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Review Article

An ecological perspective on living with fire in ponderosa pine forests of Oregon and Washington: Resistance, gone but not forgotten

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ABSTRACT

Wildland fires (WLF) have become more frequent, larger, and severe with greater impacts to society and ecosystems and dramatic increases in firefighting costs. Forests throughout the range of ponderosa pine in Oregon and Washington are jeopardized by the interaction of anomalously dense forest structure, a warming and drying climate, and an expanding human population. These forests evolved with frequent interacting disturbances including low-severity surface fires, droughts, and biological disturbance agents (BDAs). Chronic low-severity disturbances were, and still are, critical to maintaining disturbance resistance, the property of an ecosystem to withstand disturbance while maintaining its structure and ecological function. Restoration of that historical resistance offers multiple social and ecological benefits.

Moving forward, we need a shared understanding of the ecology of ponderosa pine forests to appreciate how restoring resistance can reduce the impacts of disturbances. Given contemporary forest conditions, a warming climate, and growing human populations, we predict continued elevation of tree mortality from drought, BDAs, and the large high-severity WLFs that threaten lives and property as well as ecosystem functions and services. We recommend more comprehensive planning to promote greater use of prescribed fire and management of reported fires for ecological benefits, plus increased responsibility and preparedness of local agencies, communities and individual homeowners for WLF and smoke events. Ultimately, by more effectively preparing for fire in the wildland urban interface, and by increasing the resistance of ponderosa pine forests, we can greatly enhance our ability to live with fire and other disturbances.

Introduction

Increasingly, wildland fires (WLF), drought, and biological disturbance agents are having unprecedented impacts in forests throughout the range of ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) in Oregon and Washington and on the people who call these forested landscapes home. After more than a century of fire exclusion, today's ponderosa pine forests are no longer resistant to disturbance, while droughts are increasing in frequency and severity, and human populations are increasing in and around forest land.

Historically, frequent low-severity disturbances created resistance to large severe disturbances, but 20th-century land management increased forest density, competitive stress, and the abundance and connectivity of fuels, and favored fire and drought susceptible tree species (Hessburg and Agee, 2003; Hessburg et al., 2005; Johnston, 2017; Merschel et al., 2014). More recently, a warming climate has increased the difficulty of fire suppression, and contributes to an increase in the number, extent, and severity of very large WLFs in the Pacific Northwest and western North America ((Dennison et al., 2014; Reilly et al., 2017; Westerling, 2016; Parks and Abatzoglou 2020). In ponderosa pine forests of Oregon and Washington, there has been a six-fold increase in the proportion of forest burned at high-severity in comparison to historical fire regimes (Haugo et al., 2019), over half of which is burning in uncharacteristically large patches (Reilly et al., 2017).

Abbreviations: WLF, Wildland Fire; WUI, Wildland Urban Interface; BDAs, Biological Disturbance Agents.

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In addition to ecosystem impacts, the economic and human health impacts of contemporary WLF are striking. In 2017, WLFs resulted in an estimated \$51.5 million loss to Oregon's travel and tourism industry and WLF smoke created unhealthy air quality on 160 days (Barnum, 2018). These ecological and social impacts are increasing even though the previous 10-year average annual fire suppression costs on federal land increased from \$400 million in 1995 to \$1.84 billion in 2019 (National Interagency Fire Center 2020).

Paradoxically, the past century of aggressive fire suppression that was intended to limit the impacts of WLF has unintentionally exacerbated fire effects on ecosystems and humans (Calkin et al., 2015). It also increased the susceptibility of ponderosa pine forests to the combined effects of drought and biological disturbance agents (BDAs; Table 1). BDAs are insects and pathogens that can kill or severely reduce productivity of trees and include bark beetles, defoliating insects, parasitic plants, and fungal pathogens. However, we cannot simply reintroduce WLF to ponderosa pine forests given the extensive area currently susceptible to high-severity fire, and policy that largely precludes burning near the rapidly expanding human population in the wildland urban interface (WUI). During 1990 to 2010 the WUI nearly doubled in size from 1,192 km^2 to 1,933 km^2 in the USA (Radeloff et al., 2018). Thus, learning to live with contemporary fire and human population growth is both an ecological and a societal challenge essential to the development of a sustainable and safe coexistence with ponderosa pine forest ecosystems.

Living with fire in ponderosa pine forests requires a shift in thinking by scientists, resource managers, and stakeholders about the role of fire and other disturbances in forest health. The term resilience is often used to characterize adaption strategies, but resilience is ambiguous when it is not understood in the context of a specific ecosystem (Fisichelli et al., 2016). We synthesize extensive research of historical conditions and dynamics in ponderosa pine forests to inform what adaptive resilience precisely means in ponderosa pine ecosystems. We advance that ecological resistance, rather than resilience, best describes how ponderosa pine forests can be adapted to WLF, drought, and BDAs that are exacerbated by climate change. Resistance is often considered a component of resilience, but the two ecological processes are distinct mechanisms that maintain the essential characteristics of an ecosystem including taxonomic composition, structure, ecosystem function, and process rates (Holling, 1973). Resilience is the capacity of an ecosystem to recover its essential structure and function following a disturbance, whereas resistance is the property of an ecosystem to retain its characteristic structure and function when disturbed (Grimm and Wissel, 1997).

Our synthesis of historical conditions and dynamics demonstrates resistance is how ecosystem structure and function can be maintained in ponderosa pine forests, and that the process of frequent low-severity fire develops and maintains resistance (Fig. 1, online Appendix 1). Although the importance of frequent low-severity fire in maintaining resistance in ponderosa pine forests of Oregon and Washington has long been recognized (Weaver, 1943), we have not incorporated resistant forest conditions into contemporary ponderosa pine forests at a meaningful scale (Kolden, 2019; Stephens et al., 2016). Restoring resistance means aligning forest conditions with climate change and increased disturbance frequency and intensity rather than current policy that resists or forestalls changes in contemporary forest conditions (*sensu* (Johnston et al., 2021a; Millar et al., 2007)). We recognize that restoring historical conditions and dynamics that are adapted to resist disturbances may neither be desirable nor possible across ponderosa pine forests given projections of novel climatic conditions in the coming century (Kerns et al., 2018). However, an understanding of how resistance was maintained historically can aid in regional and local planning efforts and inform decisions about whether and how to invest in restoration to realign these forests with increases in disturbance frequency and severity under a warming climate and expanding human footprint (North et al., 2015; Safford et al., 2012).

In this synthesis, we provide an ecological context for the challenge of living with fire in ponderosa pine forests of Oregon and Washington, USA. In section one, we review the ecological setting and adaptations of the major tree species to drought, fire, and BDAs to illustrate how resistance to disturbances is related to forest structure and composition, hereafter forest conditions. We then describe how the historical disturbance regime and forest conditions were dramatically altered by 20th-century land management including fire exclusion, logging, and grazing. Using an understanding of contemporary forest conditions and how they are changing with growth, management, WLF, and BDAs we forecast disturbance impacts given increasing drought caused by climate change. This summary of historical and contemporary ecology of ponderosa pine forests clarifies the importance of regular low-severity fire as a process critical to maintaining ecosystem functions of ponderosa pine forests. It also demonstrates that large mixed- and high-severity fires are inevitable in the next several decades, along with elevated tree mortality from drought and BDAs. Next, we describe the expanding WUI and challenges to sustainably managing WLF and applying prescribed fire while preparing communities for WLF impacts. We conclude by highlight tradeoffs between approaches for restoring fire and mitigating its impacts to provide a realistic assessment of what living with fire in ponderosa pine forests means in the 21st century.

The ecological setting

Our scope of inference applies only to ponderosa pine forests that historically had a frequent low-severity fire regime (online Appendix 1). Historical forest conditions, dynamics, and response to contemporary land management in these forests are distinct from forests that burned less frequently and where moderate- to high-severity fire is a major ecosystem process. Our account of historical dynamics that maintained resistant forest conditions is guided by robust and spatially extensive documentation from tree-ring reconstructions and historical records (Fig. 1; online Appendix 1). These records demonstrate that frequent low-severity fire regime was predominant across the distribution of ponderosa pine, which occupies 76,997 km^2 (14.7%) of the land area in Oregon and Washington, and primarily occurs east of the Cascade Range and in the Klamath Mountains of southwest Oregon (Fig. 1).

Historically, low-severity surface fires were extensive and burned synchronously in drought years in ponderosa pine forests (Hagmann et al., 2019; Heyerdahl et al., 2008; Johnston et al., 2017; McKenzie et al., 2004). In fact, fire history reconstructions separated by hundreds of miles share many of the same major fire years (Fig. 2). Topography, fire weather, and fuels generally did not limit chronic low-severity fire even in relatively cool-moist environments within the range of ponderosa pine where more fire sensitive Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and true fir (*Abies* spp. Mill) occurred prior to fire exclusion (Johnston et al., 2016; Wright and Agee, 2004; Heyerdahl et al. 2019; Merschel et al., 2018).

Landscape fire rotations, the years required for a defined area to experience fire equal to the area of interest (Farris et al., 2010), were substantially shorter than they are today, and high-severity fire was rare. For example, from 1700-1918, the fire rotation for fires> 20,000 ha in an 85,750-ha area in south central Oregon was < 15 years (Hagmann et al., 2019). Patches of high-severity fire historically were predominantly small (<0.5 ha) and rarely >10 ha (Agee, 1993; Heyerdahl et al. 2019; Merschel et al., 2018) because fire maintained low surface and canopy fuel loads (Johnston et al., 2017), as well as heterogeneity in horizontal structure at fine scales (< 1ha) (Churchill et al., 2013). As a result of frequent burning of tree regeneration, most basal area occurred in large fire-resistant trees (Hagmann et al., 2013, 2014, 2019). In contemporary ponderosa pine forests, the fire rotation has increased to 209 years, and ∼33% of all fire is high-severity (> 75% tree mortality; online Appendix 2).

