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The complexity of biological disturbance agents, fuels heterogeneity, and fire in coniferous forests of the western United States

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ABSTRACT

Forest biological disturbance agents (BDAs) are insects, pathogens, and parasitic plants that affect tree decline, mortality, and forest ecosystems processes. BDAs are commonly thought to increase the likelihood and severity of fire by converting live standing trees to more flammable, dead and downed fuel. However, recent research indicates that BDAs do not necessarily increase, and can reduce, the likelihood or severity of fire. This has led to confusion regarding the role of BDAs in influencing fuels and fire in fire-prone western United States forests. Here, we review the existing literature on BDAs and their effects on fuels and fire in the western US and develop a conceptual framework to better understand the complex relationships between BDAs, fuels and fire. We ask: 1) What are the major BDA groups in western US forests that affect fuels? and 2) How do BDA-affected fuels influence fire risk and outcomes? The conceptual framework is rooted in the spatiotemporal aspects of BDA life histories, which drive forest impacts, fuel characteristics and if ignited, fire outcomes. Life histories vary among BDAs from episodic, landscape-scale outbreaks (bark beetles, defoliators), to chronic, localized disturbance effects (dwarf mistletoes, root rots). Generally, BDAs convert aboveground live biomass to dead biomass, decreasing canopy fuels and increasing surface fuels. However, the rate of conversion varies with time-since-event and among BDAs and forest types, resulting in a wide range of effects on the amount of dead fuels at any given time and place, which interacts with the structure and composition of the stand before and subsequent to BDA events. A major influence on fuels may be that BDAs have emerged as dominant agents of forest heterogeneity creation. Because BDAs play complex roles in fuels and fire heterogeneity across the western US which are further complicated by interactions with climate change, drought, and forest management (fire suppression), their impacts on fuels, fire and ecological consequences cannot be categorized simply as positive or negative but need to be evaluated within the context of BDA life histories and ecosystem dynamics.

1. Introduction

Forests across much of the western US are considered to be at high risk of fire due to drought, past forest management, fire suppression, and climate change (Wickman, 1992; Hessburg et al., 2005; Stephens et al., 2018; Voelker et al., 2019; Halofsky et al., 2020). A common misconception, particularly among the lay public, is that forests infested by insects, pathogens, and parasitic plants (collectively termed biological disturbance agents, or BDAs, Table 1) are “unhealthy” and are, therefore, at greater risk of fire (Furniss and Carolin, 1977; Dale et al., 2001). However, more recent research indicates that BDAs often have a more nuanced, context-dependent influence on fire and in some cases,

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Table 1
Glossary of commonly used terms associated with BDAs, fuels and fire. For information pertaining to specific biological disturbance agents, see Table 2.

