fire suppression activities that can both facilitate and impede their formation. As patterns of
11
12 50 fire refugia are increasingly impacted by human activity, understanding their form and function
13
14 51 is becoming a priority for conservation, management, and policy. Recognition and identification
15
16 52 of fire refugia, including their spatial configuration, their physical location within the
17
18 53 surrounding burned matrix, and their composition and structure, will become increasingly
19
20 54 important for effective conservation and land management under the nexus of altered land use,
21
22 55 shifting land cover, and anthropogenic climate change, which we hereafter refer to as global
23
24 56 change.
25
26
27

28 57 Given the growing interest in and number of publications on the form, function, and
29
30 58 conservation value of contemporary fire refugia (Kolden et al. 2015a), our objective is to
31
32 59 synthesize the existing literature and characterize the current thinking about fire refugia in
33
34 60 forested ecosystems in the context of global change. By defining and identifying different
35
36 61 aspects of fire refugia we provide a clearer architecture for these important landscape elements,
37
38 62 as a crucial step forward in refugia-based science and management. We address three
39
40 63 overarching questions: 1) What are fire refugia? That is, what are the commonalities and
41
42 64 differences in the ways fire refugia have been defined in the scientific literature?; 2) What
43
44 65 theoretical frameworks underlie the ecological function of fire refugia?; 3) How can fire refugia
45
46 66 support ecosystem resilience under global change? We expand considerably upon prior efforts by
47
48 67 Robinson et al. (2013) by including flora and by focusing on refugia as micro-ecosystems, rather
49
50 68 than for a specific faunal species of interest. In addition, we characterize the temporal dynamism
51
52
53
54
55
56
57
58
59
60

1
2
3 69 of refugia by addressing drivers of formation and persistence. Finally, we address global change
4
5 70 and the role of refugia in ecosystem resilience. By clearly defining and identifying different
6
7 71 aspects of fire refugia, we gain insight into whether they will persist or whether there are given
8
9 72 thresholds that might lead to losses in fire refugia in a time of accelerating global change. To
10
11 73 support our synthesis, we conducted a comprehensive literature search utilizing standard
12
13 74 scientific search engines (e.g., Web of Science, Academic Science Premier) and searched for all
14
15 75 known terms used for fire refugia (e.g., skips, unburned islands, refuges) published as of June of
16
17 76 2018. We then compiled these to identify common themes and determine which key papers best
18
19 77 highlighted the facets of these common themes (Tables S1 and S2). We acknowledge that some
20
21 78 studies that fall within broader definitions of fire refugia and more tangential papers may be
22
23 79 omitted from these tables.
24
25
26
27
28

29 80 **What are fire refugia?**

31 81 Fire refugia are defined and characterized variably in the literature. Specific terms include
32
33 82 unburned islands, habitat refugia, remnants, residual vegetation, fire shadows, skips, stringers,
34
35 83 refuges, islands, biological legacies, and late-successional forest (Tables S1 and S2). Studies of
36
37 84 fire refugia have been concentrated primarily in the boreal and temperate forests of western
38
39 85 North America and the shrublands and forests of eastern Australia, with additional studies in
40
41 86 Europe, South America, and Africa (Tables S1 and S2). There is some ambiguity in the literature
42
43 87 regarding the distinction between refugia and refuges, which we suggest is more of a language
44
45 88 clarification than a formally defined difference. Although there are reasons to consider refugia
46
47 89 and refuges differently, we recognize that both are focused on the same core idea—areas that are
48
49 90 buffered from pressures or changes experienced by adjacent areas. From Camp et al. (1997), one
50
51 91 of the early seminal works on fire refugia, and to be consistent with the authors' more recent
52
53
54
55
56
57
58
59
60

1
2
3 92 contributions in this field, we use ‘refugia’ here, rather than ‘refuges.’ Based on the existing
4
5 93 literature, we identify four taxonomic dichotomies that delineate a conceptual framework for
6
7
8 94 characterizing fire refugia: 1) unburned versus lower severity; 2) species-specific versus
9
10 95 landscape-process characteristics; 3) predictable versus stochastic formation; and 4) ephemeral
11
12 96 versus persistent. We describe each of these in a global change context.
13
14

15 97 1. Unburned versus lower severity refugia

16
17
18 98 Some studies define fire refugia specifically as unburned areas within fire perimeters
19
20 99 (Meddens et al. 2016, Swan et al. 2016), while others include low-severity fire patches within the
21
22 100 burned area (Krawchuk et al. 2016). Many, however, do not explicitly define whether fire refugia
23
24
25 101 are unburned, low-severity, or a mixture of both (e.g., Camp et al. 1997, Schwilk and Keeley
26
27 102 2006). The widespread use of Landsat-based change detection methods to generate maps of burn
28
29 103 severity and identify fire refugia has led some studies to describe relatively large areas as
30
31 104 unburned (Kolden et al. 2015a, Kolden et al. 2012, Meddens et al. 2016, Roman-Cuesta et al.
32
33 105 2009, Wood et al. 2011), but has also yielded a growing recognition that it is difficult in some
34
35
36 106 ecosystems to accurately differentiate between unburned islands and low-severity patches from
37
38 107 such spectral reflectance-based remote sensing datasets (Kolden et al. 2015b, van Wagtenonk
39
40
41 108 and Lutz 2007). This difficulty stems from the variability of sub-canopy surface conditions
42
43 109 within a pixel when the imagery values primarily reflect conditions associated with an unaffected
44
45 110 overstory canopy (Cansler and McKenzie 2014). Further, delineation of refugia from spectral
46
47
48 111 data without additional ground observations does not provide information on the pre-fire
49
50 112 composition and structure of fire refugia (Meigs and Krawchuk 2018) or their potential
51
52 113 ecological functions.
53
54
55
56
57
58
59
60

1
2
3 114 A definition of fire refugia that includes areas that experienced underburns, surface fire, or
4
5 115 low fire severity, in addition to areas that were truly unburned, reflects a broader and more
6
7 116 inclusive perspective of refugia that supports the preponderance of taxa and fire effects of
8
9 117 interest for conservation and management concerns. For example in a forested ecosystem, a
10
11 118 stand of trees where surface has moved through the understory leaving the canopy intact, when
12
13 119 the surrounding area burned at high severity, would be considered a fire refugium. The overstory
14
15 120 trees in this fire refugium were resistant to fire, persisted as legacies on the landscape, and will
16
17 121 function as seed source for forest re-establishment. Surface fire in fire refugia may in fact
18
19 122 increase the chances of the overstory community persisting through subsequent events e.g., as
20
21 123 “fire-tended” old growth forest fire refugia. In comparison, a nearby stand may have received no
22
23 124 fire, and this unburned area is also a fire refugium but with different compositional and structural
24
25 125 attributes. Researchers and managers interested in specific ecosystem components, such as rare,
26
27 126 fire-intolerant species, understory vegetation, surface fuels, or belowground processes would
28
29 127 likely define refugia more restrictively (Tables S1 and S2). The inclusive definition of fire
30
31 128 refugia, with recognition of the distinctions between unburned versus low severity fire refugia, is
32
33 129 critical in integrating the role of refugia across broad regions and fire ecologies.
34
35
36
37
38
39
40

41 2. Species-specific refugia versus landscape process

42
43 131 Studies of fire refugia generally fall into two broad research perspectives (Lindenmayer
44
45 132 2009): fire refugia specific to a species or group of species (Table S1) and fire refugia as the
46
47 133 product of landscape-scale processes (Table S2).
48
49

50 134 A species-oriented perspective focuses on how taxa (or their habitat) respond to direct
51
52 135 exposure to combustion and fire-induced habitat change; this perspective is covered in-depth by
53
54 136 Robinson et al. (2013). Existing species-oriented fire refugia research includes studies of
55
56
57
58
59
60

1
2
3 137 butterfly populations, invertebrates, bryophytes, birds, small mammals, and vegetation (Table
4
5 138 S1). These studies stem from the need to understand specific mechanisms of survival,
6
7 139 connectivity, dispersal, and persistence of species and populations during and after wildfires,
8
9 140 particularly when a species is threatened or endangered. Species-specific refugia can refer to
10
11 141 single plants (requiring refugia of only a few m²) that remain unburned and shelter invertebrates
12
13 142 (e.g., Brennan et al. 2011) or larger areas (tens to hundreds of m²) that remain unburned and
14
15 143 promote persistence of plant species and vertebrates that rely on these structural elements as
16
17 144 habitat (e.g., Banks et al. 2012) (Fig. 1). Species-specific refugia may also involve larger
18
19 145 unburned or lightly burned patches, or collections of patches, that maintain a single species
20
21 146 across the larger landscape (e.g., *Pinus sabinana* in Schwilk and Keeley 2006). To meet
22
23 147 regulatory mandates to preserve such species under global change, however, habitat
24
25 148 requirements must be embedded in more comprehensive landscape processes that facilitate
26
27 149 specific ecosystem functions, particularly when multiple management objectives must be met.
28
29
30
31
32

33 150 Landscape-process fire refugia have primarily been characterized as landscape patches that
34
35 151 did not burn or burned less severely or frequently than adjacent areas, irrespective of species
36
37 152 composition (*but see* Berry et al. 2015b). In contrast to a species-specific approach, research
38
39 153 focused on landscape-process refugia generally seek to quantify and characterize patterns of fire
40
41 154 refugia across a range of spatiotemporal scales, and associate refugial formation with
42
43 155 environmental factors (Lindenmayer 2009, Table S2, Fig. 1). Often this approach is embedded
44
45 156 within broader landscape ecology theory or remote sensing queries and analyses (e.g., Kane et al.
46
47 157 2015, Kolden et al. 2012 Meigs and Krawchuk 2018), but landscape-process studies also include
48
49 158 modeling (Wimberly and Kennedy 2008) or quantification of forest stand structure and
50
51 159 composition from field observations (Camp et al. 1997). In contrast to species-centric
52
53
54
55
56
57
58
59
60

1
2
3 160 perspectives, landscape-process studies often lack quantifiable mechanistic links to the fine-scale
4
5 161 ecological processes that are important for understanding ecological function of fire refugia.
6
7
8 162 However, landscape-process studies (Table S2) can inform efforts focused on ecosystem process,
9
10 163 particularly those interested in trends and patterns of reforestation and plant regeneration under
11
12 164 global change (e.g., Stevens et al. 2017). Similarly, landscape-process studies may inform
13
14 165 species-specific management objectives by identifying changes in patch metrics of critical
15
16 166 habitat, such as the optimal patch-size distributions of shade for ectotherms (e.g., Sears et al.
17
18
19 167 2016).

168 3. Predictable versus stochastic refugia formation

169 For any given fire event, fire refugia are formed through fire behavior driven by the three
170 factors of the fire behavior triangle: topography, fuels, and weather. These three factors control
171 fireline intensity and direction of spread. A change in any factor can deprive a fire of available
172 fuel, creating refugia. Water features, riparian areas, roads, and clearings are some of the most
173 obvious contributors to stopping or slowing fire spread, thereby providing a degree of
174 predictability to the occurrence of fire refugia in the vicinity. Topography and edaphic factors,
175 including surface soil characteristics, are enduring features that are more stable than fuels or
176 weather, and they influence the predictability of where fire refugia occur (Camp et al. 1997,
177 Krawchuk et al. 2016, Perera and Buse 2014). Specifically, permanent topoedaphic features,
178 such as rock outcrops, ridges, or scree slopes, can function as firebreaks that protect adjacent
179 vegetated areas because they are unburnable, and they also may serve as refugia for species that
180 can inhabit these environments. At the same time, fire refugia are more likely to occur in valley
181 bottoms, local concavities, draws, or gullies (Bradstock et al. 2010, Krawchuk et al. 2016,
182 Leonard et al. 2014), potentially as a function of cold air pooling (Wilkin et al. 2016), and

1
2
3 183 through increased soil and fuel moisture (Coop and Givnish 2007, Romme and Knight 1981).
4
5 184 Slope, aspect, and elevation also can play a role, where cooler and moister sites burn less
6
7 185 frequently and support late-successional, fire-resistant individuals and populations (Camp et al.
8
9 186 1997, Wood et al. 2011). Under more extreme dry and hot weather conditions, however, these
10
11 187 facets may lose their protective characteristics and burn more severely due to high fuel
12
13
14 188 accumulation (Beaty and Taylor 2001, Krawchuk et al. 2016).
15
16

17 189 By contrast, fire refugia formation can also occur from stochastic factors. Sudden wind shifts,
18
19 190 fire-generated behavior (e.g., fire whirls and self-generating weather), and changes in weather
20
21 191 are all frequent causes of fire refugia formation, as an advancing flaming front skips over an
22
23 192 area. This is particularly characteristic of fire refugia formed in discontinuous fuels or landscapes
24
25 193 with benign terrain (Krawchuk et al. 2016), where fire spread depends strongly on wind, and thus
26
27 194 fire refugia formation is similarly related to wind patterns. Importantly, human actions related to
28
29 195 fuels management and fire suppression can be more challenging to predict consistently. People
30
31 196 build fire breaks and containment lines around resources at risk, intentionally making those
32
33 197 resource areas into fire refugia. At the same time, humans unintentionally create refugia through
34
35 198 activities that alter fuel continuity (e.g., off highway vehicles (OHV) trails, resource extraction
36
37 199 activities such as logging or drilling, or clearing of ground fuels through firewood gathering),
38
39 200 facilitating changes in fire behavior. Part of the current challenge to identifying predictable
40
41 201 versus stochastic refugia formation is that much of the science currently depends on imperfect
42
43 202 *post-hoc* reconstruction of fire events, with the most predictable refugia being those that have
44
45 203 persisted through multiple wildfires.
46
47
48
49
50

51 204
52
53

54 205
55
56
57
58
59
60

206 4. Ephemeral versus persistent fire refugia

207 Over multiple fire-return intervals fire refugia that last through only a single fire event are
208 defined here as ephemeral, while refugia that survive through multiple fires are defined as
209 persistent refugia. Generally, persistent refugia are formed through relatively predictable
210 processes and ephemeral refugia are formed through stochastic factors, but this is not always the
211 case. For example, some ephemeral refugia may be predictable if they remain unburned under
212 more benign or moderate conditions (e.g., a meadow above a certain threshold of soil moisture)
213 but burn other times (e.g., the same meadow in an extreme drought year); such refugia would be
214 predictable because the conditions prescribing their formation are known, but it is not necessarily
215 persistent through multiple fires (Berry et al. 2015a, Krawchuk et al. 2016, Perera and Buse
216 2014). Though ephemeral refugia remain only through individual fire events, the aggregate
217 population of these refugia over landscapes and regions may be important in supporting the
218 persistence of refugia-associated species over longer timeframes and under global change.