Landscapes with longer fire-free intervals and those in which high-severity fire historically created large even-aged patches of forests are outside the scope of this paper. Documented exceptions in the range of ponderosa pine are rare, but occur where ponderosa-pine dominated

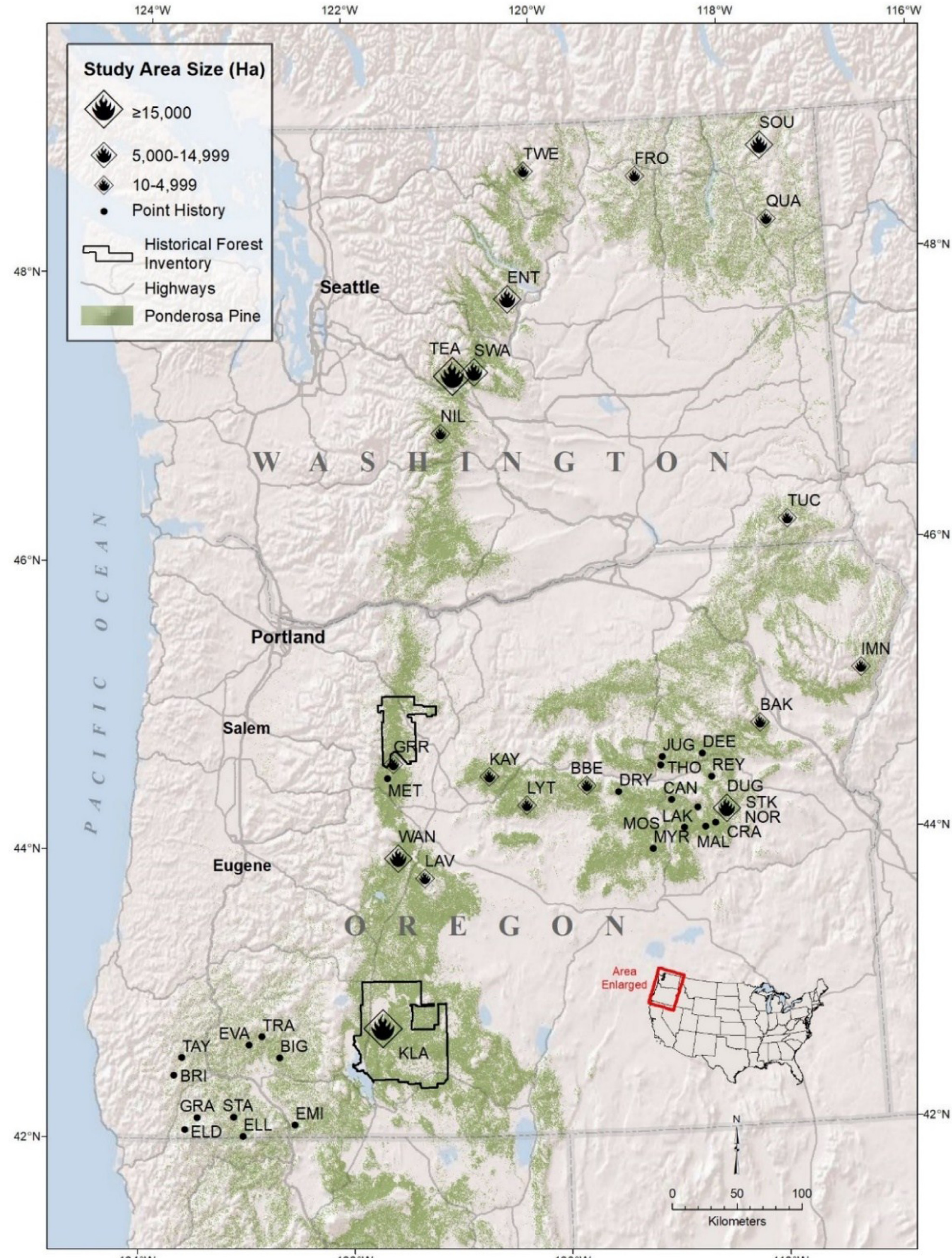

Fig. 1. Range of ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) in Oregon and Washington from the GNN forest structure model (Source: GNN maps for Washington, Oregon, and California, 2012, https://lemma.forestry.oregonstate.edu). Locations of multi-century reconstructions characterizing historical fire regimes are indicated by fire symbols scaled based on study extent. The former Klamath Indian Reservation and the Warm Springs Reservation where there are extensive systematic historical inventories of forest structure and composition are outlined in black.

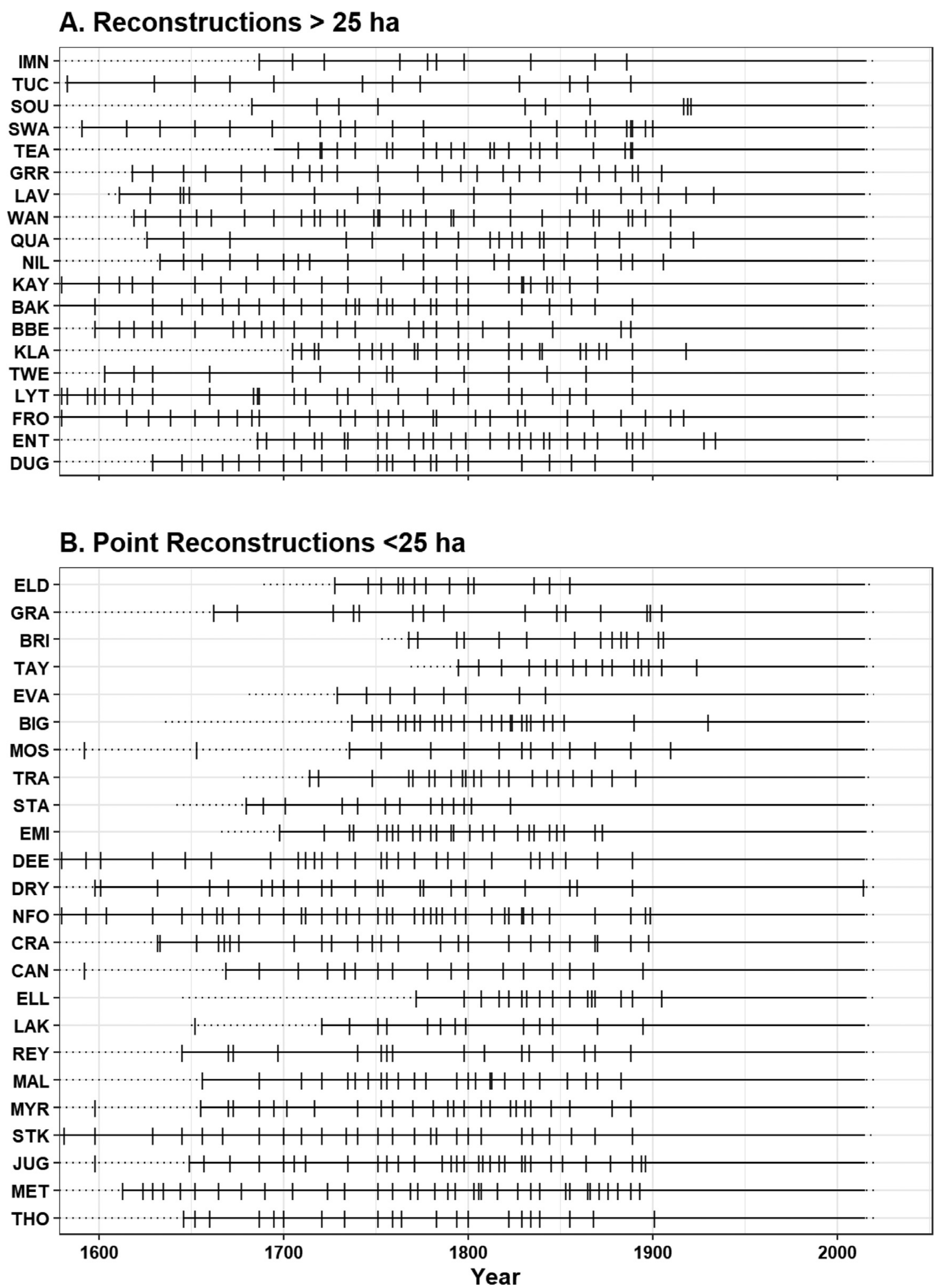

Fig. 2. Records of historical fires are depicted for reconstructions > 25 ha (A) and point reconstructions <25 ha (B). Acronyms correspond to study locations in Fig. 1, and studies are arranged from relatively hot-dry (bottom) to cool-moist (top). Each black horizontal line represents years with a fire record at each site, preceding dotted lines represent incomplete records due to insufficient sample size, and vertical tick marks indicate fires. Fires reported in (A) include only large fires that burned across a large portion of the reconstruction area. Fires reported in point reconstructions (B) include all fires recorded on at least two trees. Across these reconstructions, mean fire return intervals and fire regimes varied among and within reconstruction areas, but all would be classified as frequent fire regimes using Agee's (1993) classification. The onset of widespread fire exclusion clearly shows in the marked decrease in fires in the early 1900's. See online Appendix 1 for more detail on each reconstruction's methodology and results, and for filtering criteria for fires in Fig. 2.

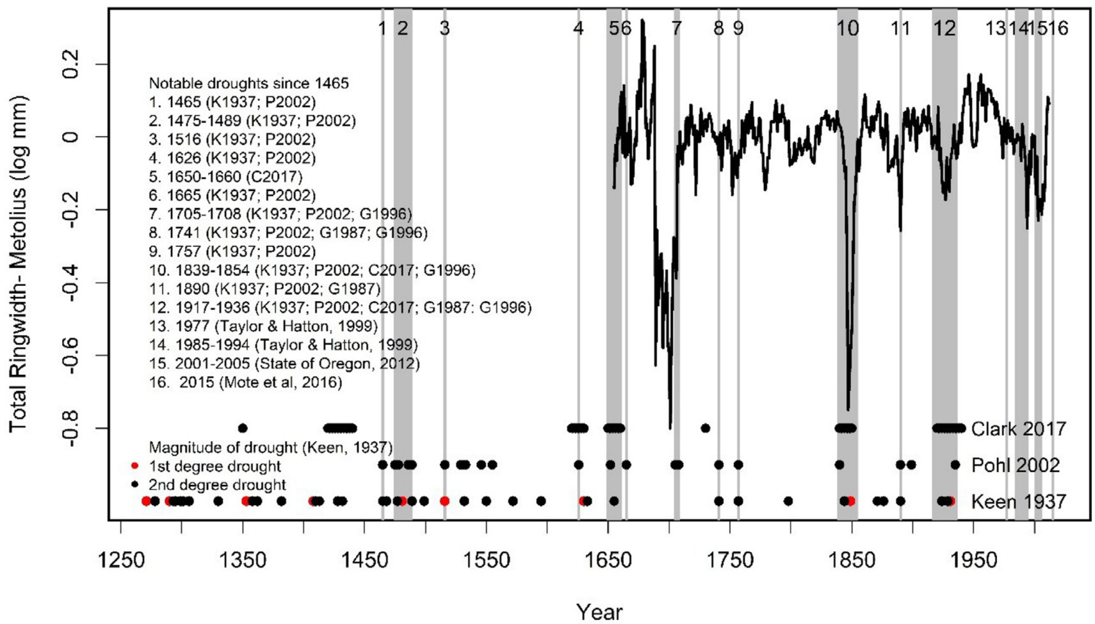

Fig. 3. History of single-year (gray lines) and prolonged droughts (gray bands) in eastern Oregon based on dendrochronological and instrumental records. The master chronology of ponderosa pine at the Metolius Research Natural Area in central Oregon (44º29'25",-121º37'54"; elevation 920 m) displays low growth anomalies associated with forest disturbances and regional droughts as well as a climate-induced negative growth trend in the most recent decades. The Metolius chronology had several extremely low growth anomalies in the decades of 1680 and 1840 which exceeded that of climate variability and were attributed to fire and Pandora moth events, respectively. Individual drought years based on three dendrochronological ponderosa pine studies are indicated at bottom of Figure.

forests transitioned to relatively cool-moist or cold forests in the east Cascades of Oregon (Hagmann et al., 2014, 2019), and in cool-moist forests with steep topography and barriers to fire spread in the Blue Mountains of Northeast Oregon and Washington ((Heyerdahl et al., 2001); see IMN and TUC in Fig. 1 and online Appendix 1B). Baker (Baker, 2012) and Odion et al. (Odion et al., 2014) challenged the paradigm that a frequent low-severity fire regime was predominant in ponderosa pine forests and contend that these forests were denser than historical and dendrochronological records report. However, the datasets they used to make these inferences contain no purposive data on historical forest conditions nor fire regimes, and their methods and inferences have been challenged in several published critiques (Fulé et al., 2014, Stevens et al., 2016, Levine et al., 2017, Levine et al., 2019). Hessburg et al. (Hessburg et al., 2007) has also been cited by Baker (Baker, 2012) as evidence of moderate and high-severity fire in ponderosa pine forests. However, Baker's (2012) evidence for high-severity fire erroneously includes grasslands and woodlands burned at high severity only in respect to their dominant vegetation (e.g., grasses and herbs), and moist or cold forest types outside our scope of inference (Spies et al., 2018).