ADS	Aerial Detection Survey; a program managed by the United States Forest Service (USFS) and State partners who monitor forests by flight and estimate acreage and intensity of damage, tree species, and causal agents.
BDA	Biological disturbance agent; insects, pathogens, and parasitic plants that cause tree decline, mortality, and affect forest ecosystem processes.
Chronic damage	Impact from BDAs where there is a low number of trees that are defoliated or killed in a given location each year, but where it is persistent across years.
Crown fire (active)	Where surface and crown fire energy are linked. Surface intensity is sufficient to ignite tree crowns, and fire spread and intensity in the tree crowns encourages surface fire spread and intensity.
Crown fire (passive)	Where surface fire intensity is sufficient to ignite tree crowns, individually or in groups, but crown fuels and winds are not sufficient to support fire propagation from tree to tree.
Endemic damage	Minor damage caused by a BDA that can become episodic, but during the periods between outbreaks.
Episodic damage	Damage or mortality patterns when large numbers of trees are defoliated or killed in a given location during an outbreak event from single to several years.
FIA	Forest Inventory and Analysis; a USFS program that maintains ground-based plots across the western US used to estimate BDA effects on tree growth, decline, mortality, and changes in forest composition and structure.
Fire intensity	The rate of heat energy released by the fire, and more precisely, the energy released per unit time per unit area of actively burning fire. It is closely related to the amount of fuel available to burn
Fire risk	Burn probability, fire intensity, susceptibility of resources/ assets, and the relative importance of resources/assets.
Fire severity	The degree of environmental change (i.e. tree mortality) caused by wildfires.
Forest decline	Tree canopy loss associated with a complex interaction of biotic and abiotic factors leading to decreasing tree vigor and mortality; forest decline is not associated with fire, wind, harvest, or land use changes.
Forest health	A subjective concept incorporating themes such as biodiversity, resilience, resistance, sustainability, ecosystem services, sustained productivity, human values, and land management objectives.
Forest structure	The quantity and spatial arrangement of forest components, including stems, branches, leaves, and air.
Fuel bed	Accumulated canopy, surface, and litter (duff) fuels.
Fuel complex	The combination of ground, surface, ladder, and canopy fuel strata
Fuel load	The mass of available fuel per unit ground area.
Fuel strata	The horizontal layers of fuels of similar general characteristics. Three primary fuel strata are recognized – ground, surface, and canopy – and ladder fuels connect surface and canopy fuels.
Ladder fuels	Fuels, such as branches, shrubs or an understory layer of trees, which allow a fire to spread from the surface to the canopy.
Outbreak	Explosive epidemic behavior, where the BDA population exceeds a control threshold and can significantly increase its population.
Residence time (fire)	"The time, in seconds, required for the flaming front of a fire to pass a stationary point at the surface of the fuel. The total length of time that the flaming front of the fire occupies one point." https://www.nwcg.gov/term/glossary/residence-time
Resilience (fire)	The capacity of a system (e,g, a forest) to be disturbed by wildfire and then, with time, recover function, structure, identity, and feedbacks.
Resinosis	An excessive outflow and accumulation of resin from coniferous plants usually resulting from injury or disease.
Resistance (fire)	The capacity of a system (e.g. a forest) to experience a wildfire and maintain the same ecological functions and structure following the disturbance.
Spotting	The non-local creation of new fires, due to downwind ignition of embers launched from a primary fire.
Torching	A surface fire that intermittently ignites the crowns of trees or shrubs as it advances

can reduce risk (Parker et al., 2006 Harvey et al., 2014b; Andrus et al., 2016). BDAs encompass a very diverse biota, including native and non-native pathogens, insects, and parasitic plants, which respond to forest composition and structure, but also influence forest composition and structure by causing tree decline and mortality and changing species composition (e.g., Hansen and Goheen, 2000; Raffa et al. 2008).

The spatiotemporal heterogeneity of forests resulting from BDA impacts on tree decline and mortality is key to understanding their influence on fuels and fire, including its likelihood, behavior, and severity. Yet, except for bark beetles, one insect defoliator (western spruce budworm, *Choristoneura freemani* Razowski (Lepidoptera: Tortricidae)), dwarf mistletoe, and the invasive sudden oak death (*Phytophthora ramorum* Werres et al.) (Hicke et al., 2012a; Flower et al., 2014; Metz et al., 2017; Shaw and Agne, 2017, Fettig et al., 2021, Cobb 2022), most BDA groups have received little attention from fire researchers, despite many being pervasive across the western United States. The role of BDAs in shaping fuel characteristics and fire risk is very relevant under today's warming and drying climate, but for most BDA groups it is uncertain whether they do or do not increase fire risk (Parker et al., 2006, Andrus et al., 2016, Kane et al., 2017, Sieg et al., 2017, Cobb 2022).

1.1. *Forest Health*

BDAs are a natural part of forest ecosystems. It is important to recognize that native BDAs are common across forest landscapes (Fig. 1), integral to biodiversity, and have interacted with forests for millennia. Further, they are essential in the functioning of forest ecosystems, including decomposition, nutrient cycling, and biomass recycling, providing important food sources for other organisms, and creating microhabitat features in forest stands (Edmonds et al., 2000; Michel and Winter, 2009; Regnery et al., 2013; Pritchard et al. 2017). The presence of numerous dead or diseased trees may be perceived to mean that a forest is "unhealthy", but dead trees do not necessarily define a forest ecosystem that is in decline. The concept of forest health can be subjective, with a wide range of definitions incorporating themes such as biodiversity, resilience, resistance, sustainability, ecosystem services, sustained productivity, human values, and land management objectives (Kolb et al., 1994; Edmonds et al., 2000; Raffa et al., 2009; Castello and Teale, 2011; Trumbore et al., 2015). The forest pathologist Paul Manion, author of "Tree Disease Concepts" (Manion 1981), is credited with saying, "A healthy forest has a healthy amount of disease." (Kim Corella, Calfire; Martin Mackenzie, USFS FHP, personal communication), meaning that a healthy forest is not without BDAs.