219 By contrast, persistent fire refugia are those that remained intact through multiple fire events
220 (including reburns; Prichard et al. 2017), and this persistence suggests that they are more likely
221 to be predictably associated with stable landscape features (Clarke 2002). Fire-resistant
222 conditions also may occur through self-reinforcing fire-vegetation feedbacks that are either
223 natural (e.g., Wood et al. 2011) or human-induced through repeated intentional burning, such as
224 annual indigenous burning to protect key resources (Kimmerer and Lake 2001). Both ephemeral
225 and persistent fire refugia can provide similar ecological functions (e.g., as seed sources;
226 Weisberg et al. 2008). However, persistent refugia are more likely to provide unique structures
227 and functions associated with late-successional structure (e.g., diverse structural conditions;
228 Camp et al. 1997, Kolden et al. 2015a), older individuals (e.g., large-diameter trees; Lutz et al.

1
2
3 229 2018, Lutz et al. 2013), or as a function of their landscape position or configuration (e.g.,
4
5 230 Russell-Smith and Bowman 1992). Persistent fire refugia may also be more vulnerable to loss
6
7 231 associated with anthropogenic climate change and changing fire regimes (Kolden et al. 2017), as
8
9 232 the climatic conditions which previously sustained persistent refugia may give way to conditions
10
11 233 that support and facilitate fire spread into a previously persistent patch. This novel introduction
12
13 234 or re-introduction of fire would have considerable implications for ecosystems that have been
14
15 235 dependent on such refugia.
16
17
18
19

20 236 **The ecological functions of fire refugia**

21
22 237 The ecological functions of fire refugia depend on the reproductive age, mobility, and fire-
23
24 238 sensitivity of the biota within them, the contrast between refugia and the surrounding burned
25
26 239 matrix, and the post-fire successional trajectories of nearby burned areas. The differential
27
28 240 ecological functions of fire refugia also change over time since fire (Perera and Buse 2014,
29
30 241 Robinson et al. 2013). For instance, refugia can shelter and protect fauna during an active
31
32 242 wildfire, function as remnant habitat immediately post-fire, or support population re-
33
34 243 establishment in the years to decades following fire (Fig. 2). In this way, refugia variably
35
36 244 function as islands in a biogeographic context or as patches in a landscape matrix.
37
38
39
40

41 245 **During the fire:** Areas within the fire perimeter that provide shelter or protection from
42
43 246 fire effects are key to maintaining populations and seed sources. Biota with limited or no
44
45 247 mobility and limited resistance to fire effects (e.g., butterflies, snails, annual plants, and fire-
46
47 248 intolerant woody plants) will be locally extirpated from the ecosystem without shelter from
48
49 249 combustion and radiant heat (Hylander 2011, Hylander and Johnson 2010). Refugia generally
50
51 250 comprise these unburned areas or slightly burned areas where fire energy is not a lethal dose
52
53 251 (Gongalsky et al. 2012, Hylander and Johnson 2010, Smith et al. 2017). More mobile taxa, such
54
55
56
57
58
59
60

1
2
3 252 as ungulates and birds, may use refugia to evade flames (Banks et al. 2011, Henriques et al.
4
5 253 2000, Lindenmayer et al. 2009), but they could be more vulnerable to the immediate and longer-
6
7 254 term post-fire effects on the landscape (Banks et al. 2012).

8
9
10 255 **Immediate post-fire:** Remnant vegetation following fire provides functional habitat and
11
12 256 other critical ecological functions days to months after fire. Refugia can supply food resources
13
14 257 (Henriques et al. 2000, Schwilk and Keeley 1998) that are otherwise consumed by fire in the
15
16 258 surrounding landscape, provide cover or protection from predators, or reduce influences from
17
18 259 exposure to abiotic stressors (e.g., wind and solar radiation). Competition within refugia may
19
20 260 increase from pre-fire to post-fire, due to decreases in available resources in the surrounding
21
22 261 burned landscape (Banks et al. 2012). In addition, these refugia can function as buffers against
23
24 262 erosion and landslides that can occur following fires (Shakesby and Doerr 2006), mediating
25
26 263 detrimental habitat loss.

27
28
29
30 264 **Recovery period:** Depending upon the severity of the surrounding burned area, refugia can
31
32 265 function as biogeographic islands during the early recovery period. They increase habitat
33
34 266 variability on the landscape, providing patches with later successional species interspersed within
35
36 267 an early successional landscape (e.g., Swanson et al. 2010), thereby increasing beta diversity
37
38 268 within a given fire perimeter. Fire refugia also can function as long-term, post-fire habitat from
39
40 269 which species can expand to neighboring areas, effectively functioning as a seed source (e.g.,
41
42 270 diffusion; Fig. 2; Schwilk and Keeley 2006, Stevens-Rumann et al. 2017). Environmental
43
44 271 conditions (e.g., climate) and the recovery trajectory of the surrounding vegetation determines
45
46 272 whether refugia merge with recovering vegetation and ultimately maintain pre-fire ecosystem
47
48 273 function (convergence) or the surrounding vegetation recovers differently from fire refugia,
49
50 274 resulting in a change of ecosystem function (e.g., divergence; Fig. 2). Relic refugia may persist
51
52
53
54
55
56
57
58
59
60

1
2
3 275 in the post-fire landscape, but if the structure and/or composition of surrounding vegetation
4
5 276 transitions to a new state, refugia may no longer support pre-fire ecosystem function;
6
7
8 277 Lindenmayer *et al.* (2011) described these as ‘landscape traps’. For example, anthropogenic
9
10 278 climate change may be facilitating type conversion of forest to shrublands in some regions by
11
12 279 inhibiting seedling regeneration (Stevens-Rumann *et al.* 2017), and relic forest refugia unable to
13
14 280 regenerate the forest around them may be vulnerable to further disturbances, such as cases where
15
16
17 281 a new surrounding vegetation matrix has a higher vegetative fuel load or shorter fire return
18
19 282 interval than the prior matrix (Fig. 2; Kolden *et al.* 2017), potentially leading to total loss of
20
21 283 forest habitat for that site.
22
23

24 284 **Fire refugia and global change**

25
26
27 285 Climate change has increased both fire potential and realized fire activity in many parts of
28
29 286 the world (Jolly *et al.* 2015, Abatzoglou and Williams 2016). The greatest recent increases have
30
31 287 been observed in boreal forests and tundra (Andela *et al.* 2017), consistent with observations of
32
33 288 the most rapid rates of climate change in high latitudes (IPCC 2013). In the western USA,
34
35 289 increased fire extent in recent decades (Westerling 2016) has been attributed to myriad factors,
36
37 290 including past fire suppression, land use and land cover changes, and increased human ignitions
38
39 291 (Balch *et al.* 2017), and anthropogenic climate change (Abatzoglou and Williams 2016). Climate
40
41 292 change is projected to continue to increase the potential for large, destructive fires across the
42
43 293 USA (Barbero *et al.* 2015) and globally (Bowman *et al.* 2017), albeit with heterogeneous impacts
44
45 294 to realized fire activity across the broader region (Kitzberger *et al.* 2017).
46
47
48
49

50 295 This considerable increase in fire has prompted questions of whether fires are also increasing
51
52 296 in severity and completeness of combustion, which should hypothetically reduce the occurrence
53
54 297 and extent of fire refugia. To date, there is mixed evidence that fires are burning more severely
55
56
57
58
59
60

1
2
3 298 over the contemporary record, outside of a few isolated subregions (e.g., Abatzoglou et al. 2017,
4
5 299 Picotte et al. 2016), and climatic conditions do not appear to be a strong driver of burn severity
6
7 300 (Abatzoglou et al. 2017, Birch et al. 2015). Some studies focusing on high-severity fire have
8
9 301 found increases in high-severity patch interior (Cansler and McKenzie 2014, Stevens et al.
10
11 302 2017), implying that small scale refugia—such as individual trees that serve as a seed source—
12
13 303 may be becoming rarer in some landscapes, but higher-resolution data are needed to confirm the
14
15 304 loss of these small-scale refugia. Studies focused solely on fire refugia have found no trends
16
17 305 towards reduced or altered patterns of refugia, suggesting that fires are burning neither more
18
19 306 completely nor more severely (Kolden et al. 2015a, Kolden et al. 2012, Meddens et al. 2018).
20
21 307 Nor are there clear or strong relationships between climate and patterns and proportions of fire
22
23 308 refugia across regions (Kolden et al. 2015a, Kolden et al. 2012, Meddens et al. 2018). Instead,
24
25 309 local-level topography seems to be a strong driver of refugia patterns, though importantly, the
26
27 310 capacity for terrain features to support refugia appears to diminish under more extreme daily fire
28
29 311 weather conditions (Krawchuk et al. 2016, Roman-Cuesta et al. 2009).
30
31
32
33
34

35 312 The climate-fire refugia studies described in the preceding paragraph defined fire refugia
36
37 313 based on landscape-process rather than the species-specific definition, so it is unknown whether
38
39 314 these trends are applicable to refugia for specific species of interest. Species-specific or
40
41 315 biodiversity-focused approaches for fire refugia may show global change trends that are not
42
43 316 evident when a landscape-process approach is used. For example, in the boreal forest of North
44
45 317 America, climate change and increased fire activity are already thought to be facilitating the loss
46
47 318 of continuous permafrost that is required for regeneration of black spruce (*Picea mariana*)
48
49 319 forests. This forest is transitioning to white spruce- and deciduous-dominated conditions, leaving
50
51 320 fire refugia vulnerable to extirpation by subsequent fire (Johnstone et al. 2016). Similarly, the
52
53
54
55
56
57
58
59
60

1
2
3 321 invasive spread of exotic annual grasses into the arid and semi-arid regions of North America
4
5 322 and Australia has induced more frequent fire, facilitating a type conversion to annual grassland.
6
7
8 323 Shrub-steppe fire refugia that serve as critical habitat for species of concern are vulnerable to
9
10 324 loss in subsequent fire, completing the type conversion by removing the regeneration seed source
11
12 325 (D'Antonio and Vitousek 1992, Rossiter *et al.* 2003).

14 326 Although changing fire regimes may influence the distribution and quantity of fire refugia,
15
16 327 fire is a naturally occurring, dynamic agent of ecosystem change in most seasonally dry
17
18 328 ecoregions. As anthropogenic changes continue to alter ecosystems, there is renewed focus on
19
20 329 refugia as key components of ecosystem resilience that will buffer some of the more immediate
21
22 330 negative impacts of climate change (Keppel and Wardell-Johnson 2012, Taylor *et al.* 2014). For
23
24 331 example, climate and land use changes increase the vulnerability of ecosystem services (Smith *et*
25
26 332 *al.* 2014), while fire refugia can mitigate the negative effects of altered disturbance regimes by
27
28 333 providing places where species that are not adapted to new disturbance regimes can persist,
29
30 334 migrate through, or adapt in place (Dobrowski 2011). In addition, plant seedling establishment
31
32 335 and persistence is related to the availability of seed sources but also to climatic conditions.
33
34 336 Juveniles tend to occupy a cooler and wetter niche (Dobrowski *et al.* 2015), so refugia such as
35
36 337 old-growth forest that foster locally moderated microclimate conditions through providing shade
37
38 338 (Frey *et al.* 2016, Lutz *et al.* 2018) may improve establishment success on adjacent sites,
39
40 339 particularly as increased summer drought may negatively impact ecosystem recovery (Harvey *et*
41
42 340 *al.* 2016, Stevens-Rumann *et al.* 2017).

49 341 Given projections of warmer and sometimes drier conditions in the future, co-location of fire
50
51 342 refugia and climate refugia will become more important for effective functioning of fire refugia
52
53 343 (Wilkin *et al.* 2016). When these refugia are not co-located, ecosystem recovery potential might
54
55
56
57
58
59
60

1
2
3 344 be severely hampered as recovering species are pushed out of their historic climatic envelope
4
5 345 (Fig 3.). Therefore, the spatial arrangement of fire refugia may play a key role in how landscape
6
7 346 heterogeneity buffers ecosystems from anthropogenic climate change. This buffering role is
8
9 347 especially important where co-located refugia support or facilitate recovery of the pre-
10
11 348 disturbance ecosystem function, whereas fire refugia that do not overlap with climate refugia are
12
13 349 more vulnerable to being compromised (Fig. 3). For example, as drought refugia are more
14
15 350 resistant to the extremes of interannual climatic variability, it is hypothesized that such locations
16
17 351 will continue to be buffered as the climate changes (McLaughlin et al. 2017), thereby harboring
18
19 352 remnant populations of sensitive species prioritized by conservation adaptation and mitigation
20
21 353 solutions (Morelli et al. 2016). However, this hypothesis depends on climate feedbacks not
22
23 354 reducing the resilience of refugia through increased ecological disturbances such as wildfire,
24
25 355 bark beetles, and drought.
26
27
28
29
30

31 356 **Research needs and management implications**

32
33
34 357 There is a critical need to prioritize fire refugia for conservation and management under
35
36 358 global change. The fire refugia taxonomic dichotomies presented here provide a framework to
37
38 359 consider conservation values and potential trends in fire refugia characteristics. Understanding
39
40 360 the distribution, abundance, composition, and function of fire refugia may help in prioritizing
41
42 361 land management activities based on concepts of resistance and resilience to fire, and
43
44 362 vulnerability to further disturbances. This prioritization likely will require a comprehensive
45
46 363 understanding of both spatial and temporal predictors of refugia, integrated with conservation
47
48 364 needs and policy limitations.
49
50

51
52 365 Because the patterns of fire refugia can be impacted by human activity, and management of
53
54 366 fire refugia has considerable implications for conservation and policy, there is a need for
55
56
57
58
59
60

1
2
3 367 research integrating different spatial and temporal methodologies to improve understanding of
4
5 368 the ecological function of fire refugia (Fig. 4, Table 1). Integration of field and remote sensing-
6
7 369 based data into both statistical and simulation modeling frameworks has been proposed to
8
9 370 facilitate dynamic species distribution modeling under global change (Franklin *et al.* 2016), and
10
11 371 such integration also holds great potential to enhance the understanding of fire refugia by scaling
12
13 372 across space and time (e.g., O'Connor *et al.* 2016). For example, consider a study identifying the
14
15 373 minimum areal extent and canopy cover for refugia required by a specific species as habitat in
16
17 374 the field. This estimate could then be extended geospatially by predicting the number of refugia
18
19 375 that meet the criteria from remote sensing and modeled into the future from downscaled global
20
21 376 climate model outputs and landscape-scale ecosystem simulations. Linking species-specific and
22
23 377 landscape-process approaches also could help to identify criteria for land managers wishing to
24
25 378 conserve species and habitats in fire-prone landscapes. The challenge is that such approaches
26
27 379 require large calibration areas to link across scales (Lutz 2015).
28
29
30
31
32