The continental climate of the ponderosa pine region is semi-arid, controlled by a rain shadow effect from the Cascade Range to the west. Summer droughts occur every year as only ∼12% of precipitation falls during June-September based on 1981-2010 precipitation data (PRISM Climate Group, Oregon State University 2021). Decadal or long term variation in climate is driven by broad-scale maritime factors including the Pacific Decadal Oscillation (PDO) (Mantua et al., 1997), El Niño-Southern Oscillation (ENSO), and Pacific North American (PNA) pattern (Abatzoglou and Redmond, 2007; Abatzoglou et al., 2014).

The sensitivity of ponderosa pine to climate and its longevity have allow reconstructions of droughts and pluvial periods prior to 1900. Annual and sustained droughts are inferred from anomalously low growth in tree rings (Fig. 3). Instrumental and dendrochronological records show a history of severe single year droughts (e.g., 1581, 1730, 1777, 1889, 1977, and 2015) and prolonged periods of sustained drought during the decades of 1420, 1430, 1620, 1650, 1750, 1840, 1920, 1930, 1990, 2000, and 2010 (Keen, 1937; Pohl et al., 2002; Pohl et al., 2006; Clark et al., 2017; Dello and Dalton, 2015; Mote et al., 2016) (Fig. 3). The mean duration of these droughts is 13 years (range 3-28) and the mean interval between sustained droughts is 83 years (range 19-219; Keen, 1937). The period that includes the late 19th and early 20th century is often the reference for studies that document historical conditions in ponderosa pine forests, but this was one of the coolest and wettest periods in at least three centuries (Fye et al., 2003; Garfin and Hughes, 1996). This pluvial was followed by the dust bowl drought (1917–1936) that was the most severe and sustained drought in at least 690 years (Keen, 1937; Pohl et al., 2002; Clark et al., 2017; Lee et al., 2017). Dendrochronological and instrumental records indicate that the 1917–1936 drought (Fig. 3) has since been exceeded by the 1990-present drought.

Characteristics of predominant tree species

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), and white fir (*Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr) are common associates of ponderosa pine across much of our geographic scope of inference. Grand fir and white fir hybridize and share a similar ecological niche (Ott et al., 2015); hereafter, we refer to them collectively as "true firs" to differentiate them from Douglas-fir. Douglas-fir and true firs are rare or absent in relatively hot-dry sites but become common and then abundant as drought stress is ameliorated by lower temperatures and higher precipitation. This transition predominantly occurs with increasing elevation (Merschel et al., 2014), but local topography is also important as Douglas-fir and true firs are also more abundant in mesic aspects and in riparian areas particularly in landscapes with larger topographic features (Johnston et al., 2016; Merschel et al., 2014; Ohmann and Spies, 1998). Lodgepole pine (*Pinus contorta* Douglas ex Loudon) is a common species in cool-moist environments at high elevations across the region (Simpson, 2007), and also at low elevations in southern Oregon where climax lodgepole forests occupy cold-air drainage basins on coarse pumice soils (Geist and Cochran 1991). Minor species in dry environments include western juniper (*Juniperus occidentalis* Hook.), Oregon white oak (*Quercus garryana* Douglas ex Hook.), and incense-cedar (*Libocedrus decurrens* Torr.), while sugar pine (*Pinus lambertiana* Douglas), western white pine (*P. monticola* Douglas ex D. Don), and western larch (*Larix occidentalis* Nutt.) occur in relatively cool-moist environments.

Ponderosa pine, Douglas-fir, and true firs have contrasting life history strategies and adaptations that influence their abundance, longevity, reproduction, and resistance to disturbance (*sensu* (Loehle, 1987; Stevens et al., 2020)). We review these to help describe resistant historical dynamics and later contrast those with dynamics in the late 20th and early 21st century. Ponderosa pine owes its longevity to drought tolerance and early and continuous investment in defensive mechanisms including phenolic compounds and resins, deep roots, fire-resistant bark, and sparsely branched tree crowns. The trade-off is that ponderosa pine has low tolerance to shade and competition because of the high synthesis costs of defensive compounds (Gershenzon 1994) and structures (Bazaaz et al. 1987). True firs are more tolerant of shade and competition, and on productive sites, can establish, outcompete, and replace ponderosa pine in dense forests with high inter-tree competition. However, true firs are less resistant to decay organisms and the combined impacts of drought and BDAs; true firs are less fire resistant, especially at young ages (Burns and Honkala, 1990). Douglas-fir and true firs both increase on productive sites in the absence of frequent fire disturbance. However, Douglas-fir has intermediate drought resistance and biochemical resistance to injury and BDAs and is fire-resistant as a mature tree (Burns and Honkala, 1990). Ponderosa pine is more fire resistant than Douglas-fir at earlier ages due to more rapid juvenile height growth and development of thicker bark, but Douglas-fir is more resilient to severe fire as a younger tree because it produces seed cones at younger ages (Rodman et al., 2020).

Ponderosa pine and true firs have contrasting investments in biochemical defenses and how they respond to wounding and BDAs, which demonstrates the disturbance resistance strategy of ponderosa pine (Phillips and Croteau, 1999). Conifers have evolved oleoresin terpene exudates (resins hereafter) to defend against attacks from BDAs (Franceschi et al., 2005). Tree resins act both as lethal chemical agents and as physical deterrents by expelling attacking BDAs. Resins are stored in bark, stems, roots, branches, cones, and needles.

Ponderosa pine has a constitutive resin response in that a large amount of resin is always produced and stored. Consequently, ponderosa pine has resin available to defend against BDAs, even when stressed by drought. True fir has an induced response where a small amount of resin is stored, but relatively large amount of resins can be produced when trees are attacked. However, resin synthesis ceases when trees are stressed by drought (Zausen et al., 2005). This explains why true fir can expel and prevent reproduction of fir-engraver beetle (*Scolytus ventralis* Lec.) under normal climatic conditions, but successful mining, reproduction, and epidemic beetle outbreaks occur during drought (Cochran, 1998, Ferrell, 1978). Evidence of drought effects on Douglas-fir resin production and defenses to BDAs is surprisingly limited. When ponderosa pine is damaged by fire, wounds can be rapidly compartmentalized with resin that prevents the entry of decay fungi (Smith et al., 2016). Frequent low-severity fire can also stimulate increased resin production and modify resin chemistry which collectively increases resistance to subsequent beetle attacks and tree mortality (Hood and Sala, 2015, Hood et al., 2016).

There is substantial variation among ponderosa pine, Douglas-fir, and true fir in drought tolerance and the fundamental strategies for coping with drought. Using factors such as long-term minimum soil water potential and site characteristics where species typically exist, (Niinemets and Valladares, 2006) developed a global-scale quantitative vegetation dynamic model that ranks species from 1 to 5 in increasing drought tolerance. On that scale, mean (± standard error) drought tolerance for true fir, Douglas-fir and ponderosa pine were 2.33 (0.33), 2.62 (0.41) and 4.32 (0.32), respectively. Physiological characteristics that relate to drought tolerance include root architecture, the ability to store water in trunks, limbs, and roots, and vulnerability to hydraulic failure (i.e., the loss of the ability of a tree to transport water). True firs develop relatively shallow root systems, followed by Douglas-fir which have moderately deep tap roots. Ponderosa pine aggressively develops deep tap roots early as seedlings (Foiles, 1965; Hermann and Petersen, 1969; Santantonio and Hermann 1985). True firs are more susceptible to hydraulic failure due to water stress than Douglas-fir, but the wood of firs has a higher capacity for storing water (McCulloh et al., 2014). Ponderosa pine roots show greater resistance to hydraulic failure than Douglas-fir (Domec et al., 2009). However, structural characteristics of wood in young Douglas-fir are associated with relatively high resistance to hydraulic failure (Miller and Johnson, 2017), and resistance to hydraulic failure in trunks and branches of mature Douglas-fir is also high (Domec et al., 2009).

Biological disturbance agents

Drought is usually not the sole or ultimate cause of most tree mortality but interacts with BDAs to influence tree mortality (Kolb et al., 2016). BDAs, including bark beetles, defoliators, root diseases, and dwarf mistletoes (Table 1), can account for more combined tree mortality than fire in Oregon and Washington (Reilly and Spies, 2016). Bark beetles (Coleoptera: Curculionidae: Scolytinae) colonize susceptible hosts and breed under the bark. Many species of bark beetles are aided by a symbiotic relationship with fungi that they introduce to infested trees which may weaken tree defenses or aid in causing tree mortality. Defoliators are typically moth or butterfly caterpillars (Leptidoptera) or sawfly larvae (Hymenoptera) that consume foliage. Root diseases caused by fungi or related microorganisms that colonize root systems of trees resulting in growth decline, increased drought susceptibility, and mortality. Finally, dwarf mistletoes (Viscaceae: *Arceuthobium* species) are parasitic flowering plants that infect conifers, causing reduced growth, deformation, increased drought susceptibility, and mortality at high infestation levels in the conifers they parasitize. Dwarf mistletoe performs more poorly on low vigor than on high vigor trees (Bickford et al., 2005).

Drought can increase mortality due to BDAs or vice versa; thus, the combined effects are thought to result in increased overall tree mortality. Trees with pre-existing infections from pathogens like root disease and dwarf mistletoe are more susceptible to drought stress and bark beetle attack (Schowalter and Filip, 1993; Bell et al. 2020). Likewise, recently defoliated trees are more susceptible to mortality from drought or beetles. Additionally, drought may increase tree susceptibility to BDAs such as bark beetles and root diseases due to decreased investment in defense and reduced ability to respond to attacks. Although climate strongly interacts with defoliators, drought as a cause of outbreaks is equivocal (Kolb et al., 2016). Forest composition and structure drive outbreaks of western spruce budworm and Douglas-fir tussock moth, but drought has also been documented before outbreaks (Flower et al., 2014).

Dynamics and conditions in disturbance resistant forests

The crucial and often overlooked function of chronic disturbance from low-severity fire is that it truncates or prevents succession from early to late successional species, which develop dense forests with multilayered canopies (Johnston, 2017; Weaver, 1943). This results in open, relatively low-density forests characterized by fine-scale heterogeneity in tree structure. This means that small areas (< 1.0 ha) have a wide range of tree ages and sizes (Johnston, 2017; Merschel et al., 2014; Merschel et al., 2018; Munger, 1917; Perry et al., 2004; Youngblood et al., 2004; Heyerdahl et al. 2019), and tree density is variable at short distances (< 25 m) as trees are arranged in a patchy mosaic of individual trees, tree clumps, and treeless openings (Churchill et al.,

Table 1
Major biotic disturbance agents, historical and current roles, and changes in habitat suitability due densification and mesophication in Ponderosa pine forests of Oregon and Washington.