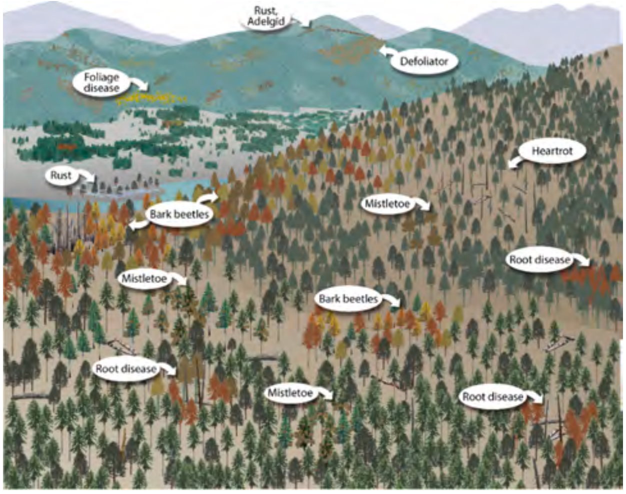

Fig. 1. A western USA coniferous forest landscape where BDAs are a common and natural feature. BDAs interact with abiotic factors such as fire and drought to determine forest composition and structure at stand and landscape scales.

From an ecosystem perspective, a healthy forest should be able to resist (“resistance”) or to recover (“resilience”) from biological disturbance (Merschel et al., 2021). The ability to be resistant or resilient is affected by a complex interaction of factors in western USA coniferous forests including: fire suppression, fuel characteristics, tree density, drought and shade tolerance, forest management effects on forest composition and structure (historic logging of large trees that were resistant to drought, fire, and BDAs), changing climate (longer hotter growing seasons combined with hotter drought, uncharacteristic fires and fire weather), as well as BDA activity (Halofsky et al., 2020; Anderegg et al., 2021; Merschel et al., 2021).

In the western US, two monitoring programs are critical to our understanding of the importance of BDAs to forest conditions and health: Aerial Detection Survey (ADS) and Forest Inventory and Analysis (FIA). The ADS program is managed by the United States Forest Service (USFS) and State partners who fly over forests and estimate acreage and intensity of damage, tree species, and causal agents (Coleman et al., 2018). The USFS FIA program maintains ground-based plots across the western US that can also be used to estimate BDA effects on tree growth declines, mortality, and changes in forest composition and structure (Barrett and Robinson, 2021). Many of the references we cite in this paper are based on ADS and FIA data.

1.2. Purpose

Here, we review the literature concerning biological disturbance agents and fire across coniferous forests of the western US (Fig. 2) to develop a conceptual framework for understanding the interactions among BDAs, fuels, and fire. Although summaries are available for bark beetles, fuels, and fire (Gibson and Negrón, 2009; Hicke et al., 2012a; Jenkins et al., 2014; Stephens et al., 2018; Fettig et al., 2021), insects and fire (Fettig et al., 2022b), forest diseases and fire (Cobb 2022), dwarf mistletoe and fire (Shaw and Agne, 2017), and broader BDA associations with fire (Parker et al., 2006; Kane et al., 2017), a conceptual framework that incorporates the spatial and temporal effects of all important BDA groups on forest heterogeneity and fuel characteristics caused by BDAs is lacking. Conceptualizing the impacts of BDAs on fuels and fire requires a recognition that the spatial and temporal patterns of BDA activity are paramount and interact with existing forest stand conditions, climate, and land management to influence fuels dynamics over time. Fuels do not remain static, and fuelbeds are continuously changing, depending on these complex interactions. In addition, more than one BDA species may be active in a mixed-conifer forest, further complicating impacts on fuels. Similarly, fire risk and outcomes are not static because they vary with changing fuels conditions and rates of decomposition. Therefore, the conceptual framework we present is driven by the dynamic, spatiotemporal interactions of multiple BDAs with heterogeneous fuelbeds across the landscape.