33 380 Because fire activity is projected to increase under future climate scenarios, fire refugia likely
34
35 381 will be important to preserving ecosystem resiliency for a variety of taxa (Tables S1 and S2).
36
37 382 Therefore, future management actions should focus on identifying, maintaining, or promoting
38
39 383 fire refugia within landscapes holistically. For example, the actual locations of ephemeral fire
40
41 384 refugia may be less important than their aggregate area and their spatial configuration. On the
42
43 385 other hand, understanding the location and environmental determinants of predictable, persistent,
44
45 386 and semi-persistent fire refugia may be vital for increasing the resilience of both natural and
46
47 387 human-occupied landscapes (Smith *et al.* 2016).
48
49
50

51 388 Management actions specifically designed to support the formation and conservation of fire
52
53 389 refugia generally do not yet exist or have not been tested for efficacy. However, one
54
55
56
57
58
59
60

1
2
3 390 management activity that would have clear positive outcomes for conserving fire refugia could
4
5 391 be reducing the use of backfires and burnouts (or ‘blackout burning’) as wildfire suppression
6
7 392 tactics where feasible. During large fire events, firefighters routinely use firing operations to
8
9 393 consume available fuel ahead of an advancing fire front; as the flaming front passes or reaches
10
11 394 containment lines, they subsequently burn out any remnant green vegetation (i.e., fire refugia) to
12
13 395 reduce potential for flare-ups and ember-ignited spot fires across the containment line. While this
14
15 396 operation tactic is highly effective for protecting critical infrastructure and resources, it may not
16
17 397 be necessary to achieve containment on fires that are remote or being managed to meet natural
18
19 398 resource objectives. One strategy for addressing the potential loss of fire refugia from this
20
21 399 practice is to embed fire refugia in national and global conservation plans through entities such
22
23 400 as The Nature Conservancy and Conservation International, which work with regional and local
24
25 401 partners to identify best management practices and policies to support ecological conservation.

26
27 402 Targeted suppression efforts can be utilized strategically to protect sensitive refugia. For
28
29 403 example, giant sequoia groves that historically burned at low severity prior to modern fire
30
31 404 suppression have specifically been protected through preventative prescribed fire, silvicultural
32
33 405 treatment, and subsequent enhanced suppression efforts in several recent fires in Yosemite and
34
35 406 Sequoia-Kings Canyon National Parks in California, USA. To date, fire refugia are generally not
36
37 407 considered ‘at risk’, or areas worth protecting during fire suppression activities. Identifying
38
39 408 ecologically valuable fire refugia or locations on the landscape where significant proportions of
40
41 409 fire refugia are desired in the post-fire mosaic would allow fire managers to integrate the
42
43 410 conservation or formation of fire refugia into their pre-planning (e.g., Dunn et al. 2017), strategy
44
45 411 and tactics.

412 **Conclusions**

413 Fire refugia are critical for the maintenance of biodiversity and ecosystem resilience under
414 global change (Keppel and Wardell-Johnson 2012) but may also be at risk due to feedbacks of a
415 changing climate, land management, and fire management practices. Projected increases in fire
416 season duration and fuel aridity in response to anthropogenic climate change alongside invasion
417 of exotic annual grasses are expected to increase future fire activity across both moist and arid
418 ecosystems, which, in turn, will increase the importance of fire refugia. The ecological functions
419 of refugia – locations where biodiversity can retreat to during and immediately after fire, and
420 persist in and expand from following fire – will continue to be important for overall ecosystem
421 resilience. The four dichotomies in our fire refugia taxonomy clarify the full spectrum of fire
422 refugia characteristics while facilitating their identification and classification. This holistic
423 approach to thinking about fire refugia, which includes both landscape-process and species-
424 specific perspectives, can help contextualize future research that investigates the formation,
425 functioning, or conservation of fire refugia, and can also be incorporated by land managers into
426 fire management strategies from local to global scales.

427 **Acknowledgements**

428 This work was partially supported by the Joint Fire Science Program (JFSP, Cooperative
429 Agreement L16AC00202), the National Science Foundation under grant no. DMS-1520873, the
430 College of Natural Resources, NASA Idaho Space Grant Consortium, and the Department of the
431 Interior Northwest Climate Science Center (NW CSC) through a Cooperative Agreement
432 G14AP00177 from the United States Geological Survey (USGS). Its contents are solely the
433 responsibility of the authors and do not necessarily represent the views of NSF, NW CSC, or
434 USGS. The views and conclusions contained in this document are those of the authors and

1
2
3 435 should not be interpreted as representing the opinions or policies of the U.S. Government.
4
5 436 Mention of trade names or commercial products does not constitute their endorsement by the
6
7
8 437 U.S. Government. This manuscript is submitted for publication with the understanding that the
9
10 438 United States Government is authorized to reproduce and distribute reprints for Governmental
11
12 439 purposes. Tyler Bleeker and Jeffrey Hicke provided helpful comments on early drafts of this
13
14
15 440 manuscript. We thank three anonymous reviewers for their helpful comments.
16
17

18 441 **References**

- 19
20 442 Abatzoglou JT, Kolden CA, Williams AP, Lutz JA, Smith AM. 2017. Climatic influences on
21 443 interannual variability in regional burn severity across western US forests. *International*
22 444 *Journal of Wildland Fire* 26:269-275.
23 445 Abatzoglou JT, Williams AP. 2016. Impact of anthropogenic climate change on wildfire across
24 446 western US forests. *Proceedings of the National Academy of Sciences* 113:11770-11775.
25 447 Agee JK. 1993. *Fire ecology of Pacific Northwest forests*. Island Press.
26 448 Allen CD, et al. 2010. A global overview of drought and heat-induced tree mortality reveals
27 449 emerging climate change risks for forests. *Forest Ecology and Management* 259:660-684.
28 450 Andela N, Morton D, Giglio L, Chen Y, van der Werf G, Kasibhatla P, DeFries R, Collatz G,
29 451 Hantson S, Kloster S. 2017. A human-driven decline in global burned area. *Science*
30 452 356:1356-1362.
31 453 Balch JK, Bradley BA, Abatzoglou JT, Nagy RC, Fusco EJ, Mahood AL. 2017. Human-started
32 454 wildfires expand the fire niche across the United States. *Proceedings of the National*
33 455 *Academy of Sciences* 114:2946-2951.
34 456 Banks SC, Blyton MDJ, Blair D, McBurney L, Lindenmayer DB. 2012. Adaptive responses and
35 457 disruptive effects: how major wildfire influences kinship-based social interactions in a
36 458 forest marsupial. *Molecular Ecology* 21:673-684.
37 459 Banks SC, Dujardin M, McBurney L, Blair D, Barker M, Lindenmayer DB. 2011. Starting points
38 460 for small mammal population recovery after wildfire: recolonisation or residual
39 461 populations? *OIKOS* 120:26-37.
40 462 Barbero R, Abatzoglou JT, Larkin NK, Kolden CA, Stocks B. 2015. Climate change presents
41 463 increased potential for very large fires in the contiguous United States. *International*
42 464 *Journal of Wildland Fire* 24:892-899.
43 465 Beaty RM, Taylor AH. 2001. Spatial and temporal variation of fire regimes in a mixed conifer
44 466 forest landscape, Southern Cascades, California, USA. *Journal of Biogeography* 28:955-
45 467 966.
46 468 Berry LE, Driscoll DA, Stein JA, Blanchard W, Banks SC, Bradstock RA, Lindenmayer DB.
47 469 2015a. Identifying the location of fire refuges in wet forest ecosystems. *Ecological*
48 470 *Applications* 25:2337-2348.
49 471 Berry LE, Lindenmayer DB, Driscoll DA. 2015b. Large unburnt areas, not small unburnt
50 472 patches, are needed to conserve avian diversity in fire - prone landscapes. *Journal of*
51 473 *Applied Ecology* 52:486-495.
52
53
54
55
56
57
58
59
60

- 1
2
3 474 Birch DS, Morgan P, Kolden CA, Abatzoglou JT, Dillon GK, Hudak AT, Smith A. 2015.
4 475 Vegetation, topography and daily weather influenced burn severity in central Idaho and
5 476 western Montana forests. *Ecosphere* 6:1-23.
- 6 477 Bowman DM, Williamson GJ, Abatzoglou JT, Kolden CA, Cochrane MA, Smith AM. 2017.
7 478 Human exposure and sensitivity to globally extreme wildfire events. *Nature ecology &*
8 479 *evolution* 1:0058.
- 9 480 Bradstock RA, Hammill KA, Collins L, Price O. 2010. Effects of weather, fuel and terrain on
10 481 fire severity in topographically diverse landscapes of south-eastern Australia. *Landscape*
11 482 *Ecology* 25:607-619.
- 12 483 Brennan KEC, Moir ML, Wittkuhn RS. 2011. Fire refugia: The mechanism governing animal
13 484 survivorship within a highly flammable plant. *Austral Ecology* 36:131-141.
- 14 485 Brubaker LB, Anderson PM, Edwards ME, Lozhkin AV. 2005. Beringia as a glacial refugium
15 486 for boreal trees and shrubs: new perspectives from mapped pollen data. *Journal of*
16 487 *Biogeography* 32:833-848.
- 17 488 Camp A, Oliver C, Hessburg P, Everett R. 1997. Predicting late-successional fire refugia pre-
18 489 dating European settlement in the Wenatchee Mountains. *Forest Ecology and*
19 490 *Management* 95:63-77.
- 20 491 Cansler CA, McKenzie D. 2014. Climate, fire size, and biophysical setting control fire severity
21 492 and spatial pattern in the northern Cascade Range, USA. *Ecological Applications*
22 493 24:1037-1056.
- 23 494 Clarke PJ. 2002. Habitat islands in fire-prone vegetation: do landscape features influence
24 495 community composition? *Journal of Biogeography* 29:677-684.
- 25 496 Coop JD, Givnish TJ. 2007. Gradient analysis of reversed treelines and grasslands of the Valles
26 497 Caldera, New Mexico. *Journal of Vegetation Science* 18:43-54.
- 27 498 D'Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses, the grass/fire cycle,
28 499 and global change. *Annual Review of Ecology and Systematics* 23:63-87.
- 29 500 Dobrowski SZ. 2011. A climatic basis for microrefugia: the influence of terrain on climate.
30 501 *Global Change Biology* 17:1022-1035.
- 31 502 Dobrowski SZ, Swanson AK, Abatzoglou JT, Holden ZA, Safford HD, Schwartz MK, Gavin
32 503 DG. 2015. Forest structure and species traits mediate projected recruitment declines in
33 504 western US tree species. *Global Ecology and Biogeography* 24:917-927.
- 34 505 Dunn CJ, Calkin DE, Thompson MP. 2017. Towards enhanced risk management: planning,
35 506 decision making and monitoring of US wildfire response. *International Journal of*
36 507 *Wildland Fire* 26:551-556.
- 37 508 Franklin J, Serra-Diaz JM, Syphard AD, Regan HM. 2016. Global change and terrestrial plant
38 509 community dynamics. *Proceedings of the National Academy of Sciences* 113:3725-3734.
- 39 510 Franklin JF, Lindenmayer DB, MacMahon JA, McKee A, Magnuson J, Perry DA, Waide R,
40 511 Foster D. 2000. Threads of continuity: ecosystem disturbance, recovery, and the theory of
41 512 biological legacies. *Conservation Biology in Practice* 1:8-17.
- 42 513 Frey SJ, Hadley AS, Johnson SL, Schulze M, Jones JA, Betts MG. 2016. Spatial models reveal
43 514 the microclimatic buffering capacity of old-growth forests. *Science advances*
44 515 2:e1501392.
- 45 516 Gill AM. 1975. Fire and the Australian flora: a review. *Australian Forestry* 38:4-25.
- 46 517 Gongalsky KB, Malmstrom A, Zaitsev AS, Shakhov SV, Bengtsson J, Persson T. 2012. Do
47 518 burned areas recover from inside? An experiment with soil fauna in a heterogeneous
48 519 landscape. *Applied Soil Ecology* 59:73-86.