Major biotic disturbance agent	Historical Habitat Suitability and Role	Changes in Habitat Suitability with Densification and Mesophication and Current Role
Root Disease & Rusts (Basidiomycota, Ascomycota) Pine: Root diseases; Armillaria (*Armillaria* spp.), Heterobasidion, (*Heteribasidion irregulare*) and Black stain root diseases (*Leptographium wageneri var. ponderosum*). Rusts; western gall rust (*Endocronartium harknessii*) and commandra blister rust (*Cronartium comandrae*) Douglas-fir: Armillaria root disease (Armillaria spp.) True fir: Armillaria (*Armillaria* spp.) and Heterobasidion (*H. occidentale*) root diseases	Low density and heterogeneous structure limited root to root connectivity and the extent and severity of root disease impacts. Mortality and growth loss were limited to patches Uneven structured forests resulted in less uniform impacts from Ponderosa pine rusts.	Increased connectivity and spread via root contacts and graphs, and an increased abundance of grand fir and Douglas-fir host species has particularly increased impacts of Armillaria and Heterobasidion root diseases (Campbell and Leigel, 1996, Hessburg et al., 1994, Thies, 2001). Armillaria has emerged as a major mortality agent of grand fir and Douglas-fir and impacts are greatest in dense stands during droughts (Cochran, 1998). Vigor of ponderosa pine can be stressed by density and competition in young even-aged stands resulting from logging and fire suppression (Hessburg et al., 1994, Parks and Flannagen 2001). Western gall rust and commandra blister rust are considered a much greater threat to ponderosa pine health in young, dense, even structured stands than in older more open and discontinuous stands ((Hessburg et al., 1994; Parks and Flanagan, 2001).
Bark beetles (Coleoptera: Curculionidae) Pine: western pine beetle (*Dendroctonus brevicomis*), mountain pine beetle (*D. ponderosae*), and pine engraver (*Ips pini*) Douglas-fir: Douglas-fir beetle (*Dendroctonus pseudotsugae*) True fir: fir engraver (*Scolytus ventralis*)	Heterogeneous forest structure, age structure, and high tree vigor in low-density stands historically limited the severity of outbreaks that caused mortality and top-kill in trees stressed by drought or injured by fire.	Increased abundance of host species for fir engraver beetle and Douglas-fir beetle, which are most successful when attacking dense forests with low-vigor trees and uniform host ages (Hayes and Daterman, 2001, Hessburg et al., 1994, Kelsey, 2001, Wickman, 1992). Decreased production and effectiveness of resin (Hood et al., 2016) Bark beetles epidemics have increased in severity and extent especially during drought and following defoliator outbreaks.
Defoliators (Lepidoptera) Pine: pine butterfly (*Neophasia menapia*), and Pandora moth (*Coloradia pandora*) Douglas-fir and true fir: western spruce budworm (WSB) (*Choristoneura freemani*) and Douglas-fir tussock moth *Orygia pseudotsugata*) (DFTM)	Episodic defoliators, associated with top kill, reduced growth, and mortality. Impacts of WDB and DFTM were limited historically because fire reduced the amount of Douglas-fir and grand fir and canopy density and layering.	Increased host abundance and susceptibility for both western spruce budworm and Douglas-fir tussock moth and increased transmission through multilayered contagious canopies (Brookes et al., 1978; Brookes et al., 1987; Hessburg et al., 1994, Wickman, 1992; Torgensen, 2001). WSB has become a chronic defoliator in dense multilayered stands with periodic outbreaks that have greater frequency intensity, duration, and extent than they did historically (Hessburg et al., 1994; Campbell and Leigel, 1996; Torgensen, 2001; Flower et al., 2014; Swetnam et al., 1995)
Dwarf mistletoe (Viscaceae) Pine: western dwarf mistletoe (*Arceuthobium campylopodum*) Douglas-fir: Douglas-fir dwarf mistletoe (*A. douglasii*) True fir: fir dwarf mistletoe (eastern Cascade slope only) (*A. abietinum*)	Agents of growth loss, branch and top dieback, and mortality. Impacts limited due to fire and wide spacing of trees.	Fire suppression has likely increased the abundance of mistletoe infection because increased tree density and canopy layering facilitates mistletoe spread, and fire is the major mortality agent of mistletoe (Shaw and Agne, 2017).

2013; Larson and Churchill, 2012; Youngblood et al., 2004). Forest development or successional phases and the structures that identify them (snags and logs, early seral shrubs and grasses, seedlings, saplings, poles, and medium, large and old-growth trees) occur simultaneously at fine scales and sustain a broad range of ecological functions (Churchill et al., 2017, 2018). Areas with homogeneous structure in a clear successional phase commonly referred to as "stands" are rare, and changes in forest conditions are not generally driven by competition among trees. Although resistant ponderosa pine forests are heterogeneous at fine scales, a 'backbone' (*sensu* (Franklin et al., 2013)) of large and old fire- and drought-tolerant trees is essential structural component of disturbance resistant forests.

The absence of homogenous stands in frequently disturbed forests means they lack the continuity in fuels, uniformity in tree ages and sizes, contagion, and high tree competition that are conducive to large high-severity disturbances. An open mosaic of trees of different ages and sizes in an intimate mixture limits the spread of disturbances and the uniformity of tree susceptibility. When disturbances occur, they generally create small patches of mortality that reinforce resistant conditions by maintaining fine-scale heterogeneity and open forest conditions. For example, root rot (*Armillaria* spp, Table 1) has always been an important fungal pathogen of true fir but spread and mortality were historically limited by lack of root contagion (contacts and grafts) in heterogeneous forests. Similarly, WLFs historically killed individual or small groups of trees, but larger patches of severe fire were rare and small because of sparse and discontinuous fuels (Everett et al., 2000; Wright and Agee, 2004; Heyerdahl et al. 2019). With respect to forest structure, frequently disturbed ponderosa pine forests are *resistant* to disturbances at scales of ~1.0 ha to thousands of hectares. Resilience, the ability to recover after disturbance (Grimm and Wissel, 1997), operates at a finer scale because trees regenerate as clumps and individuals following disturbance from wildfire, drought, and BDAs. In this way, resistance developed through the process of frequent fire results in the stability of ponderosa pine forest conditions and ecosystem functions on individual hectares (Koontz et al., 2020) and broadly across entire landscapes (Hessburg et al., 2005).

Detailed systematic inventories of historical forest conditions are available for two extensive ponderosa pine forest landscapes in the central Oregon Pumice Plateau (Fig. 4, (Hagmann et al., 2013; Hagmann et al., 2019)), and on the east slope of the central Oregon Cascades (Fig. 5, (Hagmann et al., 2014)). Maps of historical forest structure and composition from these inventories help to illustrate resistant historical forest conditions across landscapes with developed and maintained by frequent low-severity fire. Historically, open-canopied forests and woodlands were ubiquitous except at the highest elevations. Ponderosa pine was the predominant species by basal area even at higher elevations in relatively productive mixed-conifer forests, and large trees with diameter at breast height (DBH) > 50 cm were found at moderate (11-25 trees/ha) to high (>26 trees/ha) densities across most of the landscape. The consistent presence of the structural framework of large trees across the landscape attests to the disturbance resistance of these landscapes given the history of fires, droughts, and BDAs.

Multiple lines of evidence demonstrate that resistant forest conditions resulting from frequent low-severity fire were historically pervasive in ponderosa pine forests. Although detailed records of historical conditions (Figs. 4 and 5) are not available for most ponderosa pine forests, dendrochronological reconstructions of fire regimes and forest development history document the extent of frequent low-severity fire and predominance of resistant structure and composition in the east Cascades of Washington (Everett et al., 2000; Everett et al., 2007; Wright and Agee, 2004), the east Cascades of Oregon (Hagmann et al., 2019; Heyerdahl et al., 2019; Merschel et al., 2014; Merschel et al., 2018; Perry et al., 2004; Youngblood et al., 2004), the central and southern Blue Mountains (Heyerdahl et al., 2001; Heyerdahl et al., 2019; Johnston, 2017), and in the Rogue Basin of southwestern Oregon (Metlen et al., 2018).

Changes in Forest Conditions and Dynamics in the 20th Century

Land use changes in the late 19th century including logging, grazing, and fire suppression, initiated changes in ponderosa pine forests that led to progressively decreasing resistance to drought, fire, and BDAs through the 20th and into the 21st century (Figs. 4 and 5; online Appendix 1). Extensive and heavy grazing removed bunchgrass that historically limited tree reproduction and density (Rummell, 1951; Kolb and Robberecht, 1996) and provided the surface fuels that carried frequent fires (Heyerdahl et al., 2001). In the absence of frequent fire, tree establishment and survival profoundly increased in the late 19th and early 20th centuries (Johnston, 2017; Merschel et al., 2014) resulting in denser, more homogeneous forests characterized by increased homogeneity in horizontal structure, increased canopy layering and connectivity, inter-tree competition, and canopy cover (Hessburg et al., 2005). This densification combined with widespread logging of large and old fire-resistant trees (Hessburg and Agee, 2003; Naficy et al., 2010) contributed to mesophication—a shift from drought- and fire-resistant shade-intolerant species to shade-tolerant species but not as resistant to drought and fire (*sensu* (Nowacki and Abrams, 2008)). Finally, aggressive fire suppression since ~1910 ensured densification and mesophication continued to the present.

The magnitude of densification and mesophication varies with productivity, but dramatic changes in forest conditions at large spatial scales are consistently documented in studies across the region (Figs. 4 and 5, online Appendix 1). For example, the proportion of fire-intolerant species by basal area increased from 17% to 91% in relatively moist environments that historically supported true fir in the southern Blue Mountains (Johnston, 2017). Large trees > 53 cm in diameter were historically found in nearly equal proportions to small trees, but today, small trees are up to 9 times more abundant than they were historically in the south-central Cascades (Hagmann et al., 2019). Because trees established over a short period of time following fire exclusion, age structure in contemporary forests is often homogeneous especially where old trees were selectively logged (Merschel et al., 2014). A common misconception is that densification and mesophication associated with land use changes have had less impacts in cool-moist environments. On the contrary, land use changes have had the greatest impacts in relatively cool-moist environments where higher moisture and productivity allows more abundant establishment and faster growth (Johnston, 2017; Merschel et al., 2014).

Profound landscape scale examples of densification, mesophication, and the loss of large fire-resistant trees and resistant forest conditions between the early and late 20th century are illustrated in Figs. 4 and 5. Densification dramatically increased canopy cover while mesophication increased the basal area of fire and drought sensitive species especially at higher elevations. The backbone of large old trees, predominantly ponderosa pine, was extensively compromised by logging. Since 1985, densification and mesophication have largely continued except where WLFs have occurred. WLF activity and impacts are disproportionate in different landscapes within the ponderosa pine region. WLFs have been relatively rare on the former Klamath Indian Reservation where gentle terrain aides fire suppression (Fig. 4), whereas much of the more topographically complex Warm Springs Indian Reservation (Fig. 5) has experienced WLF. Contemporary WLFs in these landscapes are abruptly reducing canopy cover and reversing densification, but are also drastically reducing remnant large tree populations that are no longer resistant to WLF because of densification and increased surface and canopy fuels. Large tree populations are recovering outside of WLFs but are increasingly composed of Douglas-fir and grand fir.