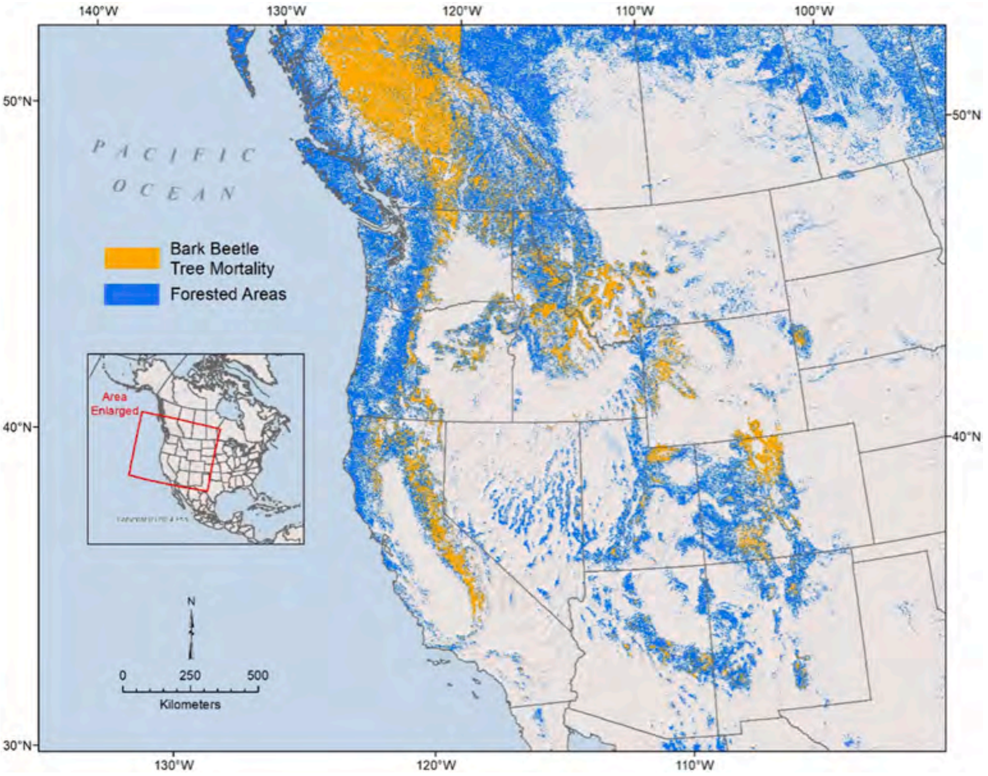

Fig. 2. Forests (blue) of western continental United States and adjacent Canada. The occurrence of tree mortality associated with seven major bark beetles in the western US from 1990 to 2020 is overlaid in light orange. Bark beetles include mountain pine beetle (*Dendroctonus ponderosae* Hopkins), western pine beetle (*D. brevicomis* LeConte), Douglas-fir beetle (*D. pseudotsugae* Hopkins), spruce beetle (*D. rufipennis* (Kirby)), fir engraver (*Scolytus ventralis* LeConte), engraver beetles (*Ips* species), and western balsam bark beetle (*Dryocoetes confusus* Swaine). Data from US Forest Service, Aerial Detection Survey: https://www.fs.fed.us/foresthealth/applied-sciences/mapping-reporting/detection-surveys.shtml#collapseSeven (last checked, 7-7-2022) and British Columbia, Canada Aerial Overview Survey: https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-health/aerial-overview-surveys/data-files (last checked, 7-7-2022) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

This framework provides a generalized approach to characterizing fuel dynamics in relation to BDAs over time and space, which can help develop hypotheses on their subsequent effects on fire risk and severity. We use this framework to address the following questions: 1) What are the major BDA groups in western US forests that can affect fuels? and 2) How do BDA-affected fuels influence fire risk and outcomes? These questions are very relevant to fuels and fire management, as well as a better understanding of western US forest dynamics, because of the ubiquitous impacts of climate-mediated BDAs across the western US (Barrett and Robinson, 2021). As the fire literature is lacking for most BDA groups, we also explore ecological understanding of BDA effects on forest structure, composition, and fuels to postulate how they potentially influence fire risk and outcomes. We feel our approach is a major step forward in integrating all BDAs into fuels and fire science, but there are still major knowledge gaps in our understanding of BDAs and their influence on fuel and fire.