- 1
2
3 520 Haffer J. 1969. Speciation in Amazonian forest birds. *Science* 165:131-137.
- 4 521 Haire SL, McGarigal K. 2010. Effects of landscape patterns of fire severity on regenerating
5 522 ponderosa pine forests (*Pinus ponderosa*) in New Mexico and Arizona, USA. *Landscape*
6 523 *Ecology* 25:1055-1069.
- 7 524 Harvey BJ, Donato DC, Turner MG. 2016. High and dry: post-fire tree seedling establishment in
8 525 subalpine forests decreases with post-fire drought and large stand-replacing burn patches.
9 526 *Global Ecology and Biogeography* 25:655-669.
- 10 527 Henriques RPB, Bizerril MXA, Palma ART. 2000. Changes in small mammal populations after
11 528 fire in a patch of unburned cerrado in Central Brazil. *Mammalia* 64:173-185.
- 12 529 Hylander K. 2011. The response of land snail assemblages below aspens to forest fire and clear-
13 530 cutting in Fennoscandian boreal forests. *Forest Ecology and Management* 261:1811-
14 531 1819.
- 15 532 Hylander K, Johnson S. 2010. In situ survival of forest bryophytes in small-scale refugia after an
16 533 intense forest fire. *Journal of Vegetation Science* 21:1099-1109.
- 17 534 IPCC. 2013. *Climate Change 2013: The physical science basis*. Working Group 1 (WG1)
18 535 Contribution to the Intergovernmental Panel on Climate Change (IPCC) Stocker, T.F., D.
19 536 Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and
20 537 P.M. Midgley, (eds.). 5th Assessment Report (AR5). Cambridge, United Kingdom and
21 538 New York, NY 1535 pp. Cambridge, UK and New York, New York, USA.
- 22 539 Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC,
23 540 Meentemeyer RK, Metz MR, Perry GL. 2016. Changing disturbance regimes, ecological
24 541 memory, and forest resilience. *Frontiers in Ecology and the Environment* 14:369-378.
- 25 542 Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DM.
26 543 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature*
27 544 *communications* 6.
- 28 545 Kane VR, Lutz JA, Cansler CA, Povak NA, Churchill DJ, Smith DF, Kane JT, North MP. 2015.
29 546 Water balance and topography predict fire and forest structure patterns. *Forest Ecology*
30 547 *and Management* 338:1-13.
- 31 548 Keppel G, Mokany K, Wardell-Johnson GW, Phillips BL, Welbergen JA, Reside AE. 2015. The
32 549 capacity of refugia for conservation planning under climate change. *Frontiers in Ecology*
33 550 *and the Environment* 13:106-112.
- 34 551 Keppel G, Van Niel KP, Wardell-Johnson GW, Yates CJ, Byrne M, Mucina L, Schut AG,
35 552 Hopper SD, Franklin SE. 2012. Refugia: identifying and understanding safe havens for
36 553 biodiversity under climate change. *Global Ecology and Biogeography* 21:393-404.
- 37 554 Keppel G, Wardell-Johnson GW. 2012. Refugia: keys to climate change management. *Global*
38 555 *Change Biology* 18:2389-2391.
- 39 556 Kimmerer RW, Lake FK. 2001. The role of indigenous burning in land management. *Journal of*
40 557 *Forestry* 99:36-41.
- 41 558 Kitzberger T, Falk DA, Westerling AL, Swetnam TW. 2017. Direct and indirect climate controls
42 559 predict heterogeneous early-mid 21st century wildfire burned area across western and
43 560 boreal North America. *Plos One* 12:e0188486.
- 44 561 Kolden CA, Abatzoglou JT, Lutz JA, Cansler CA, Kane JT, van Wagendonk JW, Key CH.
45 562 2015a. Climate contributors to forest mosaics: ecological persistence following wildfire.
46 563 *Northwest Science* 89:219-238.
- 47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 564 Kolden CA, Abatzoglou JT, Smith AMS. 2015b. Limitations and utilisation of Monitoring
4 565 Trends in Burn Severity products for assessing wildfire severity in the USA. *International*
5 566 *Journal of Wildland Fire* 24:1023-1028.
- 6 567 Kolden CA, Bleeker TM, Smith A, Poulos HM, Camp AE. 2017. Fire effects on historical
7 568 wildfire refugia in contemporary wildfires. *Forests* 8:400.
- 8 569 Kolden CA, Lutz JA, Key CH, Kane JT, van Wagendonk JW. 2012. Mapped versus actual
9 570 burned area within wildfire perimeters: characterizing the unburned. *Forest Ecology and*
10 571 *Management* 286:38-47.
- 11 572 Krawchuk MA, Haire SL, Coop J, Parisien MA, Whitman E, Chong G, Miller C. 2016.
12 573 Topographic and fire weather controls of fire refugia in forested ecosystems of
13 574 northwestern North America. *Ecosphere* 7:1-18.
- 14 575 Leonard SWJ, Bennett AF, Clarke MF. 2014. Determinants of the occurrence of unburnt forest
15 576 patches: Potential biotic refuges within a large, intense wildfire in south-eastern
16 577 Australia. *Forest Ecology and Management* 314:85-93.
- 17 578 Lindenmayer DB. 2009. Large-scale landscape experiments: lessons from Tumut. Cambridge
18 579 University Press.
- 19 580 Lindenmayer DB, Hobbs RJ, Likens GE, Krebs CJ, Banks SC. 2011. Newly discovered
20 581 landscape traps produce regime shifts in wet forests. *Proceedings of the National*
21 582 *Academy of Sciences* 108:15887-15891.
- 22 583 Lindenmayer DB, et al. 2009. What factors influence rapid post-fire site re-occupancy? A case
23 584 study of the endangered Eastern Bristlebird in eastern Australia. *International Journal of*
24 585 *Wildland Fire* 18:84-95.
- 25 586 Lutz JA. 2015. The evolution of long-term data for forestry: large temperate research plots in an
26 587 era of global change. *Northwest Science* 89:255-269.
- 27 588 Lutz JA, Furniss TJ, Johnson DJ, Davies SJ, Allen D, Alonso A, Anderson-Teixeira KJ, Andrade
28 589 A, Baltzer J, Becker KM. 2018. Global importance of large-diameter trees. *Global*
29 590 *Ecology and Biogeography* 1–16, <https://doi.org/10.1111/geb.12747>
- 30 591 Lutz JA, Larson AJ, Freund JA, Swanson ME, Bible KJ. 2013. The importance of large-diameter
31 592 trees to forest structural heterogeneity. *Plos One* 8:e82784.
- 32 593 Mackey B, Lindenmayer D, Gill M, McCarthy M, J L. 2002. Wildfire, fire and future climate: a
33 594 forest ecosystem analysis. CSIRO Publishing.
- 34 595 McLaughlin BC, Ackerly DD, Klos PZ, Natali J, Dawson TE, Thompson SE. 2017. Hydrologic
35 596 refugia, plants, and climate change. *Global Change Biology* 23:2941-2961.
- 36 597 Meddens AJ, Kolden CA, Lutz JA. 2016. Detecting unburned areas within wildfire perimeters
37 598 using Landsat and ancillary data across the northwestern United States. *Remote Sensing*
38 599 *of Environment* 186:275-285.
- 39 600 Meddens AJ, Kolden CA, Lutz JA, Abatzoglou JT, Hudak AT. 2018. Spatial and temporal
40 601 patterns of unburned areas within fire perimeters in the northwestern United States from
41 602 1984 to 2014. *Ecosphere* 9:DOI: e02029.02010.01002/ecs02022.02029.
- 42 603 Meigs GW, Krawchuk MA. 2018. Composition and Structure of Forest Fire Refugia: What Are
43 604 the Ecosystem Legacies across Burned Landscapes? *Forests* 9:243.
- 44 605 Morelli TL, Daly C, Dobrowski SZ, Dulen DM, Ebersole JL, Jackson ST, Lundquist JD, Millar
45 606 CI, Maher SP, Monahan WB. 2016. Managing climate change refugia for climate
46 607 adaptation. *Plos One* 11:e0159909. doi:0159910.0151371 / journal.pone.0159909.

- 1
2
3 608 O'Connor CD, Thompson MP, Rodríguez y Silva F. 2016. Getting ahead of the wildfire
4 609 problem: quantifying and mapping management challenges and opportunities.
5 610 *Geosciences* 6:35.
- 6
7 611 Perera A, Buse L. 2014. Ecology of wildfire residuals in boreal forests. John Wiley & Sons.
- 8 612 Petit RJ, et al. 2003. Glacial refugia: Hotspots but not melting pots of genetic diversity. *Science*
9 613 300:1563-1565.
- 10 614 Picotte JJ, Peterson B, Meier G, Howard SM. 2016. 1984–2010 trends in fire burn severity and
11 615 area for the conterminous US. *International Journal of Wildland Fire* 25:413-420.
- 12 616 Prichard SJ, Stevens-Rumann CS, Hessburg PF. 2017. Tamm Review: shifting global fire
13 617 regimes: Lessons from reburns and research needs. *Forest Ecology and Management*
14 618 396:217-233.
- 15
16 619 Robinson NM, Leonard SWJ, Ritchie EG, Bassett M, Chia EK, Buckingham S, Gibb H, Bennett
17 620 AF, Clarke MF. 2013. Refuges for fauna in fire-prone landscapes: their ecological
18 621 function and importance. *Journal of Applied Ecology* 50:1321-1329.
- 19 622 Roman-Cuesta RM, Gracia M, Retana J. 2009. Factors influencing the formation of unburned
20 623 forest islands within the perimeter of a large forest fire. *Forest Ecology and Management*
21 624 258:71-80.
- 22
23 625 Romme WH, Knight DH. 1981. Fire frequency and subalpine forest succession along a
24 626 topographic gradient in Wyoming. *Ecology* 62:319-326.
- 25 627 Rossiter NA, Setterfield SA, Douglas MM, Hutley LB. 2003. Testing the grass-fire cycle: alien
26 628 grass invasion in the tropical savannas of northern Australia. *Diversity and Distributions*
27 629 9:169-176.
- 28
29 630 Russell-Smith J, Bowman D. 1992. Conservation of monsoon rainforest isolates in the Northern
30 631 Territory, Australia. *Biological Conservation* 59:51-63.
- 31 632 Schwilk DW, Keeley JE. 1998. Rodent populations after a large wildfire in California chaparral
32 633 and coastal sage scrub. *The Southwestern Naturalist*:480-483.
- 33 634 Schwilk DW, Keeley JE. 2006. The role of fire refugia in the distribution of *Pinus sabiniana*
34 635 (Pinaceae) in the southern Sierra Nevada. *Madrono* 53:364-372.
- 35 636 Sears MW, Angilletta MJ, Schuler MS, Borchert J, Dilliplane KF, Stegman M, Rusch TW,
36 637 Mitchell WA. 2016. Configuration of the thermal landscape determines thermoregulatory
37 638 performance of ectotherms. *Proceedings of the National Academy of Sciences*
38 639 113:10595–10600.
- 39
40 640 Shakesby R, Doerr S. 2006. Wildfire as a hydrological and geomorphological agent. *Earth-*
41 641 *Science Reviews* 74:269-307.
- 42 642 Smith A, Kolden CA, Tinkham WT, Talhelm AF, Marshall JD, Hudak AT, Boschetti L,
43 643 Falkowski MJ, Greenberg JA, Anderson JW. 2014. Remote sensing the vulnerability of
44 644 vegetation in natural terrestrial ecosystems. *Remote Sensing of Environment* 154:322-
45 645 337.
- 46
47 646 Smith AM, et al. 2016. The science of firescapes: achieving fire-resilient communities.
48 647 *Bioscience* 66:130-146.
- 49 648 Smith AM, Talhelm AF, Johnson DM, Sparks AM, Kolden CA, Yedinak KM, Apostol KG,
50 649 Tinkham WT, Abatzoglou JT, Lutz JA. 2017. Effects of fire radiative energy density
51 650 dose on *Pinus contorta* and *Larix occidentalis* seedling physiology and mortality.
52 651 *International Journal of Wildland Fire* 26:82-94.
- 53
54
55
56
57
58
59
60

- 1
2
3 652 Stevens JT, Collins BM, Miller JD, North MP, Stephens SL. 2017. Changing spatial patterns of
4 653 stand-replacing fire in California conifer forests. *Forest Ecology and Management*
5 654 406:28-36.
- 6 655 Stevens-Rumann CS, Kemp KB, Higuera PE, Harvey BJ, Rother MT, Donato DC, Morgan P,
7 656 Veblen TT. 2017. Evidence for declining forest resilience to wildfires under climate
8 657 change. *Ecology Letters*.
- 9 658 Swan M, Galindez-Silva C, Christie F, York A, Di Stefano J. 2016. Contrasting responses of
10 659 small mammals to fire and topographic refugia. *Austral Ecology* 41:437-445.
- 11 660 Swanson ME, Franklin JF, Beschta RL, Crisafulli CM, DellaSala DA, Hutto RL, Lindenmayer
12 661 DB, Swanson FJ. 2010. The forgotten stage of forest succession: early-successional
13 662 ecosystems on forest sites. *Frontiers in Ecology and the Environment* 9:117-125.
- 14 663 Taylor C, McCarthy MA, Lindenmayer DB. 2014. Nonlinear effects of stand age on fire
15 664 severity. *Conservation Letters* 7:355-370.
- 16 665 Turner MG. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833-
17 666 2849.
- 18 667 van Wagtenonk JW, Lutz JA. 2007. Fire regime attributes of wildland fires in Yosemite
19 668 National Park, USA. *Fire Ecology* 3:34-52.
- 20 669 Weisberg PJ, Ko D, Py C, Bauer JM. 2008. Modeling fire and landform influences on the
21 670 distribution of old-growth pinyon-juniper woodland. *Landscape Ecology* 23:931-943.
- 22 671 Westerling AL. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the
23 672 timing of spring. *Phil. Trans. R. Soc. B* 371:20150178.
- 24 673 Wilkin KM, Ackerly DD, Stephens SL. 2016. Climate change refugia, fire ecology and
25 674 management. *Forests* 7:77.
- 26 675 Wimberly MC, Kennedy RSH. 2008. Spatially explicit modeling of mixed-severity fire regimes
27 676 and landscape dynamics. *Forest Ecology and Management* 254:511-523.
- 28 677 Wood SW, Murphy BP, Bowman DM. 2011. Firescape ecology: how topography determines the
29 678 contrasting distribution of fire and rain forest in the south-west of the Tasmanian
30 679 Wilderness World Heritage Area. *Journal of Biogeography* 38:1807-1820.
- 31 680
- 32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Tables

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 ^{1, 2, 3, 4, 5, 6}	How do we facilitate refugia through ecosystem restoration tactics (e.g., prescribed fire)?
Refugia characteristics	Ranked importance of refugia characteristics by key species ^{2, 5}	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 ^{5, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17}	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) ^{5, 18, 19, 20, 21, 22, 23}	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 ^{4, 5, 24}	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 ^{25, 26}	How do we identify and protect critical fire refugia as seed sources and biodiversity hot spots?
Successional pathways	Probabilities of different successional pathways for refugia ^{5, 23, 27, 28, 29}	How do we protect the ecological integrity of fire refugia years to decades post-fire?

Literature that in some way or form contributes to or highlights the need for (a) research, (b) management and/or (c) applications, related to fire refugia: ¹Meddens et al 2016, ²Meddens et al 2018, ³Kolden et al 2012, ⁴Krawchuk et al 2016, ⁵Perera and Buse 2014, ⁶Robinson 2013, ⁷Banks et al 2012, ⁸Banks et al 2011, ⁹Berry et al 2015b, ¹⁰Brennan et al 2011, ¹¹Gongalsky et al 2012, ¹²Henriques et al 2000, ¹³Hylander 2011, ¹⁴Hylander and Johnson 2010, ¹⁵Lindenmayer et al. 2009, ¹⁶Schwilk and Keeley 1998, ¹⁷Swan et al 2017, ¹⁸Berry et al 2015a, ¹⁹Clarke 2002, ²⁰Leonard et al 2014, ²¹Roman-Cuesta et al 2009, ²²Wilkin et al 2016, ²³Schwilk and Keeley 2006, ²⁴Wimberly and Kennedy 2008, ²⁵Abatzoglou et al 2017, ²⁶Kolden et al 2015, ²⁷Camp et al 1997, ²⁸Harvey et al 2016, ²⁹Kolden et al 2017.