Contemporary forest conditions and dynamics

The ponderosa pine forests we see today are the cumulative result of tree establishment and growth versus mortality from drought, BDAs, WLF, and land management (e.g. timber harvesting, thinning,

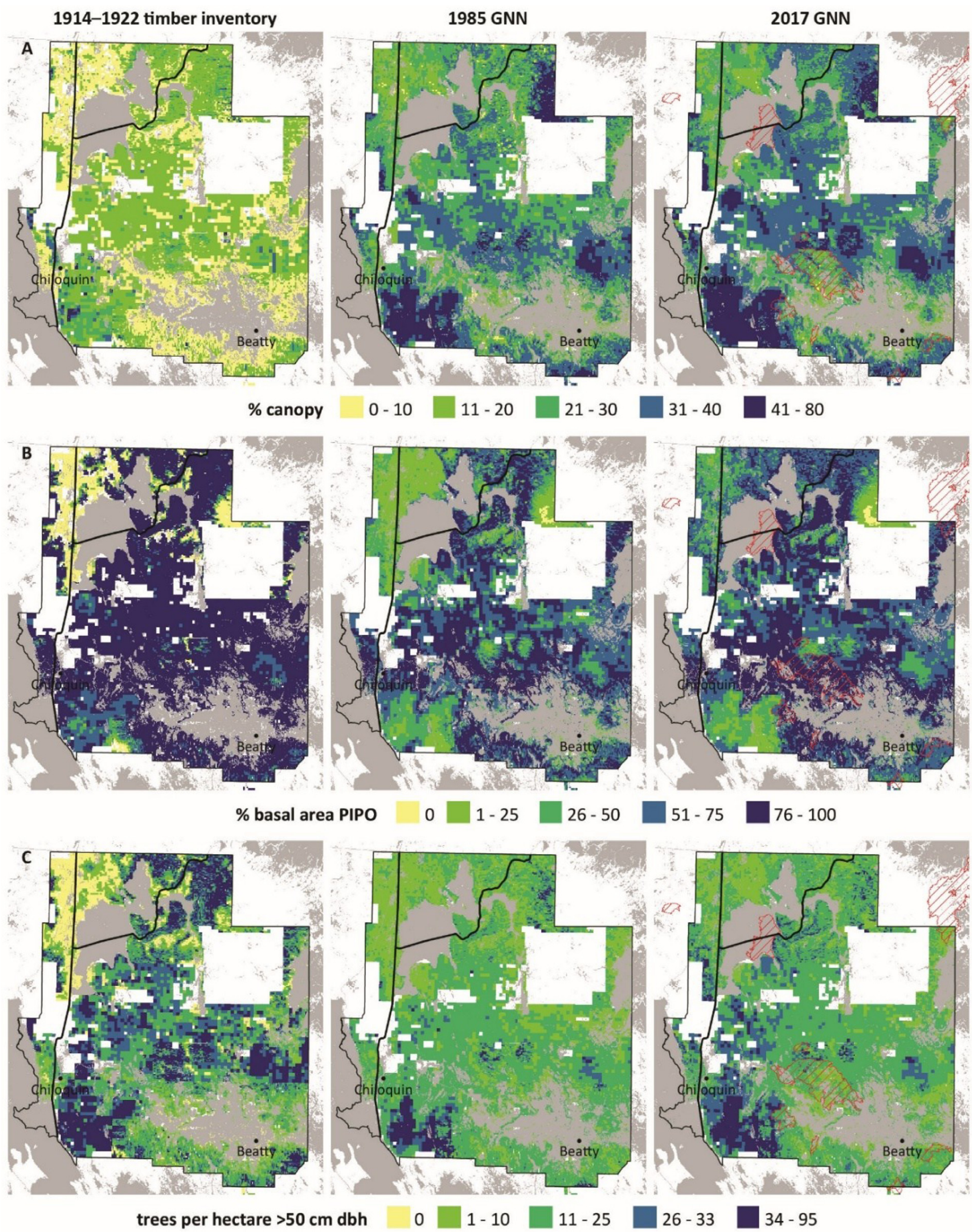

Fig. 4. Changes in forest structure and composition during fire exclusion over the last century across the 375,000 ha former Klamath Indian Reservation located in south central Oregon (Fig. 1). The first column maps conditions recorded in the 1914-1922 timber inventory (Hagmann et al., 2013), and second and third columns map conditions predicted by the GNN forest structure model in 1985 and 2017 ((Bell et al., 2021); https://lemma.forestry.oregonstate.edu). Perimeters for fires during 1984-2016 are mapped in red in the third column (MTBS Data Access: Burned Areas Boundaries Dataset, 2017 https://www.mtbs.gov/direct-download).

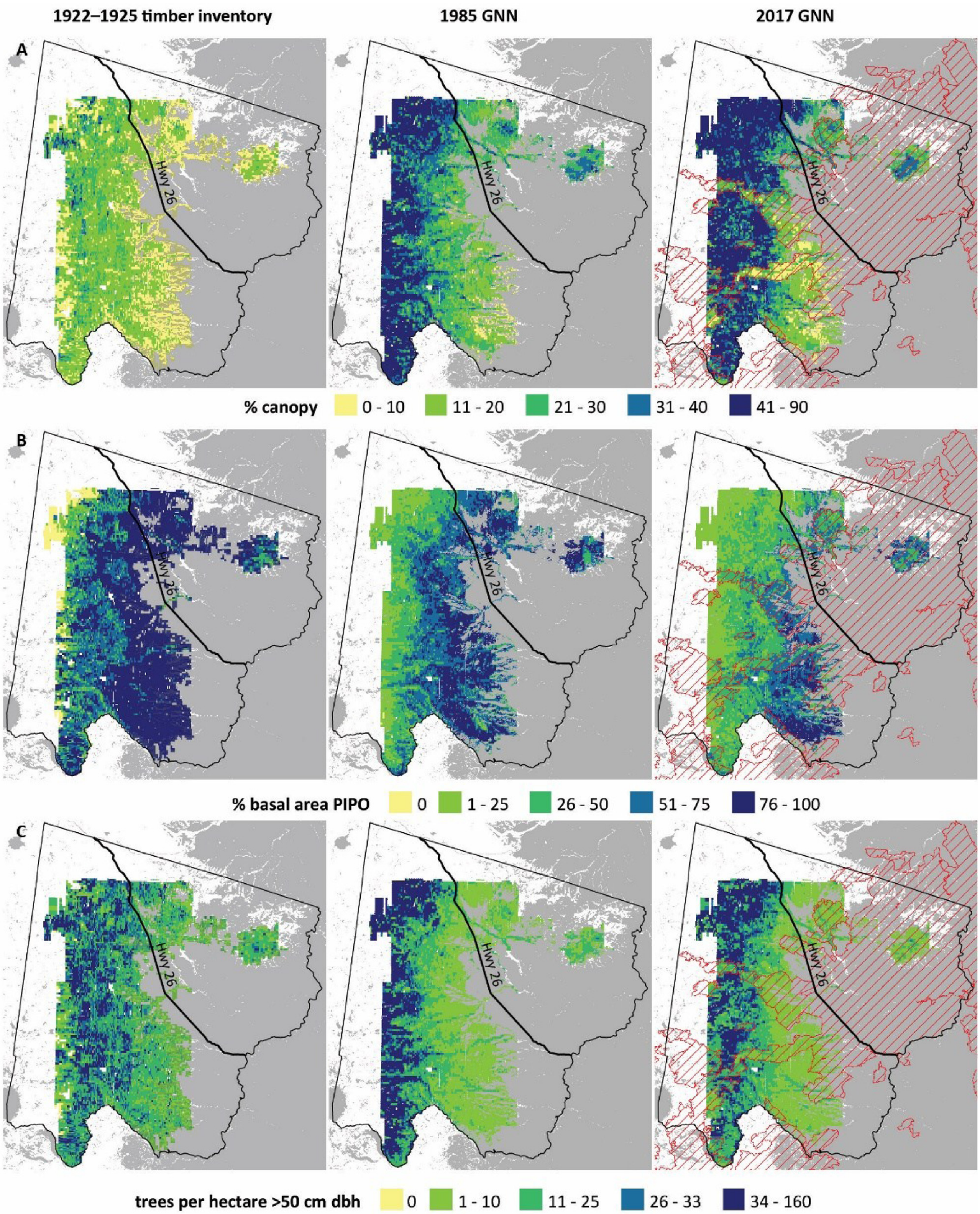

Fig. 5. Changes in forest structure and composition during fire exclusion and the contemporary period across the ~50,000 ha of forest on the Warm Springs Indian Reservation located in central Oregon (Fig. 1). The first column maps conditions recorded in a 1922-1925 timber inventory (Hagmann et al., 2014), and second and third columns map conditions predicted by the GNN forest structure model in 1985 and 2017 ((Bell et al., 2021); https://lemma.forestry.oregonstate.edu). Perimeters for fires during 1984-2016 are mapped in red in the third column (MTBS Data Access: Burned Areas Boundaries Dataset, 2017 https://www.mtbs.gov/direct-download).

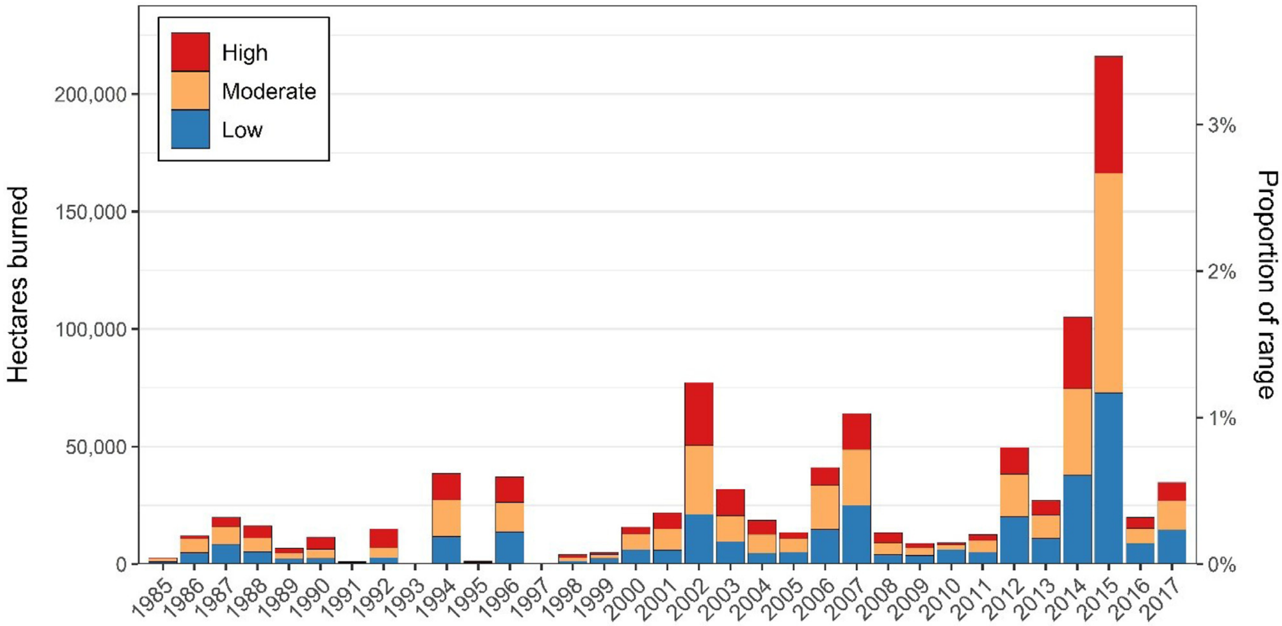

Fig. 6. WLF area by year and remotely sensed severity class during 1985-2017, and the proportion of ponderosa pine forests affected. Burn severity classes follow (Reilly et al., 2017) and are based on the percent basal area tree mortality: low (<25%), moderate (25 to 75%), and high (>75%). See online Appendix 2 for methodology.

prescribed fire). Disturbance agents, particularly fire and management, alter forest conditions within landscapes at relatively short temporal scales. At longer time scales, tree establishment and growth result in densification and mesophication at regional scales. Ultimately, changes over decades are driven by the balance of tree mortality versus regeneration and growth and can be tracked based on the abundance of various structural conditions over time.