2. Major BDAs in the western US

Given the wide variety of BDAs in the western US (Table 2), we use standardized, regional field guides developed by US Forest Service, Forest Health Protection (Hagle et al. 2003, Wood et al. 2003, Forest Health Protection, Rocky Mountain Region 2010, Forest Health Protection, Southwest Region, 2013, Goheen and Willhite 2021) and relevant literature to assess the major BDAs important to western US forests. BDAs include three major groups: 1. Insects (defoliators, bark beetles, wood borers, sap-feeders, insect root, stem and tip feeders); 2. Pathogens (root diseases, heartrots, foliage diseases, cankers and shoot blights, rusts, *Phytophthora* spp); 3. Parasitic plants (dwarf mistletoes, leafy mistletoes). Vertebrates also play a role in forest dynamics but are not included here. The most significant BDAs that cause mortality and decline in western conifer forests are native and include bark beetles, defoliators, root pathogens, rust fungi, and dwarf mistletoe. However, several invasive, non-native, mortality and defoliation agents are present, including *Cronartium ribicola* J.C. Fisch. (white pine blister rust), *Phytophthora lateralis* Tucker & Milbrath (Port Orford cedar root disease), *P. ramorum* Werres et al. (sudden oak death), *Adelges piceae* (Ratzeburg) (Homoptera: Adelgidae) (balsam woolly adelgid), *Elatobium abietinum* (Walker) (Homoptera: Aphididae) (spruce aphid), *Coleophora laricella* (Hubner) (Lepidoptera: Coleophoridae) (larch casebearer), and *Agrilus planipennis* Fairemaire (Coleoptera: Buprestidae) (emerald ash borer).

BDAs play many roles in shaping forest structure, composition, and fuel profiles at a range of temporal and spatial scales (Castello et al., 1995; Hansen and Goheen, 2000; Meigs et al., 2011; Hicke et al. 2012b) (Fig. 3). Spatial scales range from the individual tree to the stand, landscape and region. Temporal scales range from episodic outbreaks to chronic mortality that can continue for decades. Chronic damage and mortality occur when a BDA defoliates or kills low numbers of trees in a given location each year but is persistent across years. Chronic damage can be confined to discrete spatial scales acting on the individual or entire stand. An episodic damage or mortality pattern occurs when large numbers of trees are defoliated or killed in a given stand during an event spanning one to several years. Endemic refers only to BDAs that are episodic, but describes the period when they are not in an outbreak (e.g. Smith et al., 2011 for bark beetles). Berryman (1982) refers to this period as, "controlled endemic behavior" where the pest insect is kept at low population levels by host resistance and/or predators and parasites. Alternatively, he refers to an outbreak as, "explosive epidemic behavior", where the pest population exceeds a control threshold and can significantly increase its population. Some BDAs, such as bark beetles, defoliators, and foliage diseases, can erupt with major tree defoliation (Fig. 4) and tree killing outbreaks that have a distinct time-since-event influence on forest structure and fuels across large landscapes (Meigs et al. 2011, Hicke et al. 2012a). Other BDAs, such as root diseases (Fig. 5) and dwarf mistletoes, may cause tree decline and

Table 2
Common BDA groups, common BDA examples, and spatial and temporal patterns of BDA damage to trees in the western US. Based on regional field guides to common and important BDAs in the western US (Hagle et al., 2003; Wood et al., 2003; Forest Health Protection, Rocky Mt. Region, 2010; Forest Health Protection, Southwest Region, 2013; and Goheen and Willhite, 2021). Invasive examples listed in bold.