Figure captions

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

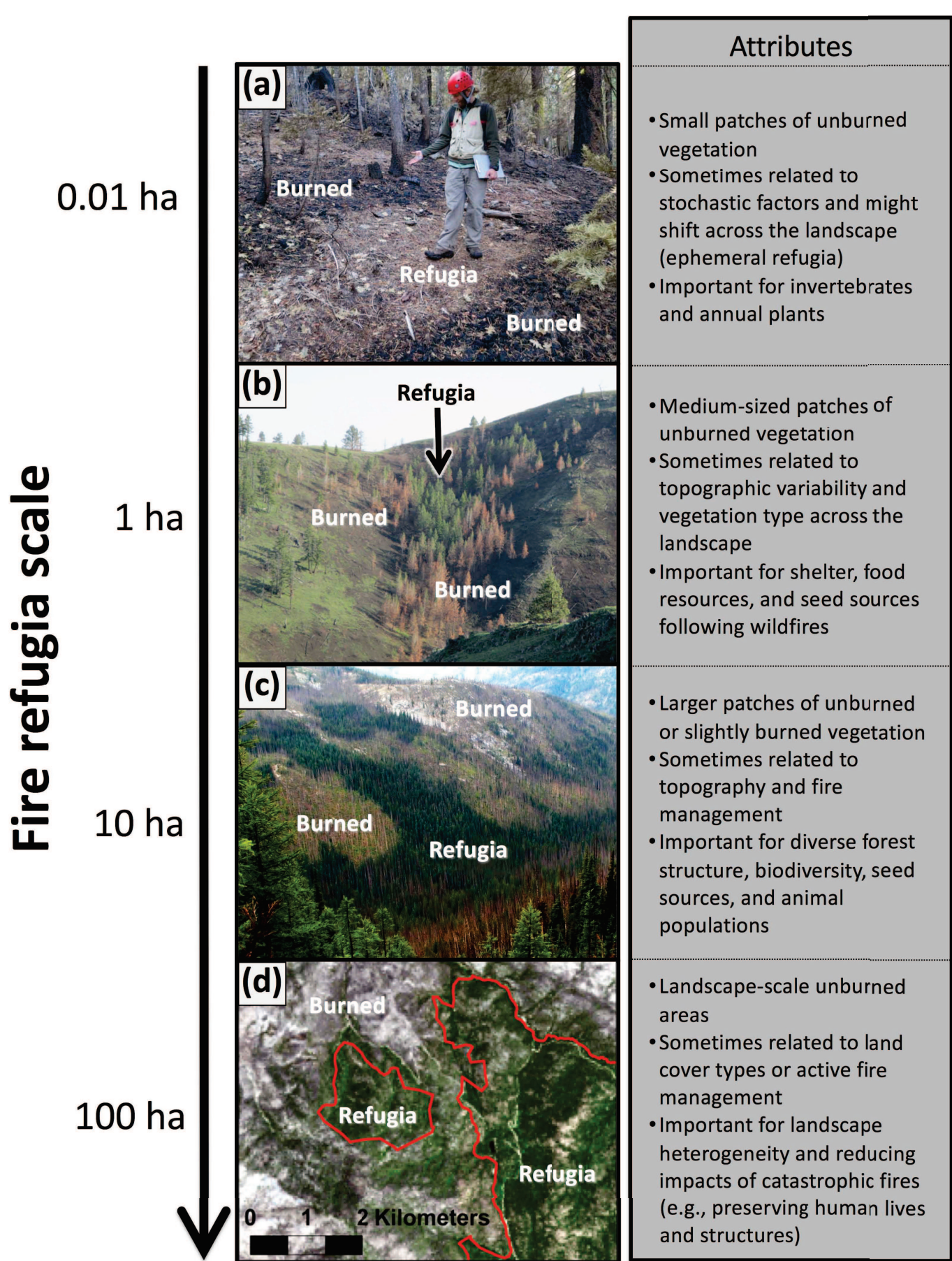
Figure 2. Successional pathways of refugia and non-refugia following fires in relation to the broader ecosystem. During and immediately after fire, refugia provide shelter or food resources, whereas over longer time periods fire refugia facilitate ecosystem recovery by providing seed sources and increasing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

Figure 3. Conceptual effect of global change on ecosystem recovery in relation to climate and fire refugia, adapted from Allen *et al.* (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, as climate refugia are more

1
2
3 buffered from these global changes. Identifying the geospatial overlap between fire refugia
4
5 and climate refugia is an important research need.
6
7
8
9

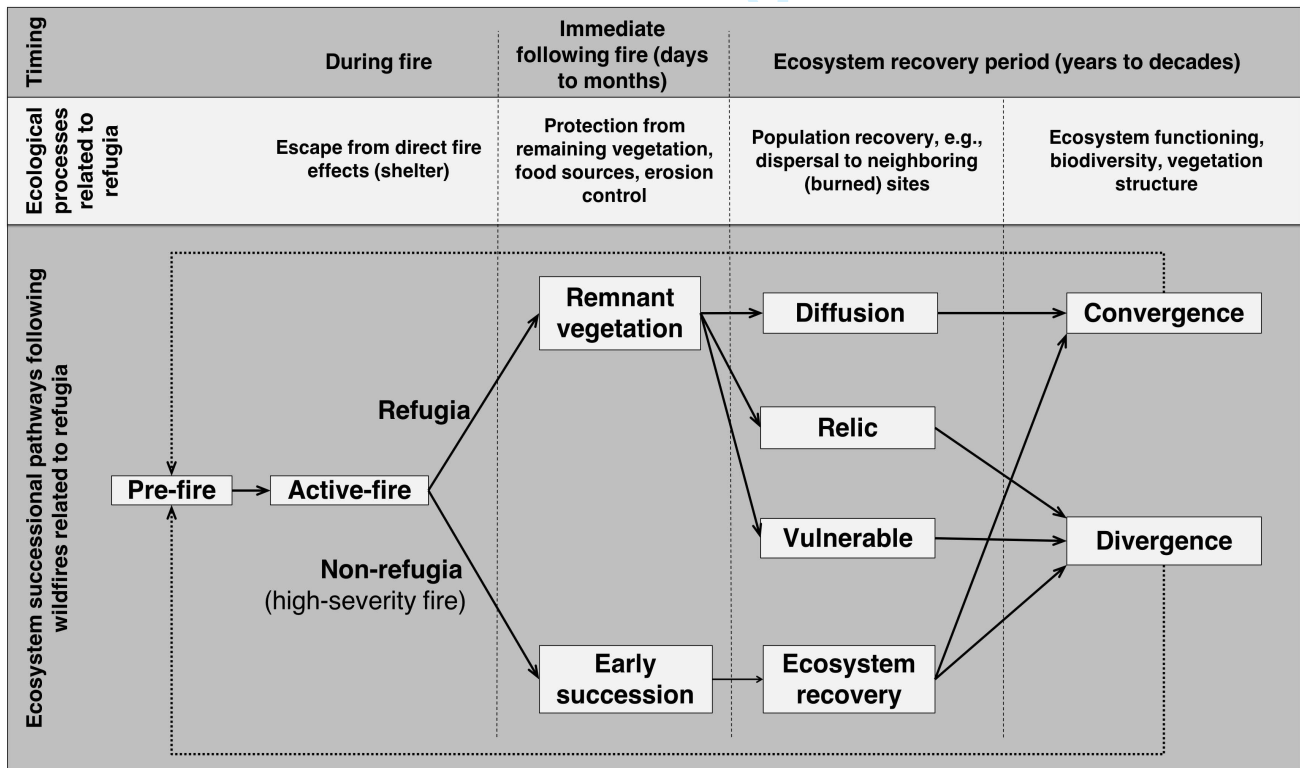
10 Figure 4. Examples of approximate timescales at which different methods or instruments can
11
12 contribute to understanding of wildland fire and the occurrence of fire refugia. Average fire
13
14 return intervals for three different ecosystems across the western United States are given with
15
16 the bars representing the time period across the time axis.
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Draft Manuscript



1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

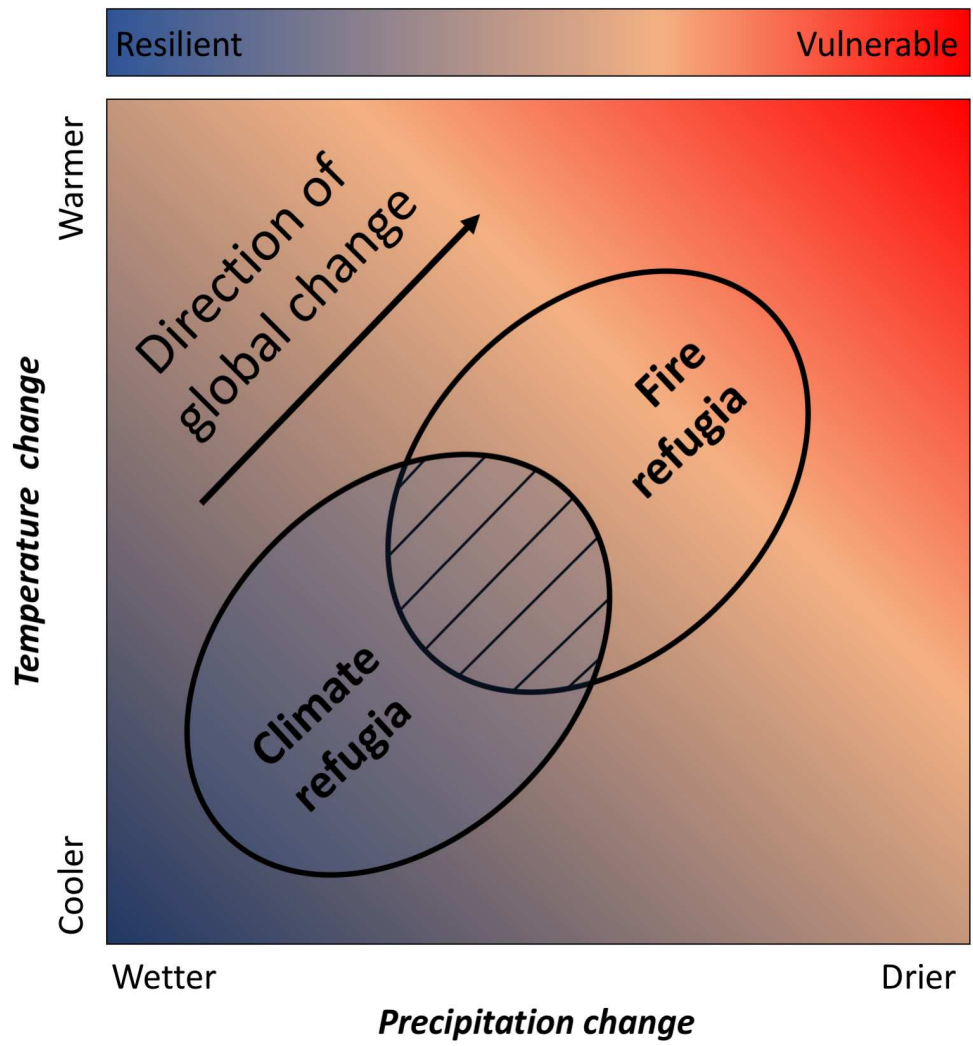
Draft Manuscript



1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

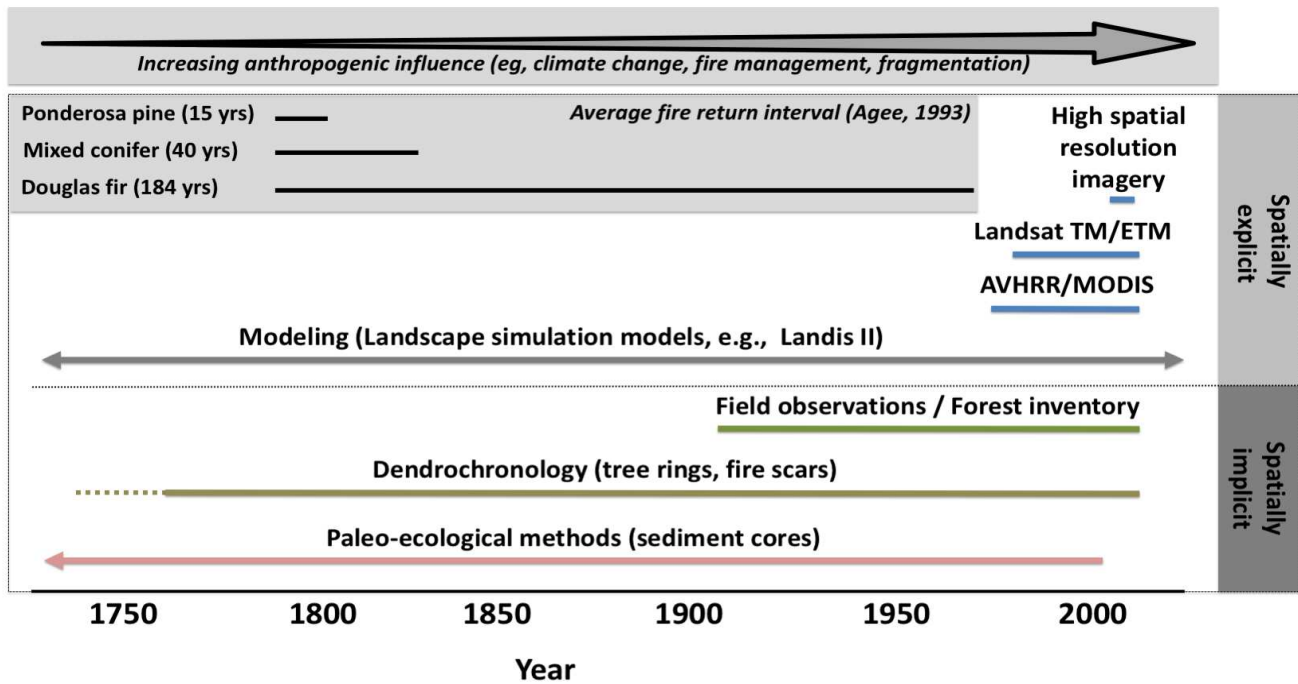


Ecosystem recovery



1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Draft Ma



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, Meg A. Krawchuk

Supplementary material

Contents:

Table S1. Summary of reviewed studies involving species-specific wildfire refugia.

Table S2. Summary of reviewed studies involving landscape-scale wildfire refugia.

WebTable 1. Summary of reviewed studies involving species-specific wildfire refugia.