WLFs create abrupt and dramatic changes, sometimes creating large patches of early seral vegetation characterized by abundant snags, and at other times simply reducing the density of small understory trees. Despite the obvious local effects of WLF, they currently affect a relatively small proportion of ponderosa pine forests in the Pacific Northwest ((Reilly et al., 2017); Fig. 6). Timber harvest, the primary agent of stand-replacing disturbance in the region besides fire, has declined on all lands since the 1980s (Adams and Latta, 2007). Although the frequency and severity of WLF is increasing in the PNW and broadly in western North America (Dennison et al., 2014), area burned is still far below historical rates. For example, there were 952,000 ha of WLF that burned 15% of the 6.2 million ha range of ponderosa pine in Oregon and Washington during 1985-2017 (Fig. 6). Approximately one-third of that WLF burned at high-severity, which is four to six times more high-severity fire than historical estimates (Hagmann et al., 2019; Haugo et al., 2019).

Although there is increased emphasis on the use of controlled WLF to reduce the risk of catastrophic fire, in 2018, 97% of 3,686 reported fires in Oregon and Washington were suppressed during initial attack, burning < 40 ha (forest) or 120 ha (grassland) ((Bureau of Land Management, US Forest Service, Region 6. 2019) Bureau of Land Management, USFS Region 6 2019). Compared to the area burned historically (Fig. 2), there is currently an enormous fire deficit especially for low-severity fire (Haugo et al., 2019; Reilly et al., 2017). Open forests with most of the basal area in large trees was historically the most common structural condition in ponderosa pine forests in historical inventories (Hagmann et al., 2013, 2014). Today, open structure with medium trees or open structure with large trees accounts for 23% and < 0.1% of forest area respectively in ponderosa pine forests across Oregon and Washington (Fig. 7).

In the absence of fire and widespread timber harvesting, densification and mesophication continues across ponderosa pine forests

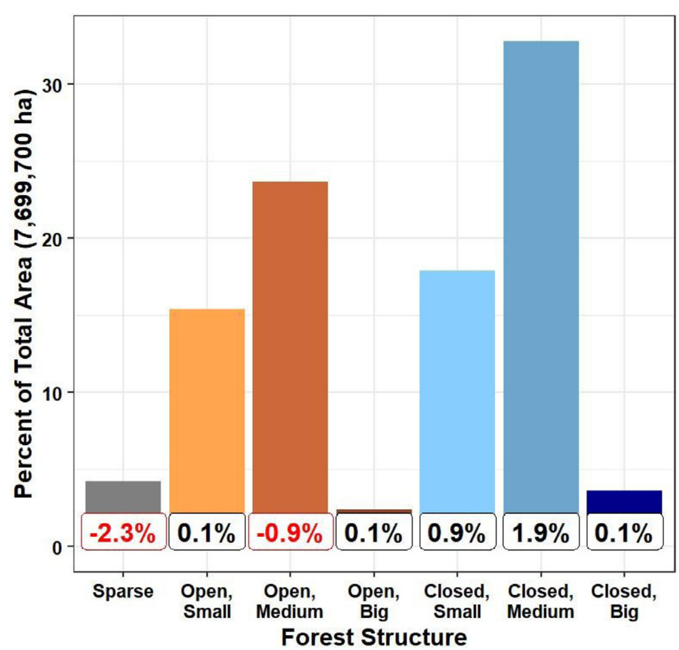

Fig. 7. Contemporary area of structure classes (Reilly et al., 2017) in ponderosa pine forests in 2017, and percent changes in area of each class from 1984-2017. Label color indicates either an increase (black) or decrease (red) for each structural class from 1984-2017. Structural classes describe canopy cover (Sparse < 10%, Open – 10-40%, Closed > 40%) and tree size represented by Quadratic Mean Diameter (QMD; Small - QMD < 25 cm, Medium QMD 25-50 cm, Large – QMD > 50cm. Despite increased WLF and emphasis on thinning and prescribed fire, dense closed forest structure is abundant and increasing.

(Figs. 4A, 5A and 7). Although this succession occurs slowly, it proceeds continuously across most of the region, and is currently the major driver of change. The cumulative effects of tree regeneration and growth versus mortality from disturbances in contemporary times are the loss of open-canopied resistant forest structure and composition, sparse woodlands, and non-forest cover. Currently, the forest area being managed to reduce density, restore large ponderosa pine trees, and reintroduce low-intensity, frequent fire is very small compared to that experiencing continued densification and succession.

Novel impacts of drought and biological disturbance agents

Anthropogenic climate change is exacerbating drought in the region (Mote et al., 2019; Williams et al., 2020). Dendroclimatic and instrumental records demonstrate that sustained droughts occurred approximately once per century until the mid-1980s. Since 1985, several sustained droughts occurred with each drought surpassing preceding droughts in intensity. The 1917-1936 drought in Oregon (Keen, 1937) has since been surpassed by a series of notable single and multi-year droughts from 1990 to 2018 as indicated by a declining growth rate of ponderosa pine (Fig. 3). Forests throughout the state suffered from a lack of moisture during the 1985-1994 drought, notably in 1992 when a drought emergency was declared for all of Oregon. The 2001-2002 drought was the third most intense drought in Oregon history, surpassed by the brief but intense droughts during 1977 and 2015. The snow drought of 2015 in Oregon and Washington was the most severe on record by far (Dello and Dalton, 2015; Mote et al., 2016; Mote et al., 2019). Sustained drought intensity during 2000-2004 was unprecedented in the past 800 years (Schwalm et al., 2012), but this was quickly eclipsed by drought during 2012-2018 (Williams et al., 2020). Overall drought conditions occurred in 15 of 18 years during 2000-2017 when temperatures were increasing at an accelerated rate of 0.3ºC/decade (Abatzoglou et al., 2014). The recent prolonged drought in the PNW was felt across the entire western U.S. and the 2000-2018 drought in southwestern North America was the driest 19-year period since the late 1500s (Williams et al., 2020). Recent drought in western North America was partially a product of natural variability, but its concurrence with anthropogenic warming resulted in intensity and duration on par with the most extreme drought events since 800 CE (Williams et al., 2020). Drought likely represents the new normal as the region is projected to continue to warm in the 21st century (Fourth National Climate Assessment, 2019).

Severe water stress related to more frequent and severe drought can lead to widespread tree mortality (Anderegg et al., 2019) and increased vulnerability to BDAs (Cochran, 1998; Kolb et al., 2016; Stephenson et al., 2019). The frequency and magnitude of drought-related tree mortality events have increased in recent years, particularly in the western United States (Buotte et al., 2019). Progressively increasing temperatures (Abatzoglou et al., 2014) and increasing drought severity (Dello and Dalton, 2015; Mote et al., 2019; Williams et al., 2020) combined with contemporary forest conditions suggest that the recent tree mortality in fire-excluded dry conifer forests in California may forecast mortality in ponderosa pine forests of Oregon and Washington. In California, at least 147 million trees died as a result of the record setting 2012-2016 drought with both ponderosa pine and true firs experiencing high levels of mortality, the majority of which involved BDAs (USDA 2019). Mortality reduced tree density but did not restore historical structure and composition because mortality for ponderosa was highest (50%) for large (> 50 cm DBH) trees that are already depauperate (Stephenson et al., 2019).

Forest densification and mesophication in Oregon and Washington have profoundly changed habitat suitability for BDAs and the susceptibility of host species (Table 1; (Hayes and Daterman, 2001; Hessburg et al., 1994; Oester et al., 2018; Wickman, 1992)). Coupled with a warming climate, this suggests drought and BDAs may be equal or more important drivers of change than WLF in the 21st century. Unlike WLF where ignitions can be broadly suppressed, disturbance from drought and BDAs cannot be mitigated in practical ways due to the extensive area where forest conditions are susceptible, and BDAs occur.

History also demonstrates the potential for epidemic mortality from interacting BDAs and drought both before and after densification and mesophication. For example at the onset of the 1917-1936 drought in the East Cascades of Oregon, five years of Pandora moth defoliation resulted in minimal tree mortality, but this was followed by epidemic levels of mountain pine and western pine beetle-induced tree mortality in defoliated trees (Cochran and Barrett, 1999; Weaver 2014). Following logging and fire exclusion true firs grew rapidly for 60 years on four research sites that received less than 13 cm of precipitation annually (Cochran, 1998). These sites were experimentally thinned to remove suppressed trees, reduce mortality, and monitor growth. However, the study abruptly collapsed because of heavy mortality from root rot (*Armillaria ostoyea*), western spruce budworm (*Choristoneura occidentalis*) and fir engraver beetles (*Scolytus venrtalis*) that occurred during the 1985-1995 drought.

Expansion of the WUI

WLF risk and costs have increased in recent decades not only because of a century of fire suppression and climate warming, but also because more people are choosing to live in fire-prone ponderosa pine forests. The WiIdland-Urban Interface (WUI), where communities are near wild lands, is the fastest growing land use type in the conterminous U.S. From 1990 to 2010 new houses in the WUI increased by 41%, from 30.8 to 43.4 million and land area increased 33%, from 581,000 to 770,000 km^2 (Radeloff et al., 2018). In the ponderosa pine forests of Oregon and Washington, the land area of WUI nearly doubled during the same period and now occupies 8.1% of the range of ponderosa pine (Fig. 8). In Oregon and Washington, most of the WUI in ponderosa pine forests is concentrated around three rapidly growing urban areas that are regularly impacted by WLFs (Fig. 9). However, within the WUI areas the risk from WLF is not uniform. A recent report (Bureau of Land Management 2018) found that in the communities most at risk from WLF in Oregon and Washington, a relatively small proportion of the houses (15%) bore most of the risk (76%). Further, the report found 74% of fires were caused by humans and fires that threated homes tended to start near them, and not on federally owned lands.

Challenges to living in Ponderosa pine forests in the 21st century

From an ecological perspective, a goal of re-establishing low-severity surface fire in ponderosa pine forest ecosystems is fundamental to successful fire management (Allen et al., 2002). In Oregon and Washington, studies demonstrate that fire management based on historical landscape conditions where fires are allowed to burn can result, over time, in landscapes much less susceptible to catastrophic fires (Prichard et al., 2017). This promotes key ecological benefits to wildlife and humans (Pausas and Keeley, 2019) including reduced public exposure to smoke (Schweizer et al., 2019) and improved water quality (Chow et al., 2018). Frequent, low-severity surface fire can not only reduce the severity of later fires, it can increase resistance to drought and BDAs exacerbated by climate change (Spies et al., 2019; Vose et al., 2019; Westlind and Kerns 2020), while reducing the costs associated with fire suppression (Ingalsbee and Urooj, 2015).