BDA group	Common BDA Examples	Spatial Patterns	Temporal Patterns
Bark Beetles (Coleoptera: Curculionidae)	Mt. pine beetle (*Dendroctonus ponderosae* Hopkins) Western pine beetle (*D. brevicomis* LeConte) Douglas-fir beetle (*D. pseudotsugae* Hopkins) Spruce beetle (*D. rufipennis* (Kirby)) Fir engraver (*Scolytus ventralis* LeConte) Engraver beetles (*Ips* species) Western balsam bark beetle (*Dryocoetes confusus* Swaine)	Local to landscape Can cause widespread landscape scale mortality events	Associated with low vigor tree mortality during the endemic phase Outbreaks common, usually end after most susceptible hosts are killed or weather conditions change. Increased bark beetle-caused tree mortality often associated with drought
Defoliators (Lepidoptera: Tortricidae, Erebidae, Pieridae, Saturnidae, Geometridae Coleophoridae) Sawflies (Hymenoptera: Diprionidae)	Western spruce budworm (*Choristoneura freemani* Razowski) Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough)) Pine butterfly (*Neophasia menapia* (C. & R. Felder)) Pandora moth (*Coloradia pandora* C. A. Blake) Western hemlock looper (*Lambdina fiscellaria lugubrosa* (Hulst)) **Larch casebearer** (*Coleophora laricella* (Hubner)) (invasive) Pine sawflies (*Neodiprion* species)	Widespread defoliation during outbreaks, causing growth impacts, crown decline, and sometimes tree mortality across landscapes	Distinct outbreaks can last from 2 to over 10 years
Woodborers (Coleoptera and Hymenoptera)	Flatheaded wood borers (Buprestidae) Flatheaded fir borer (*Phaenops drummondi* Kirby) **Emerald ash borer (*Agrilus planipennis* Fairmaire)** Roundheaded wood borers (Cerambycidae) Ambrosia beetles (Curculionidae) Horntail wasps (Siricidae)	Tend to be localized in dead and down material. Invasives most significant threat to tree mortality. Flatheaded fir borer is associated with widespread lower elevation Douglas-fir mortality in dry forests. Emerald ash	Increase with increasing host material; recently dead or severely stressed trees. Flatheaded fir borer impacts appear to increase with drought. Emerald ash borer will likely increase until the food source (ash) is effectively gone.

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Table 2 (*continued*)