Study	Objective of study	Species of interest	Location	Extent / spatial domain of study	Ecosystem type	Fire refugia definition or characteristics	Refugia age	Refugia size	Main conclusions	Severity ^a	Predictability ^b	Persistence ^c
Schwilk and Keeley 1998	Evaluate relationship between rodent populations and distance to unburned brush	Rodents (Eight different species)	Big Sycamore Canyon, Point Muga State Park, California, USA	A 110 m transect with traps every 5 m, at six sites ranging in elevation from 75 m to 210 m within the canyon	Coastal sage scrub and chaparral	Unburned vegetation outside fire perimeter (chaparral or coastal sage)	N/A	N/A	Rodent response to distance to unburned areas differed by species, and by habitat type (coastal sage scrub vs. chaparral)	U	N/A	N/A
Pfab and Witkowski 1999	Determine whether an endangered succulent survives fire in refugia or via fire tolerance	A succulent species (<i>Euphorbia clivicola</i>)	Northern Province of South Africa	An unknown number of transects 5 m apart	Savannah, grassland	Rocky patches with lower fuel amounts	N/A	N/A	Fire refugia were not associated with survivorship of the plant species studied. In contrast, plant seems to be fire tolerant and a resprouter that regenerates following low severity fire	U/L	P	P
Henriques et al. 2000	Describe the changes in small mammal populations in a patch of unburned woodland	Seven species of small mammals (6 rodents and 1 marsupial)	Southwest Brasilia, Brazil	Two sampling grids with 49 stations 10 m apart (one in the unburned areas and one in the burned area)	Semi-deciduous cerrado woodland	One unburned patch of 1 ha	Measured 6 months after the fire	1 ha	Data suggest that many species use the unburned cerrado patch as shelter during the fire and/or as a food sources after the fire	U	S	E
Swengel and Swengel 2007	Determine the spatial and temporal patterns of fire refugia in association with butterfly abundance	Butterfly species (Lepidoptera species)	Three sites in Wisconsin, USA	Crex Meadows: 12,180 ha Bauer-Brockway: 125 ha Muralt Bluff: 25 ha	Pine barren, prairie fields, oak savanna	Unburned units compared to surrounding sites with more frequent fire	>6-8 years	Ave: 7 ha (range: 3-14ha)	Areas started functioning as refugia for butterflies 6-8 years after burning	U	N/A	E
Gandhi et al. 2001	Determine whether fire residuals are important for beetles and whether patch size is correlated with beetle population diversity	Litter-dwelling beetles (Coleoptera: <i>Carabidae</i> and <i>Staphylinidae</i>)	Western Alberta, Canada	Sixteen refugial patches across two wildfires that burned 1,015 ha	Montane and boreal forest	Fire residuals were wet, late successional patches of fir and spruce stands	Average 180 years, oldest trees were 300 years	Ave: 1.5 ha (range: 0.012 – 10.8 ha)	1) Trees in residual significantly older than surrounding; 2) greater diversity in residuals compared to burned areas; 3) no relationship between residual size and species diversity	N/A	N/A	N/A
Brotons et al. 2005	Determine importance of dispersal on avian post-fire colonization	Nine open-habitat bird species	Catalonia, Northeastern Iberian Peninsula, Spain	Transects on 8 wildfires (273–5,905 ha), which were at least 10 km from each another	Mediterranean forest (pine, cork-oak, or holm-oak) and shrubland, including grasslands and rocky outcrops	N/A	N/A	N/A	Strong significant differences in post-fire species composition between burnt areas, indicating the importance of landscape heterogeneity (including unburned areas) resulting from wildfires	N/A	N/A	N/A
Schwilk and Keeley 2006	Test hypothesis whether gray pines spread from unburned areas to upland chaparral ecotones in the region	Gray pines, <i>Pinus sabiniana</i>	McNally fire, California, USA	Seven (50×500 m) transects in a 25,100-ha fire	Gray pine and chaparral	Gray pine populations persist in reduced fire severity riparian areas	N/A	Average widths of riparian valleys: 79-177 m	Maximum age of gray pines declined significantly with distance to riparian areas, suggesting the need for fire refuges for reinvasion of slopes after being eliminated by severe fires	L	P	P

Lindenmayer et al. 2009	Quantify post-fire recovery of the Eastern Bristlebird	Eastern Bristlebird (<i>Dasyornis brachypterus</i>)	Booderee National Park, southeastern Australia	Bird occurrence was recorded at 110 sites a year before and for 3 years after a fire	Different vegetation types including heathland, woodland, shrubland, forest and rainforest	Field surveys indicating unburned sites	Measured up to 3 years post-fire	N/A	Rapid bird population recovery of burned sites was most likely due to movement by resident birds to unburned parts elsewhere within their territories	U	N/A	N/A
Hylander and Johnson 2010	Do unburned areas support higher diversity and abundance of bryophytes?	Boreal forest bryophytes	Tyresta National Park, Sweden	Fourteen burned and 12 forest reference plots (50 by 50 m) within each plot 15 random 1-m ² micro-plots	Boreal forest (pine, spruce, broadleaf)	Refugia generally related to rocky or mesic conditions rather than wet conditions	Measured 7-8 years post fire	Not stated but generally on the scale of m ²	(1) Refugia were associated with rocky sites (fuel breaks) rather than wet sites (2) Refugia within the fire perimeter were more like the surrounding unburned forest than the burned forest (3) Colonization from refugia unclear	U	N/A	N/A
Banks et al. 2011	Quantify the effects of high severity forest fire on the population characteristics of mammal species	Two small mammal species (<i>Antechinus agilis</i> and <i>Rattus fuscipes</i>)	Black Saturday fires, Victoria, Australia	Fifteen trapping sites, dispersed over the fire (including unburned areas)	Tall eucalypt forest (dominated by <i>Eucalyptus regnans</i>)	Unburned sites outside fire perimeter	N/A	N/A	Survival during the fire (by utilizing unburned areas) and not recolonization (from unburned areas), was the most plausible explanation of the population dynamics following fire	U (Outside perimeter)	N/A	N/A
Hylander 2011	Investigate survival of forest floor dwelling snails within harvest units, burned areas and undisturbed controls	Forest floor dwelling land snails	Southern Stockholm county, Sweden	Six to 7 samples under aspen trees in each of five burned sites and 7 forest reference sites	Scots pine and Norway spruce dominated forests with aspen trees	Selection of nearby reference (unburned) forest	Measured 2-7 years post fire	N/A	Lower abundance of snails in the burned sites as compared to the unburned reference sites	U (Outside perimeter)	N/A	N/A
Brennan et al. 2011	Determine invertebrate survival in burned plants	Invertebrates	Western Australia	Nine plants	Eucalyptus forest/ woodland	Portions of plants that did not burn	N/A	One plant	Even burned plants can provide refugia for some taxa in portions of their canopy	U/L	P	P
Banks et al. 2012	Understand animal behavior (i.e., den sharing) differences within burned areas compared to fire refugia	Mountain brushtail possum (<i>Trichosurus cunninghami</i>)	Cambarville, Victoria, south-eastern Australia	Fifty ha of burned and unburned areas	Mountain ash dominated forest	Unburned mountain ash, containing trees over 12–200 years old that contained hollows	N/A	Approximately half of a 50 ha study site	(1) Den sharing with kin was reduced in the burned area, likely because post-fire range-shifts by individuals caused kin to no longer be in close proximity (2) In unburned areas den sharing with kin increased, likely because the local population in refugia more than doubled (due to migration out of the fire) increasing competition for dens	U	S	N/A
Watson et al. 2012	Examine the avifauna at recently burned sites within extensive semi-arid shrublands of south-eastern Australia	Avifauna	Southeastern Australia	Seventy-two sites <5 years since fire and 26 sites 10 years since fire	Semi-arid shrublands	Unburned area outside of fire perimeter	Greater than 27 years	>5 ha	Species richness was higher at places close to the unburned areas <5 years after the fire, however these patterns were not evident 10 years following the fire	U (Outside perimeter)	N/A	N/A

Borchert and Borchert 2013	Compare rodent abundance and species composition in burned and unburned chaparral along fire perimeter	Four species of small mammals	Southern California, USA	Two 8×12 trap 10m grids 110 m apart	Chamise chaparral	Unburned area outside of fire perimeter artificially created by a bulldozer	Measurements up to 9 years after fire	N/A	(1) Some species did not return to the burn site 10 years after the burn, (2) some species had higher abundances in unburned areas, (3) longer-term studies are needed to capture the full dynamics of population recovery following a fire	U (Outside perimeter)	S	N/A
Radford et al. 2013	Examine whether patches of <i>Callitris intratropica</i> act as refuges for other fire-sensitive biota	Cypress Pine <i>Callitris intratropica</i> (a fire-sensitive tree)	Northwestern Australia	Surveyed several <i>Callitris</i> patches at 3 different sites	Eucalypt savannas	Patches of the fires intolerant <i>Callitris</i>	N/A	50 m to 100 m in diameter	<i>Callitris</i> patches were not found to have an abundance of fire sensitive species and might therefore not act as important fire refuges	U/L	P	P
Cullinane-Anthony et al. 2014	Examine bird diversity and uniqueness of species in fire refugia vs. burned areas	Northern Lower Michigan, USA	Seven sites ranging from 9825 ha to 65 ha	Jack pine (<i>Pinus banksiana</i>) forests	“Stringers” or “patches of residual forest” – contiguous areas of mature trees within burn perimeters	Aerial photo interpretation	N/A	N/A	Bird assemblages differed between refugia and surrounding burned landscape when burn were < 12 years old, but not when burns were >30 years old	U/L	S	N/A
Zaitsev et al. 2014	Evaluate the connectivity of (relatively) unburned litter and soil in the recovery of soil fauna communities after a fire	Soil fauna communities	Central Sweden	Three transects with 4 plots each	Sparse forest of Scots pine and common silver birch	Unburned areas, 20 m from forest edge	N/A	2–10 m ²	External colonization (of the unburned forest edge) dominates over the local survival and recovery from small refuges nearby	U/L	S	N/A
Berry et al. 2015b	Assess bird responses to the spatial patterns of unburned areas in a woodland area	All observed and heard birds	Southern Australia	Five replicated blocks within a recently burned woodland area of 28,000 ha compared to 6 sites adjacent to fire	Mallee woodland area	Unburned residuals or unburned patches	Five years following fire	Study included large (5–7 ha) and small (1–3 ha) unburned areas	Large rather than small unburned areas are needed to conserve avian diversity in fire-prone landscapes	U	S	N/A
Swan et al. 2016	Investigate how two small mammal species used unburned gully systems after prescribed fire	Bush rat <i>Rattus fuscipes</i> , agile antechinus <i>Antechinus agilis</i>	Victoria, Australia	400 ha prescribed burn area, 300 ha control	Eucalypt forest	Unburned gullies within a prescribed burned matrix	Measured twice post-fire within 1 year of burn	52% of treated area was unburned (208 ha)	<i>Agile antechinus</i> abundance increased in gullies post-fire; fire effects has little impact on bush rat abundance in refugia	U	P	P
Adie et al. 2017	Compare richness, composition and functional traits of refugia to contiguous forest	Tree species	Drakensberg mountains, South Africa	Census of woody plants in refugia, 25x10 m random plots in forests	Afrotemperate forests	Small patches of forest surrounded by grassland matrix	N/A	10 – 100s m ²	Richness, composition, and functional traits were indistinguishable between refugia and forests	U/L	P	P
Barbé et al. 2017	Investigate the role of residual boreal forest patches as refugia for bryophytes and compare to undisturbed forest	192 bryophyte taxa	Western Quebec	303 5x10 m plots (117 in undisturbed, 108 in residual patches, 78 in burned matrix)	Black spuce boreal forest	Areas of surviving overstory forest	Measurements 8 to 42 years post-fire	0.05 – 1820 ha	Residual patches house bryophyte species absent in burned matrix, but do not conserve all diversity present in undisturbed forest	U/L	S	E

Lutz et al. 2017	Investigate the role of pre-fire shrub cover to post-fire burned and unburned shrubs	16 species of riparian, generalist, and montane shrubs	Central Sierra Nevada	1204 shrub patches ≥ 2 m ² within a 25.6 ha spatially explicit forest plot	Sierra Nevada mixed-conifer forest	Areas of unburned shrub cover	N/A	N/A	Unburned shrub patches persist on the landscape at a density and abundance potentially important for post-fire regeneration	U/L	P/S	N/A
Landesmann and Morales 2018	Characterize post-fire seedling establishment of a fire-sensitive conifer species as a function of refugial seed source and site characteristics	Cordilleran Cypress (<i>Austrocedrus chilensis</i>)	Northwestern Patagonia, Argentina	7 residual stands of <i>Austrocedrus chilensis</i> within recent large fire perimeters	Fire-sensitive conifer (<i>Austrocedrus chilensis</i>) forest	Remnant stands of <i>Austrocedrus chilensis</i> that survived fire	3 sites sampled 14 years post-fire, 4 sites sampled 17 years post-fire	N/A	Fire refugia and the surviving seed sources they contain are critical for the post-fire reestablishment of a fire sensitive conifer species	U/L	P	P

^a Burn severity; studies that include only unburned (U) or also low severity fires (L) into their fire refugia definition. ^b Predictability; studies that mainly investigate or describe predictable (P) or stochastic (S) fire refugia. ^c Persistence; studies that mainly investigate or describe persistent (P) or ephemeral (E) fire refugia. N/A indicates that there was no clear indication of the studied refugia belonging to a given fire refugia taxonomy class.

WebTable 2. Summary of reviewed studies involving landscape-scale wildfire refugia.