However, the ecological reality is that the extent of historically departed forest conditions that are susceptible to uncharacteristically high-severity fire and tree mortality from the combination of drought and BDAs is currently far greater than the acreage of resistant forest conditions. More than 55% or 4.2 million ha of ponderosa pine forests have dense and closed canopy structure (Fig. 7) and that area is increasing. Managed WLF and prescribed fire is not being adopted into management practices at a scale necessary to reduce the fire deficit in the western U.S. and reduce the potential for more WLF disasters; the area burned by prescribed fire has actually decreased in the Pacific Northwest from 1998-2018 (Kolden, 2019). Ongoing fire suppression outpaces restoration of resistant conditions, while densification and mesophication are increasing across the range of ponderosa pine.

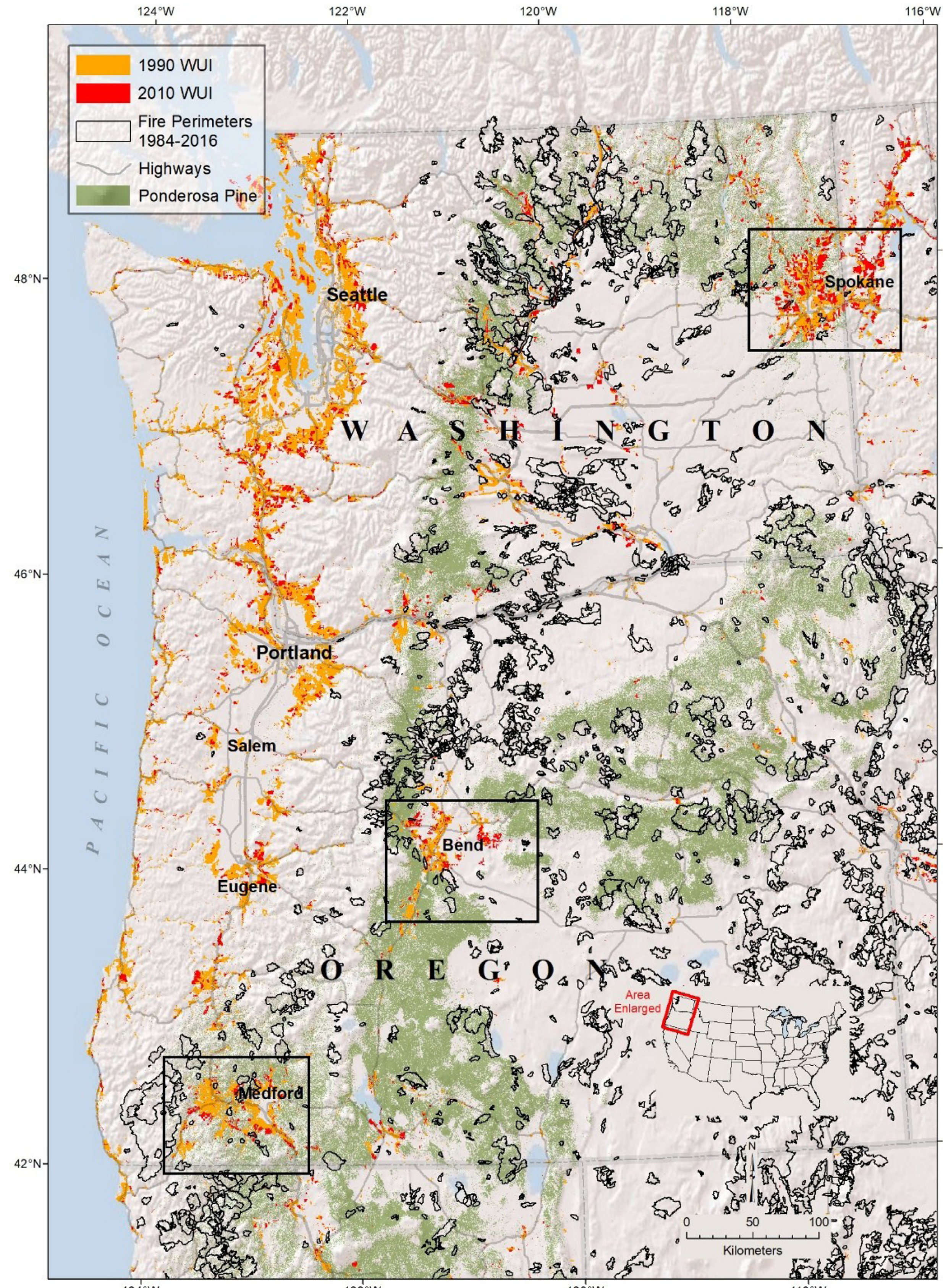

Fig. 8. Distribution and expansion of the WUI (data from (Radeloff et al., 2017)) in Oregon and Washington. The distribution of ponderosa pine and recent fire perimeters highlight how recent fire activity in dry fire prone forest interacts with the WUI that expanded from 18,859 km^2 (4.6% of total land area) to 24,003 km^2 (6.0% of total land area) from 1990 to 2010. The proportion for WUI in ponderosa pine forests rose from 6.3% (1,192 km^2) in 1990 to 8.1% (1,933 km^2) in 2010.

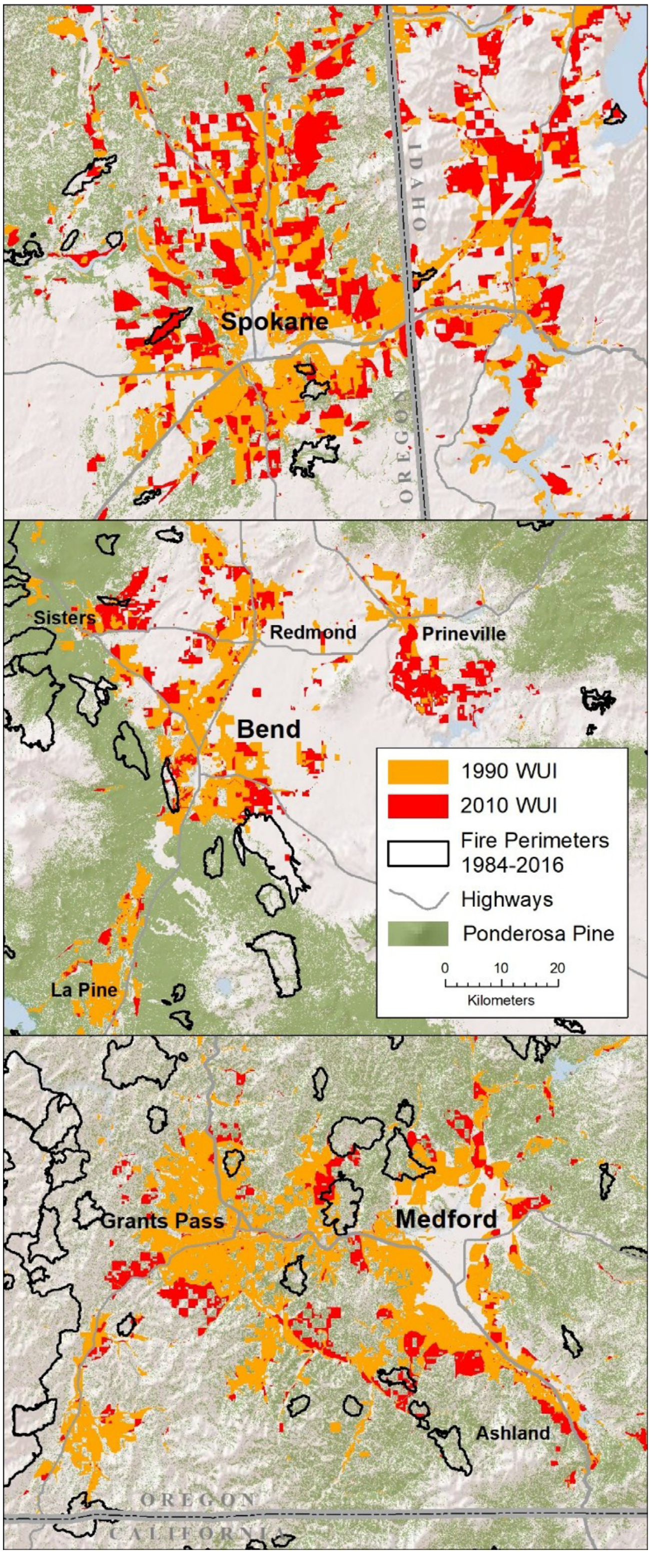

Fig. 9. Focal areas from Fig. 8 show that expansion of the WUI in ponderosa pine forests is concentrated in three expanding metropolitan areas that have been frequently impacted by WLFs from 1984-2016 (data from (Radeloff et al., 2017)).

Modeling of future WLFs and management on forest conditions demonstrate that even if the area treated by prescribed fire and mechanical treatments tripled over the next 50 years, we would likely see modest reductions in severe WLF and impacts on ecosystem services and humans (Barros et al., 2017). Similarly, if one large (e.g. 5000- 20,000 ha) WLF was allowed to burn to restore forest structure every year for the next 50 years (23% increase in area burned) this would result in a small reduction in the size of high-severity wildfires (Barros et al., 2018). This is because both high-severity wildfires and restored resistant forest conditions are relatively rare in either scenario and have a low probability of overlapping. Ultimately current forest conditions (Fig. 7) and contemporary fire-climate relationships suggest there will be an increase in large WLFs (Westerling, 2016) and high-severity fire effects (Parks and Abatzoglou 2020) that will impact ecosystem services and the WUI. Even so, it's important to keep in mind that most areas will not be directly affected by fire, but nearly all will be affected by drought, BDAs, and smoke from regional WLF.

The costs of suppressing WLF over the vast area of ponderosa pine forests are increasingly prohibitive, largely because the expanding WUI demands more costly fire protection (Ingalsbee and Urooj, 2015). At the same time, barriers to restoring resistant forest structure and maintaining it with controlled fire are greatest on public lands in and adjacent to the WUI (Coughlan et al., 2019). Fuel treatments and prescribed fire in proximity to the WUI are vulnerable to conflicts with stakeholders due to their high visibility, smoke, and values people attach to forests (Brenkert-Smith et al., 2020). Across the west, there is broad public support for managing fuels to reduce the risk of ecologically destructive WLF, damage to property, and health impacts (McCaffrey and Olsen, 2012). However, treatments are often delayed, reduced in area, or abandoned when local stakeholders view the precise details of proposed treatments. These details include the treament types, detail (e.g. prescribed fire, WLF use, or thinning), their location and proximity to private property, and how they will affect the aesthetics of treated areas (Brenkert-Smith et al., 2020).

Public trust in management agencies is critical to developing treatment plans with public support. This trust is built by representing the range of stakeholder perspectives throughout the development of proposed treatments in a forum that allows public input and an equitable understanding of the science and rationale behind proposed actions (Davis et al., 2017). Forest collaboratives can connect stakeholders, managers, and scientists to develop alternative management scenarios (Johnston et al., 2021b) and have proven to be effective at increasing the amount and quality of restoration because they bring together a diversity of stakeholder values and scientific information that help identify restoration priorities that benefit several social and ecological objectives (Davis et al., 2019).