BDA group	Common BDA Examples	Spatial Patterns	Temporal Patterns
		borer has been discovered on the west coast and will likely kill all ash on the west coast within a decade or so.	
Sap-feeders (Homoptera: Adelgidae, Aphididae, Diaspididae) Also includes Hemiptera	**Balsam woolly adelgid** (*Adelges piceae* (Ratzeburg)) **Spruce aphid** (*Elatobium abietinum* (Walker)) Black pineleaf scale (*Dynaspidiotus californicus* (Coleman)) Pine needle scale (*Chionaspis pinifoliae* (Fitch))	Balsam woolly adelgid and spruce aphid are non-native invasive insects. Sap-feeders occur where susceptible hosts occur in appropriate climate, tree to landscape.	Spruce aphid is eruptive. Balsam woolly adelgid appears to cause significant mortality as it spreads into new areas and then persists as a chronic agent of decline.
Insect root, stem, and tip feeders (several orders)	White pine weevil (*Pissodes strobi* (Peck) (Coleoptera: Curculionidae) Sequoia pitch moth (*Synanthedon sequoia* (Edwards)) (Lepidoptera: Sesiidae) Gouty pitch midge (*Cecidomyia piniinopis* Osten Sacken) (Diptera: Cecidomyiadae)	Tend to be localized although can have stand and regional upswings. Non-native invasives are the most threatening.	Ebb and flow with weather, host conditions and management activities.
Root pathogens (Fungi: Basidiomycetes and Ascomycetes)	Laminated root rot (*Coniferiporia sulphurascens* (Pilát) L. W. Shou & Y.C. Dai) Heterobasidion root diseases (*Heterobasidion occidentale* Ostrosina & Garbelotto) (*H. irregulare* Garbelotto & Ostrosina) Armillaria root disease (*Armillaria* species, especially *A. ostoyae* Romagn.) Black stain root disease (*Leptographium wageneri* (W.B. Kendrick) M.J. Wingfield) Schweinitzii root and butt rot (*Phaeolus schweinitzii* (Fr:Fr.) Pat.) Tomentosus root disease (*Onia tomentosus* (Fr.: Fr.)P. Karst.)	Root pathogens can be quite aggressive and cause tree decline and mortality or be secondary pathogens that attack stressed trees. Root pathogens can occur in distinct spatially explicit infection centers or dispersed through forest stands.	Root pathogens tend to cause chronic tree decline and mortality, but may exacerbate mortality during droughts.
Live wood decays (Fungi, Basidiomycetes)	Indian Paint fungus (*Echinodontium tinctorium* (Ellis & Everh.) Ellis & Everh.) Red ring rot (*Porodaedalia pini* (Brot.) Murrill) Quinine conk (*Fomitopsis officionalis* (Villar.:Fr..) Bondartsev & Singer) Brown top rot (*Fomitopsis cajanderi* (P.Karst.) Kotl & Pouzar)	Widely distributed, but live wood decays typically increase in significance with tree age and wounding history	Chronic development although can increase significantly after storm events that cause top breakage for example.
Foliage pathogens (Fungi, Ascomycetes)	Dothistroma needle blight (*Dothistroma septosporum* (Dorog.) M.Morelet) Swiss needle cast (*Nothophaeocryptopus gaeumannii* (T.Rohde) Videira et al.) Larch needle cast (*Rhabdocline laricis* (Vuill.) J.K. Stone) Needle casts of pine (*Lophodermella* and *Lophodermium* species)	Foliage diseases are closely associated with seasonal weather patterns and local site conditions. Can be limited to humid microsites or occur at landscape scales in major epidemics.	Foliage diseases tend to flare up if seasonal weather allows and then subside when conditions shift. If long term shifts in weather patterns occur (wetter summers) can outbreak at the landscape scale.
Canker, branch and tip dieback fungi (Fungi, Ascomycetes)	Atropellis canker (*Atropellis piniphila* (Weir) M.L. Lohman & Cash) Diplodia tip blight (*Diplodia sapinea* (Fr.) Fuckel) Phomopsis canker (*Diaporthe lokoyae* Funk) Cytospora canker (*Cytospora abietis* Sacc.)	Occur at the individual and patch scale but can become ubiquitous. Often associated with stress.	Some annual cankers and tip blights are closely associated with episodic drought stress or weather events such as hail.
Rust fungi (Fungi, Basidiomycetes, Pucciniales)	**White pine blister rust** (*Cronartium ribicola* J.C. Fisch.) Western gall rust (*Endocronartium harknessii* (J.P. Moore) Y. Hirats.) Comandra blister rust (*Cronartium commandrae* Peck) Stalactiform rust (*Cronartium coleosporidoides* Arthur) Foliage rusts (*Pucciniastrum* species)	Rust diseases can cause significant localized damage. Some cause brooming of branches others foliage diseases or cankers. White pine blister rust is a non-native invasive rust that kills five-needle pines and has affected composition of forests throughout the western US (except Utah)	Can occur chronically in a stand, or flare up with weather, local to regional. Many rust fungi are tightly linked to weather patterns at a critical time of year and may have ‘wave years’ when rust spore dispersal and weather synchronize with host phenology to allow significant increases in infections.
Phytophthora (Water mold, Oomycota)	**Sudden oak death** (*Phytophthora ramorum* Werres et al.) **Port Orford cedar root disease** (*P. lateralis* Tucker & Milbrath) **Phytophthora dieback** (*P. cinnamomi* Rands)	Most *Phytophthora* spp. that cause significant damage are invasive, non-native pathogens. They can cause major mortality at the local to	Tendency for invasive Phytophthora to invade an area, kill most the hosts and then become chronic over the long term.

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Table 2 (*continued*)