Study	Objective of study	Location	Extent / spatial domain of study	Ecosystem type	Fire refugia definition or characteristics	Method for spatial characterization of refugia	Refugia age	Refugia size	Main conclusions	Severity ^a	Predictability ^b	Persistence ^c
Eberhart and Woodard 1987	Assess number and size of unburned islands within fire perimeters	Alberta, Canada	Alberta north of 54N; about 400,000 km ²	Boreal forest	An unburned patch as determined from aerial photos	Aerial photography, supplemented by field data	N/A	Ave: 2–9 ha, except for fires less than 40 ha (where there were zero)	There are unburned patches in fires of all sizes (size increasing with fire size), but the unburned patch size is not always big enough for taxa of interest (i.e., elk herds)	U/L	P	E
Camp et al. 1997	Identify occurrence and attributes of late-successional wildfire refugia	Swauk Late Successional Reserve, Washington, USA	487 plots across 47,000 ha, ~12% late successional forest	Dry forests of the Inland West	(1) different (forest) structure from surrounding matrix, (2) different fire regime from surrounding matrix, (3) presence of old individuals of fire-intolerant tree species	(1) Plots, (2) GIS (characterized potential late successional forest)	130–150 years	Range: <10–41 ha	Different combinations of topographic characteristics best predicted refugial presence	U/L	P	P
Kushla and Ripple 1997	Investigate the role of terrain variables on fire-related forest mortality	Willamette National Forest, Oregon, USA	Sample points (23, 31, 71 and 71) within 4 physiographic areas within a 3,669 ha burned area	Conifer dominated, moist, temperate forests	Refugia not used; but live canopy ratios could be interpreted as refugia indicating high survival of trees during the fire	Aerial photo interpretation	N/A	N/A	Topography and vegetation variables were significant predictors of live canopy ratio, but the specific predictors that were important varied between four physiographic areas within the burned area	U/L	P	N/A
Turner et al. 1999	Quantify (1) pre-fire heterogeneity effects of the landscape on fire severity (2) post-fire patterns of burn severities on plant reestablishment	Yellowstone, Wyoming, USA	Three sites (100 sampling points within 3 1×1-km grids)	Subalpine Forests	Unburned areas: no sign of fire effects, Light surface burn: low-intensity surface fire in which canopy trees retain green needles	Aerial observation, field observations (plots) for burn severity situation within grid	Measured up to 4 years after fire	Total: 9.7 ha (unburned); 31.3 ha (unburned+ slightly burned) of 1×1 km grid	(1) In lightly burned areas, percent cover returned to unburned levels within 3 years, (2) biotic cover tended to be higher near unburned or lightly burned areas	U/L	N/A	N/A
DeLong and Kessler 2000	Compare fire refugia forest structure to the surrounding high-severity burned landscape matrix	British Columbia, Canada	About 660,000 ha	Sub-boreal spruce forest	A remnant forest patch is older forest surrounded by younger (previously burned) forest	Maps of stand age	Assessed as a chronosequence based on persistence of different fire refugia	<10 ha	Remnant patches were different from the surrounding, younger matrix, remnant patches were also different from matrix of same age class	U/L	N/A	N/A

Clarke 2002	Compare vegetative species composition and fire response traits on habitat islands (created by topography) and surrounding open forest matrix	Four coastal and sub-coastal locations in Australia	Approximately 32 paired 0.1 ha samples of rocky outcrops versus forest matrix	Open Eucalypt forest	Fire shadows are areas that receive less fire than the surrounding matrix (mainly due to topographical effects and fuel discontinuity)	Aerial photography	Outcrops have fire return interval different from forest matrix	Size >0.1 ha (mainly for sampling purposes)	(1) Fire effects less on outcrops than in the forest matrix because the physical barrier of rock edges, (2) more frequent fires lead to less obligate seeders in the forest matrix, (3) in contrast, there is convergence towards resprouters in the forest matrix	U/L	P	P
Wimberly and Kennedy 2008	Model the sensitivity of fire spread in relation to (1) different successional stages, and (2) the distribution of fire refugia	Experimental model runs in landscapes in the interior Pacific Northwest, USA	Grids of 200×200 cells (cell size undefined)	Dry forests of the interior Pacific Northwest	Refugia in the model were defined as a land types with a lower probability of fire spread	Prescribed in modeling exercise	Old closed-canopy forests <10% of the landscape after 100,000 simulations years	Prescribed at 25–50% of landscape (in 32×32 or 64×64 squares)	The area of old closed-canopy forests increased when fire spread was less rapid in these forests, and when the physical landscape incorporated more fire refugia	U/L	S	P
Weisberg et al. 2008	Compare old-growth distributions with spatial models of fire risk to determine if old-growth pinyon-juniper woodlands are limited to sites with lower fire risk	Shosone Mountain Range, central Nevada, USA	Nineteen-km ² watershed, age classes of stand were mapped over a 10-km ² area	Piñon-juniper woodlands in central Great Basin	Old-growth pinyon-juniper woodlands	Aerial photo interpretation and field-based adjustments to GIS layers	800-1350 years (based on old growth ages)	Ave: 9.32 ha	Old-growth piñon-juniper woodlands occupy isolated sites with low fire risk; statistical relationships between old growth and fire risk were weak implying that woodland expansion may be driven by other factors than fire exclusion	U/L	P	P
Burton et al. 2008	Examine how large fires generate landscape heterogeneity in the North American boreal forest	All boreal ecozones in Canada	All large fires across Canada from 1959 to 1999	Boreal ecosystems	Unburned islands as determined by dNBR from satellite data. Severity thresholds established based on field data (CBI)	Landsat	N/A	Ave: 14.5 ha (range: 1.3–24.2 ha; of 5 fires)	The occurrence of unburned islands was related to more unburned area within the perimeters of larger fires	U	N/A	N/A
Roman-Cuesta et al. 2009	Evaluate the importance of biotic/abiotic variables influencing the number and size of unburned islands	The Solsones wildfire, northeastern Spain	One 3,400 ha wildfire	Mixed conifer and oak	Satellite-derived land cover classes including unburned vegetation	Satellite derived fire severity map (three classes) using the Indian satellite IRS LISSIII	N/A	Ave: 0.42 (+/- 0.05 se) ha (range: <0.5–135 ha)	Unburned islands occur at continuous slopes with more forest cover and lower percentage broadleaf species	U/L	N/A	N/A
Kolden et al. 2012	Characterize abundance, distribution, and shape of unburned patches with respect to fire size and severity	Yosemite, Glacier and Yukon-Charley National Parks, USA	Yosemite: 4,771 km ² Glacier: 29,850 km ² Yukon-Charley: 30,980 km ²	Yosemite: mixed conifer shrubland Glacier: subalpine and submontane; Yukon-Charley: boreal forest	Either a 0.09 ha or a 0.81 ha area with a dNBR not detectable as burned	Classification from Landsat-derived dNBR, unburned patches were classified using thresholds (-100 ≤ dNBR ≤ 100)	N/A	Yosemite: ave. ~4 ha (range: 0.09–300 ha) Glacier and Yukon-Charley: ave. ~1 ha (range: 0.09–20 ha)	Unburned proportion significant in all areas but amount, spatial pattern, and distance within the fire to unburned varies among regions	U/L	N/A	N/A

Mackey et al. 2012	Identifying ecosystem 'greenspots' that may have functioned as habitat refuges	Great Eastern Ranges, New South Wales, Australia	24 million ha	Coastal forests, heathland, rainforests, aline herbfields, and semiarid woodlands	Greenspots are defined as locations that may have functioned as drought and fire micro-refuges for multiple species	Satellite imagery (MODIS)	Minimally disturbed pixels from 10 year time series	Greenspots were 0.2% of total study area (Range: 86–15,238 ha)	Ecosystem greenspot index can be used to map locations that may have functioned as micro-refuges from drought and fire for a decade following the year 2000	N/A	P	P
Collins et al. 2012	Assess the effect of fire frequency on forest structure	Eastern Australia	Not explicitly stated, but about 250 km ²	Eucalyptus forest	Sites burnt two or fewer times over 27 years or >18 years between the two most recent fires	Digitized fire history layers	N/A	20×20m quadrats, size not explicitly delineated	Gullies or areas of markedly different topography in a landscape allow persistence of complex structure (generally, fire burns less severely and consumption is lower)	U/L	P	P
Kashian et al. 2012	Describe the natural range of variability in fire refugia spatial pattern	Northern Lower Michigan, USA	Not explicitly state but about 300 km ² . 54 wildfires > 80 ha examined and 11 had refugia.	Jack pine (<i>Pinus banksiana</i>) forests	“Stringers” or “patches of residual forest” where contiguous areas of mature trees within burn perimeters	Aerial photo interpretation	N/A	Mean patch area within each fire ranged from 0.1 ha – 22.9 ha	All stringers were long and narrow in size, and made up 3%-14% of burned landscapes. Fires < 80 ha did not have refugia, but larger fires had a lower proportion of their landscape as refugia, but refugia patches were larger. Neither pre-fire species composition nor topography were related to refugia creation	U/L	N/A	N/A
Andison and McCleary 2014	Quantify (1) historical range of burn severity and (2) differences in fine-scale burn patterns across ecological zones	Western boreal Canada	Wildfires across more than 100 million ha of western boreal Canada	Five Canadian boreal ecozones	Undisturbed island remnants: Unburned or partially burned areas within fire perimeter not connected to the outer unburned edge, Matrix remnants: unburned areas connected to the outer unburned edge	Aerial photo interpretation	N/A	12% (undisturbed remnants) 41% (partially burned) (range: >0 – 58% area of undisturbed remnants)	The southwestern parts (2 ecoregions) had less area in partially disturbed island remnants relative other areas, but most metrics were ecozone invariant	U/L	N/A	N/A
Leonard et al. 2014	Characterize unburned patches within a large wildfire and identify contributing factors	Victoria, Australia	250,000 ha	Eucalypt forest	Unburned as delineated from 15cm aerial imagery	Aerial imagery and SPOT-derived dNBR	N/A	Ave: 27.1 ha (range: 1-306 ha)	Unburned area was <1% of fire and mostly topography-driven	U	P	P
Perera and Buse 2014	Synthesize literature, create awareness, and explore future knowledge requirements of wildfire residuals in boreal forests	The boreal biome in the northern hemisphere	Approximately 12x10 ⁶ km ²	Boreal forests	All vegetation structure remaining following a fire	Synthesis of scientific literature	N/A	N/A	0.5×10 ⁶ ha of residual patches are produced every year across the boreal biome; growing recognition of the importance of boreal wildfire residuals will prompt answering many questions on their ecology	N/A	N/A	N/A

1 2 3 4 5 6 7 8	Kolden et al. 2015	Correlate unburned islands to climate predictor variables	Yosemite, Glacier and Yukon-Charley National Parks, USA	Yosemite: 4,771 km ² Glacier: 29,850 km ² Yukon-Charley: 30,980 km ²	Yosemite: mixed conifer shrubland Glacier: subalpine and submontane; Yukon-Charley: boreal forest	Persistent patches which have no significant spectral change between pre- and post-fire Landsat-derived dNBR;	Classification from Landsat-derived dNBR	N/A	Same as Kolden et al. 2012	No trend in unburned proportion over time and relationships between unburned islands and climate echo broader fire-climate relationships	U/L	N/A	N/A
9 10 11 12 13 14 15 16 17 18	Berry et al. 2015a	(1) Validate predictive fire refugia model using burn severity from a large, recent wildfire (2) examine the extent to which local fire severity was influenced by the severity of the surrounding landscape	Victoria Central Highlands, northeast of Melbourne, Australia	Not explicitly given, based on maps, each of the 2 catchments were roughly 12 by 12 km	Australian wet montane forest	Unburned or lightly burned habitat patches within the boundaries of a large fire	Normalized Burn Ratio from SPOT satellite imagery	N/A	N/A	Modeled fire refuges were strong predictors of fire severity, but under extreme fire conditions fire refuges were limited to areas with extremely high probability of refuge occurrence: deep, extremely sheltered mesic gullies and late successional vegetation communities; under moderate conditions fire severity was topographically mediated	U/L	P	P
19 20 21 22 23 24 25	Landesmann et al. 2015	Contribute to understanding of the ecological functioning of fire refuges, i.e., examine buffering capacity for fire-sensitive tree species which inhabit fire-prone landscapes	Nahuel Huapi National Park, northwestern Patagonia, Argentina	Thirty-one forest remnants throughout the national park: 24 within the area burned more than 100 years ago and 7 in the area burned less than 20 years ago	Fire-sensitive conifer (<i>Austrocedrus chilensis</i>) forest	Fixed locations where physical conditions decrease fire severity, allowing the persistence of fire-sensitive forest taxa or communities	Distribution map of <i>A. chilensis</i> forest	>100 years	N/A	<i>A. chilensis</i> forest remnants in northwestern Patagonia are persistent entities, i.e., fire refuges associated with particular biophysical attributes	U/L	P	P
26 27 28 29 30 31 32	Krawchuk et al. 2016	Determine predictability of fire refugia location across topographic and weather gradients	Western Canada	Seven study fires in conifer-dominated forest of the Western Cordillera of Canada	Conifer forest	Unburned or low-severity burned areas fires (-200 ≤ dNBR ≤ 200)	Normalized Burn Ratio from Landsat TM and ETM imagery	N/A	N/A	The predictability of refugia was lowest under higher fire weather conditions and increased with topographic complexity. Topographic predictors associated with refugia changed in importance with fire weather and topographic complexity	U/L	P	P
33 34 35 36 37	Wilkin et al. 2016	Compare fire occurrence, frequency and severity within cold air pools to the surrounding landscape matrix	Yosemite National Park, USA	Mixed conifer forests of Yosemite National Park between 1000 and 3600 m	Mixed conifer forest and scattered meadows and shrublands	Unchanged areas as determined by RdNBR fire severity maps	Relative differenced Normalized Burn Ratio (RdNBR) from satellite data	N/A	N/A	The landscape scale study suggests that cold-air pools have lower fire occurrence, frequency, and severity patterns, possibly leading small-scale refugia	U/L	P	P
38 39 40 41 42 43	Ouarmim et al. 2016	Test if particular environmental conditions and stand characteristics explain the presence of fire refugia	Northwest Quebec, Canada	11,000 ha natural forest mosaic	Boreal mixedwood forest	Late-successional conifer stands which escaped two of more consecutive fires	Stand composition maps, dendrochronological and palaeoecological fire histories	> 250 years	N/A	Fuel moisture is the dominant factor influencing the distribution of fire refugia, which are assumed to not be randomly distributed	U/L	L	P