Strategies for living with fire and their trade-offs

Forest policy and management practices are slowly changing from predominantly fire suppression to managing fire and associated risks to communities (Ingalsbee and Urooj, 2015; Thompson et al., 2018). This requires using a complementary set of restoration approaches that restores disturbance resistance including wildland fire use, prescribed fire, and mechanical fuels treatments which include tree thinning and mowing or mastication of surface fuels. Key to living with fire in ponderosa pine forests is an all-lands and all ownerships approach to forest management planning that helps determine where prescribed fire and mechanical treatments are appropriate and could be prioritized, and where fires can safely be allowed to burn (Dunn et al., 2020). The what, where, when, and how of forest restoration requires careful planning (Franklin and Agee, 2003). Taking the costs, location, and frequency of each approach in relation to co-occurring infrastructure as well as highly valued natural resources and forest conditions can help prioritization (Ager et al., 2007; Barros et al., 2017). For example, source watersheds for communities are a high priority for fire mitigation because WLF can severely degrade water quality for at least several months (Hallema et al., 2018).

If the goal of living with fire is to be realized, fire needs to be used in a comprehensive, strategic way. Directing some WLFs rather than suppressing them can control costs while protecting communities and restoring dry forest ecosystems (Ingalsbee and Urooj, 2015). In Oregon and Washington, the mean annual number of fires during 2008-18 was 3,678; lightning caused 57% of fires on average (National Interagency Fire Center (NIFC) 2019). Therefore, lightning fires represent ∼ 2100 annual potential opportunities to reintroduce WLF for resource benefits. One option is to allow more of these to burn and to be managed with strategies other than aggressive, full suppression. Pre-incident planning for large WLFs is the first step to increase WLF use on the landscape (Dunn et al., 2017). Ranking areas within the landscape based on high to low risk of loss from WLF, and prioritizing where and how fuels are treated to reduce WLF risk allows land managers to distinguish areas that must be protected from fire using mechanical fuel treatments, from those that can be treated with prescribed fire, and those that can make use of directed WLF (Thompson et al. 2016). Geospatial decision-support tools can help evaluate the likelihood that unplanned ignitions could be hazardous (Barnett et al., 2016). Identifying strategic response zones can also guide the initial response to WLF ignition (Thompson et al. 2016; Dunn et al., 2017). Collectively, strategic response zones represent a gradient from complete fire suppression to monitoring fires while allowing them to burn, e.g. the protect-restore-maintain continuum (Thompson et al. 2016).

Despite these advanced technologies and analytics, implementing multiple risk-based strategies may depend on adopting an alternative fire management approach: adaptive co-management of wildfire risk (Dunn et al., 2020). This approach relies on continual collaborative planning using common information and shared expertise and decision-making by fire managers from all jurisdictional levels and ownerships within the spatial extent of a fire-prone landscape. This approach has proven especially useful for fire management in multi-jurisdictional landscapes, e.g. dry-forest communities, because across ownerships/jurisdictions the relationship of highly valued resources, fire risk, and control boundaries can be analyzed cooperatively, and fire responses pre-planned and cross-boundary mitigations identified and prioritized accordingly. Although many future WLFs will require a full suppression response, there will likely be hundreds of low-risk opportunities each year for using managed fire to increase ecological benefits while lowering fire deficits and future suppression costs. Seizing upon these opportunities will potentially be more viable in the context of adaptive co-management of wildfire (Dunn et al., 2020).

Given the extent of hazardous forest conditions and associated risks to public safety and ecosystem health, WLF use can be most effective when be accompanied by both prescribed fire and mechanical treatments that reduce fuel loads (Ager et al., 2020). WLFs will be perpetually suppressed unless there are treated boundary areas that allow fire to be contained or directed while ensuring firefighter safety (Dunn et al., 2020). Furthermore, fire as a restoration tool is simply not practical in many areas in and adjacent to the WUI given safety risks, potential property damage, and smoke impacts (North et al., 2015). Ecologically, many contemporary WLFs are not restoring historical conditions because they occur during extreme fire weather (Calkin et al., 2005), where fuels support high-severity fire. This has resulted in large patches of stand-replacing fire with no known historical analogue (Reilly et al., 2017).

Large stand-replacing patches of WLF potentially involve a type conversion from a forest to a non-forest state. Invasion on non-native plants, particularly annual grasses, may accelerate such changes (Kerns et al., 2020). However, existing research from Oregon and Washington suggests that post-fire regeneration failure due to climate or seed dispersal is limited to warm, dry low elevation sites (Dodson and Root, 2013) while relatively more productive ponderosa pine forests have generally been resilient (Downing et al., 2019). When and where severe WLF results in type conversion, managers may consider accepting and potentially directing postfire outcomes to align with human values (Coop et al., 2020).

The cost of mechanical treatments is usually higher than prescribed fire treatments, but similar if merchantable wood is available to partially or completely offset costs (Nicholls et al., 2018). Typically, mechanical treatments are emphasized in the WUI, while both mechanical and prescribed fire treatments, alone or in combination, are used in adjacent forest lands from which WLF might spread into the WUI (Barros et al., 2019). Biomass utilization may be a key component of the economic feasibility of fuel treatments, not only to offset treatment costs but also to stimulate economic activity (Davis et al., 2010). Still, there are grand challenges ahead to sustain long-term programs to reduce fire severity and promote resistant forest structure; particularly, the need for innovative, non-timber orientated, silvicultural prescriptions (e.g., (Larson and Churchill, 2012)) and the subsequent increased use of non-lumber orientated wood products (Nicholls et al., 2018). Charnley et al. (Charnley et al., 2017) estimate that federally owned ponderosa pine forests managed with proposed forest thinning, prescribed fire, managed WLF, and fire suppression where necessary could reduce the land area susceptible to high-severity fire from 62% to 37% over the next five decades in south central Oregon. In comparison, ~75% of land area would remain susceptible to high-severity fire on land owned by private corporations that prioritize fire suppression and uniform forest structure in order to maximize revenue and produce a sustainable flow of wood products.

Preparing people and property for smoke and fire

Protecting human health from prescribed fire and WLF smoke is a challenge to local, state, and federal agencies. Ultimately, smoke from either prescribed, managed, or uncontrolled WLF will inevitably affect people's lives far into the future. A recent study found that U.S. adults are willing to pay an average of $373 to avoid one day of WLF smoke over their county of residence within a six month period, and residents of rural areas are willing to pay $130 more than urban residents to avoid one smoke day (Jones, 2017).

It is well known that WLF smoke contains numerous hazardous air pollutants and many studies have documented negative human health effects, but more research is needed to resolve which components in smoke, and which sources of smoke are most hazardous. There remains an outstanding need to better define the risk for adverse health outcomes, identify the sensitive populations, and assess the influence of social factors on the relationship between exposure and health outcomes (Cascio, 2018; Reid et al., 2016). From a fire management perspective, questions remain regarding forecasting air quality, the effects of prescribed burns compared to uncontrolled fire, length of exposure on the health burden of smoke, as well as the effectiveness of personal actions, such as using masks or filters, in reducing smoke exposures (Jaffe et al., 2020). Community planners are faced with questions about designing air filtration systems and providing safe places for vulnerable populations (Cascio, 2018).

Decision tools are also needed to help individuals and communities live with fire (Long et al., 2017). The U.S. Environmental Protection Agency (EPA), the U.S. Forest Service (USFS) and other federal, state and community agencies and organizations are working together to identify ways in which the public can prepare to reduce their health risk before a WLF. Public health officials and others can use the resources in the Environmental Protection Agency's Smoke Ready Toolbox to help educate people about the risks of smoke exposure and actions they can take to protect their health (https://www.epa.gov/air-research/smoke-ready-toolbox-wildfires). The 2019 document Wildfire Smoke: A Guide for Public Health Officials (http://www.epa.gov/airnow/wildfire-smoke/wildfire-smoke-guide-revised-2019.pdf) is designed to help local public health officials prepare for smoke events, to take measures to protect the public when smoke is present and communicate with the public about WLF smoke and health. The National Fire Protection Association sponsors a program, *Firewise USA,* that teaches people how to adapt to living with WLF and encourages neighbors to work together and take action to prevent losses (https://www.nfpa.org/Public-Education/Fire-causes-and-risks/Wildfire/Firewise-USA). The Community Health Vulnerability Index (CHVI) was developed based on socioeconomic and health variables at the county level to identify the most vulnerable counties in the U.S. to air pollution and wildland fire smoke (Rappold et al., 2017). Continuously updated websites provide information on when and where prescribed burns are planned, which should help those who are particularly sensitive to smoke avoid it and help people understand why prescribed burning is important to healthy forests and public safety while maintaining healthy air quality (see http://www.centraloregonfire.org/).

Re-introducing low-severity fire and disturbance resistance to ponderosa pine forests will increase opportunities to safely manage fire and reduce smoke emissions and property damage, but it cannot eliminate property risk in the WUI. Unfortunately, landowner expectations and responsibilities for fuel treatments and fire protection measures on surrounding public lands are often counter to living with fire. For example, the flammability of homes is primarily determined by conditions on private property even if the surrounded wildland has been thinned or treated with prescribed fire leaving the primary responsibility for preventing home destruction with homeowners rather than public land managers (Calkin et al. 2014). It follows that more of the cost of WLF protection could also be shared by those who build homes and the local governments who issue building permits (Ingalsbee and Urooj, 2015). Along with land managers, communities the responsibility of planning for fire and providing the means to live with fire. Community planning in the WUl could benefit from including socio-health aspects: dangers, sheltering, community actions [e.g., canceling sporting events]. Tools are available to aid communities in developing flexible, scenario-based approaches for addressing WLF adaptation applicable across a variety of situations (Paveglio et al., 2018).

Conclusions

From an ecological perspective, building disturbance resistance through restoration of frequent low-severity fire is an essential goal to sustain ponderosa pine forest ecosystems. However, extensive densification and mesophication of PNW dry ecosystems due to land management practices in the 20th century, followed by an increase in frequency of high-severity WLF, drought, and BDAs, and a rapid expansion of the WUI pose serious ecological and socioeconomic challenges to living with disturbances in the 21st century.

We expect a continued increase in large and uncharacteristically severe WLFs along with increased tree mortality from drought and BDAs under a warming climate in the 21st century. Resource managers will likely be unable to affect the increasing trend in WLF events for several decades, as this trend is influenced by climate and the broad susceptibility of contemporary forests to severe WLF. Ultimately, people will have to adapt to living with more fire; including low-intensity prescribed and managed fire, and episodic mixed-severity fires that can have substantial and lasting impacts on ecosystem services, human health, and property. For society, living with fire could be aided by a shift in responsibility towards homeowners for prevention of property damage and respiratory distress and illnesses. Protecting ponderosa pine ecosystems will require a shift in policy towards less aggressive fire suppression, and an increase in prescribed fire and fuel treatments where reintroduction of fire is not feasible. By facilitating changes in forests conditions that increase disturbance resistance and align with a warmer and drier climate, we can gradually reduce the socioecological impacts of disturbances in ponderosa pine forests in the 21st century.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. This paper has been subjected to review by the Center for Public Health and Environmental Assessment, Pacific Ecological Systems Division and approved for publication. Approval does not signify that the contents reflect the views of the Agency, nor does mention of trade names or commercial products constitute endorsement or recommendation for use.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2021.100074.

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