1 2 3 4 5 6 7 8	Meddens et al. 2016	Develop a model for classifying unburned areas within wildfire perimeters using moderate resolution satellite and ancillary data	Interior Pacific Northwest, USA	Twenty fires and 868 field plots	Forests and rangelands of the Inland Northwest	Unburned plot locations evaluated by field visits	Multi-temporal Landsat and ancillary data	N/A	Ave unburned by fire: 19% (standard deviation 16%)	(1) Using multi-date Landsat scenes improved classification accuracy of unburned areas, (2) the total area of unburned islands in non-forest was significantly higher than the unburned areas in forest	U	N/A	N/A
9 10 11 12 13	Nielsen et al. 2016	Assess influence of lake pattern on fire frequency and the predictability of fire refugia	Boreal Shield and Boreal Plain, northern Saskatchewan Canada	All large fires (>200 ha) between 1980 and 2014	Boreal forest	Parts of the landscape where intense crown fires are rare	Mapped fire perimeters from Canadian Forest Service National Fire Database	N/A	N/A	Persistent landscape features can reduce the likelihood of wildfire. Areas close to lakes are more likely to lead to long-term fire refugia	U	P	P
14 15 16 17 18	Haire et al. 2017	Quantify neighborhood spatial patterns of refugia and characterize plant species composition along a neighborhood gradient	Jemez Mountains, New Mexico, USA	Las Conchas fire (2011, 61,000 ha)	Mixed conifer forest	Areas which have no significant spectral change between pre- and post-fire Landsat-derived dNBR; (-200 ≤ dNBR ≤ 200)	Classification from Landsat-derived dNBR	N/A	N/A	Neighborhood patterns were correlated with topographic predictors. Most refugial neighborhoods overlap with refugia from previous fires	U/L	P	P
19 20 21 22 23 24	Banks et al. 2017	Simulation experiment to investigate how fire regimes interact with topography and weather to shape genetic diversity	Australian Alps, Australia	9,125 km ²	Montane forests	Upper 20 th percentile of mean interference interval	Simulation	N/A	N/A	Topographic relief and weather variability influence occurrence of refugia. Refugia patterns have implications for genetic diversity and spatial structure	U/L	P	P
25 26 27 28 29 30 31 32	Kolden et al. 2017	Sustainability of previously classified wildfire refugia following a contemporary fire event	Swauk Late Successional Reserve, Washington, USA	Plots (122) across 3 drainages, approximately 11 ha in total	Dry forests of Inland Northwest	Does not transition between successional stage due to fire	Field data and supplemental information	Same as Camp et al. 1997	Same as Camp et al. 1997	(1) Extreme fires can maintain historic range of variability of successional stages across landscape, (2) historic refugia burned more severely in 2012 than surrounding forest, (3) new refugia formed, suggesting refugia are ephemeral or "shift" over time	U/L	S	E
33 34 35 36 37 38 39 40 41 42	Meddens et al. 2018	Determine unburned proportion trends across the Northwestern US from 1984–2014 and assess patterns across space	Interior Pacific Northwest, USA	Entire interior Pacific Northwest, USA	Forests and rangelands of the Inland Northwest	Unburned plot locations as determined by Meddens et al. 2016	Multi-temporal Landsat data	N/A	Ave. unburned patch size is 1.2 ha (sd: 25.4 ha) Ave. unburned proportion by fire: 9.6%,	Unburned area proportion exhibited no change over the three decades; ecoregional differences in mean unburned proportion, patch area, and patch density, suggests influences of vegetation and topography on the formation of unburned areas	U	N/A	2.6% of total unburned area was unburned for >2 fires

Rogean et al. 2018	Investigate the influence of topographic features on fire refugia persistence	Alberta Rockies, CA	911,951 ha	Forest capable landscapes in the Alberta Rockies	Stands >300 years old	Field-based fire history data	>300 years	N/A	Topographic features were strong predictors of persistent fire refugia; sustainability of fire refugia may be decreasing with warming climate and current fuel conditions	U/L	P	P
Meigs and Krawchuk 2018	Characterize abundance, structure, and composition of fire refugia in the Pacific Northwest, USA	Oregon and Washington, USA	612,629 ha	Forest and non-forest area in Oregon and Washington	0 – 10% basal area mortality according to fire severity inferred from Landsat imagery	Classification from Landsat-derived RdNBR	N/A	N/A	(1) Ecological role of fire refugia depends on site-specific pre-fire conditions, as well as the broader burn severity mosaic, (2) non-forest vegetation accounted for a substantial component of fire refugia	U/L	N/A	N/A

^a Burn severity; studies that include only unburned (U) or also low severity fires (L) into their fire refugia definition. ^b Predictability; studies that mainly investigate or describe predictable (P) or stochastic (S) fire refugia. ^c Persistence; studies that mainly investigate or describe persistent (P) or ephemeral (E) fire refugia. N/A indicates that there was no clear indication of the studied refugia belonging to a given fire refugia taxonomy class.

References: web-only material

- Adie H, Kotze DJ, Lawes MJ. 2017. Small fire refugia in the grassy matrix and the persistence of Afrotropical forest in the Drakensberg mountains. *Scientific reports* 7:6549.
- Andison DW, McCleary K. 2014. Detecting regional differences in within-wildfire burn patterns in western boreal Canada. *The Forestry Chronicle* 90:59-69.
- 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, Davies ID, Cary GJ. 2017. When can refuges mediate the genetic effects of fire regimes? A simulation study of the effects of topography and weather on neutral and adaptive genetic diversity in fire-prone landscapes. *Molecular Ecology* 26: 4935-4954.
- 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.
- Barbé M, Fenton NJ, Bergeron Y. 2017. Are post-fire residual forest patches refugia for boreal bryophyte species? Implications for ecosystem based management and conservation. *Biodiversity and Conservation* 26:943-965.
- 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.
- Borchert M, Borchert SM. 2013. Small mammal use of the burn perimeter following a chaparral wildfire in southern California. *Bulletin, Southern California Academy of Sciences* 112:63-73.
- Brennan KEC, Moir ML, Wittkuhn RS. 2011. Fire refugia: The mechanism governing animal survivorship within a highly flammable plant. *Austral Ecology* 36:131-141.
- Brotans L, Pons P, Herrando S. 2005. Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? *Journal of Biogeography* 32:789-798.
- Burton PJ, Parisien M-A, Hicke JA, Hall RJ, Freeburn JT. 2008. Large fires as agents of ecological diversity in the North American boreal forest. *International Journal of Wildland Fire* 17:754-767.
- 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.
- Clarke PJ. 2002. Habitat islands in fire-prone vegetation: do landscape features influence community composition? *Journal of Biogeography* 29:677-684.
- Collins L, Bradstock RA, Tasker EM, Whelan RJ. 2012. Can gullies preserve complex forest structure in frequently burnt landscapes? *Biological Conservation* 153:177-186.
- Cullinane-Anthony BL, Seefelt NE, Corace RG, Kashian DM, Gehring TM. 2014. Influence of residual forest patches on post-fire bird diversity patterns in jack pine-dominated ecosystems of northern Lower Michigan. *Forest Ecology and Management* 331:93-103.
- DeLong SC, Kessler WB. 2000. Ecological characteristics of mature forest remnants left by wildfire. *Forest Ecology and Management* 131:93-106.
- Eberhart KE, Woodard PM. 1987. Distribution of residual vegetation associated with large fires in Alberta. *Canadian Journal of Forest Research* 17:1207-1212.

- 1
2
3 Gandhi KJK, Spence JR, Langor DW, Morgantini LE. 2001. Fire residuals as habitat reserves for
4 epigaeic beetles (Coleoptera: Carabidae and Staphylinidae). *Biological Conservation* 102:131-
5 141.
- 6 Haire SL, Coop JD, Miller C. 2017. Characterizing Spatial Neighborhoods of Refugia Following
7 Large Fires in Northern New Mexico USA. *Land* 6:19.
- 8 Henriques RPB, Bizerril MXA, Palma ART. 2000. Changes in small mammal populations after
9 fire in a patch of unburned cerrado in Central Brazil. *Mammalia* 64:173-185.
- 10 Hylander K. 2011. The response of land snail assemblages below aspens to forest fire and clear-
11 cutting in Fennoscandian boreal forests. *Forest Ecology and Management* 261:1811-1819.
- 12 Hylander K, Johnson S. 2010. In situ survival of forest bryophytes in small-scale refugia after an
13 intense forest fire. *Journal of Vegetation Science* 21:1099-1109.
- 14 Kashian DM, Corace RG, Shartell LM, Donner DM, Huber PW. 2012. Variability and
15 persistence of post-fire biological legacies in jack pine-dominated ecosystems of northern
16 Lower Michigan. *Forest Ecology and Management* 263:148-158.
- 17 Kolden CA, Abatzoglou JT, Lutz JA, Cansler CA, Kane JT, van Wagtenonk JW, Key CH.
18 2015. Climate contributors to forest mosaics: ecological persistence following wildfire.
19 *Northwest Science* 89:219-238.
- 20 Kolden CA, Bleeker TM, Smith A, Poulos HM, Camp AE. 2017. Fire Effects on Historical
21 Wildfire Refugia in Contemporary Wildfires. *Forests* 8:400.
- 22 Kolden CA, Lutz JA, Key CH, Kane JT, van Wagtenonk JW. 2012. Mapped versus actual
23 burned area within wildfire perimeters: characterizing the unburned. *Forest Ecology and*
24 *Management* 286:38-47.
- 25 Krawchuk MA, Haire SL, Coop J, Parisien MA, Whitman E, Chong G, Miller C. 2016.
26 Topographic and fire weather controls of fire refugia in forested ecosystems of northwestern
27 North America. *Ecosphere* 7:1-18.
- 28 Kushla JD, Ripple WJ. 1997. The role of terrain in a fire mosaic of a temperate coniferous forest.
29 *Forest Ecology and Management* 95:97-107.
- 30 Landesmann JB, Gowda JH, Garibaldi LA, Kitzberger T. 2015. Survival, growth and
31 vulnerability to drought in fire refuges: implications for the persistence of a fire-sensitive
32 conifer in northern Patagonia. *Oecologia* 179:1111-1122.
- 33 Landesmann JB, Morales JM. 2018. The importance of fire refugia in the recolonization of a
34 fire-sensitive conifer in northern Patagonia. *Plant Ecology* 219:455-466.
- 35 Leonard SWJ, Bennett AF, Clarke MF. 2014. Determinants of the occurrence of unburnt forest
36 patches: Potential biotic refuges within a large, intense wildfire in south-eastern Australia.
37 *Forest Ecology and Management* 314:85-93.
- 38 Lindenmayer DB, et al. 2009. What factors influence rapid post-fire site re-occupancy? A case
39 study of the endangered Eastern Bristlebird in eastern Australia. *International Journal of*
40 *Wildland Fire* 18:84-95.
- 41 Lutz J, Furniss T, Germain S, Becker K, Blomdahl E, Jeroni-mo S, Cansler CA, Freund J,
42 Swanson M, Larson A. 2017. Shrub communities, spatial patterns, and shrub-mediated tree
43 mortality following reintroduced fire in Yosemite National Park, California, USA. *Fire*
44 *Ecology* 13:104-126.
- 45 Mackey B, Berry S, Hugh S, Ferrier S, Harwood TD, Williams KJ. 2012. Ecosystem greenspots:
46 identifying potential drought, fire, and climate-change micro-refuges. *Ecological Applications*
47 *22:1852-1864.*
- 48
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3 Meddens AJ, Kolden CA, Lutz JA. 2016. Detecting unburned areas within wildfire perimeters
4 using Landsat and ancillary data across the northwestern United States. *Remote Sensing of*
5 *Environment* 186:275-285.
- 6 Meddens AJ, Kolden CA, Lutz JA, Abatzoglou JT, Hudak AT. 2018. Spatial and temporal
7 patterns of unburned areas within fire perimeters in the northwestern United States from 1984
8 to 2014. *Ecosphere* 9:2.
- 9 Meigs GW, Krawchuk MA. 2018. Composition and Structure of Forest Fire Refugia: What Are
10 the Ecosystem Legacies across Burned Landscapes? *Forests* 9:243.
- 11 Nielsen SE, DeLancey ER, Reinhardt K, Parisien M-A. 2016. Effects of lakes on wildfire
12 activity in the boreal forests of Saskatchewan, Canada. *Forests* 7:265.
- 13 Ouarmim S, Paradis L, Asselin H, Bergeron Y, Ali AA, Hély C. 2016. Burning potential of fire
14 refuges in the boreal mixedwood forest. *Forests* 7:246.
- 15 Perera A, Buse L. 2014. *Ecology of wildfire residuals in boreal forests*. John Wiley & Sons.
- 16 Pfab MF, Witkowski ETF. 1999. Fire survival of the Critically Endangered succulent, *Euphorbia*
17 *clivicola* – fire-avoider or fire-tolerant? *African Journal of Ecology* 37:249-257.
- 18 Radford IJ, Andersen AN, Graham G, Trauernicht C. 2013. The fire refuge value of patches of a
19 fire-sensitive tree in fire-prone savannas: *Callitris intratropica* in Northern Australia.
20 *Biotropica* 45:594-601.
- 21 Rogeau MP, Barber QE, Parisien MA. 2018. Effect of Topography on Persistent Fire Refugia of
22 the Canadian Rocky Mountains. *Forests* 9:285.
- 23 Roman-Cuesta RM, Gracia M, Retana J. 2009. Factors influencing the formation of unburned
24 forest islands within the perimeter of a large forest fire. *Forest Ecology and Management*
25 258:71-80.
- 26 Schwilk DW, Keeley JE. 1998. Rodent populations after a large wildfire in California chaparral
27 and coastal sage scrub. *The Southwestern Naturalist*:480-483.
- 28 Schwilk DW, Keeley JE. 2006. The role of fire refugia in the distribution of *Pinus sabiniana*
29 (*Pinaceae*) in the southern Sierra Nevada. *Madrono* 53:364-372.
- 30 Swan M, Galindez-Silva C, Christie F, York A, Di Stefano J. 2016. Contrasting responses of
31 small mammals to fire and topographic refugia. *Austral Ecology* 41:437-445.
- 32 Swengel AB, Swengel SR. 2007. Benefit of permanent non-fire refugia for Lepidoptera
33 conservation in fire-managed sites. *Journal of Insect Conservation* 11:263-279.
- 34 Turner MG, Romme WH, Gardner RH. 1999. Prefire heterogeneity, fire severity, and early
35 postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming.
36 *International Journal of Wildland Fire* 9:21-36.
- 37 Watson SJ, Taylor RS, Nimmo DG, Kelly LT, Clarke MF, Bennett AF. 2012. The influence of
38 unburnt patches and distance from refuges on post-fire bird communities. *Animal*
39 *Conservation* 15:499-507.
- 40 Weisberg PJ, Ko D, Py C, Bauer JM. 2008. Modeling fire and landform influences on the
41 distribution of old-growth pinyon-juniper woodland. *Landscape Ecology* 23:931-943.
- 42 Wilkin KM, Ackerly DD, Stephens SL. 2016. Climate change refugia, fire ecology and
43 management. *Forests* 7:77.
- 44 Wimberly MC, Kennedy RSH. 2008. Spatially explicit modeling of mixed-severity fire regimes
45 and landscape dynamics. *Forest Ecology and Management* 254:511-523.
- 46 Zaitsev AS, Gongalsky KB, Persson T, Bengtsson J. 2014. Connectivity of litter islands
47 remaining after a fire and unburnt forest determines the recovery of soil fauna. *Applied Soil*
48 *Ecology* 83:101-108.
- 49
50
51
52
53
54
55
56
57
58
59
60