BDA group	Common BDA Examples	Spatial Patterns	Temporal Patterns
		landscape scales.	
Dwarf mistletoe (Flowering plant, *Arceuthobium*, Viscaceae)	Diverse in the western USA, four common ones:Lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nuttall ex Engelmann) Western dwarf mistletoe (*A. campylopodum* Engelmann) Douglas-fir dwarf mistletoe (*A. douglasii* Engelmann) Southwestern dwarf mistletoe (*A. vaginatum* ssp. *cryptododum* (Engelmann) Hawksworth & Wiens)	Dispersed by explosive discharge of the seed. Dwarf mistletoes tend to occur in spatially distinct infection centers and slowly expand. Fire, and time-since-fire, is the major control on landscape patterns.	Dwarf mistletoe slowly intensifies within a tree crown over decades and host impacts increase with intensity of infection. Chronic impacts.
Leafy mistletoe (Flowering plant, *Phoradendron,* Viscaceae)	White fir mistletoe (*Phoradendron pauciflorum* Torr.) Incense-cedar mistletoe (*P. libocedri* (Engelm.) Howell) Juniper mistletoe (*P. juniperinum* Engelm. ex. A. Gray)	Dispersed by birds and tends to occur aggregated across the landscape and in largest host trees. Limited to southern/central western NA.	Chronic impacts, slowly intensifies within hosts. Not considered as pathogenic as dwarf mistletoe.

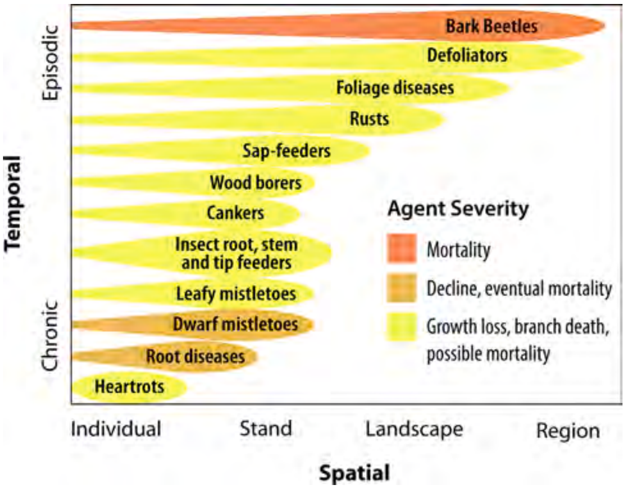

Fig. 3. Proposed relationships of major BDA groups in the western US that represent the temporal and spatial scales at which they can predominantly influence tree mortality and fuels. All BDAs function at the individual tree scale as well as the stand, and the positioning of the main "bubble" of BDA groups is meant to indicate relationships to maximum effects on fuel structure. Chronic damage and mortality occur when low numbers of trees are defoliated or killed/ha each year, but it is persistent across years. Chronic damage can be confined to discrete spatial scales acting on the individual or entire stand. An episodic damage or mortality pattern occurs when large numbers of trees are defoliated or killed/ha in a single-several years. Endemic patterns (not shown in this figure) refer to BDAs that can be episodic, but for periods of time between outbreaks.

Fig. 4. A defoliator outbreak: Pine butterfly (*Neophasia menapia* (C. & R. Felder)) (Lepidoptera: Pieridae) defoliation of ponderosa pine in the southern Malheur National Forest, Oregon. Note the removal of almost all foliage. The outbreak peaked at ∼ 100,000 ha.

Fig. 5. A root disease center: Black stain root disease (*Leptographium wageneri* (W.B. Kendrick) M.J. Wingfield) at Blacks Mountain Experimental Forest, Northern California. *Leptographium wageneri* has been killing ponderosa pine in this photo for several decades. Note the creation of a canopy gap, removal of ponderosa pine from the canopy within the disease center, increase in surface fuels, lower density of trees, and persistence of non-host white fir (*Abies concolor* (Gordon) Lindley ex Hildebrand) within the mortality pocket. Tree in foreground right is a snag.

mortality chronically over long periods of time at the patch and stand scale but are discontinuous across the landscape. Other BDAs such as rust and canker-causing fungi as well as native and naturalized sap-feeders, may be intermediate between the chronic and episodic temporal scales and between the individual and regional spatial scales (Fig. 3).

2.1. BDA impacts in western US forests

Bark beetle activity in the western US during the period from 2000 to

2020 increased compared to the mid-to late 20th century (Fettig et al, 2022a). Based on ADS data since 1997, bark beetle-induced tree mortality has been extensive in the western US, affecting 4.3 million ha (4.7%) of forest area (Hicke et al., 2020) (Fig. 2). The massive mortality of 147 million trees from 2010 to 2018, notably in the Sierra Nevada, California, was attributed to a combination of the unprecedented 2012–2016 drought and native bark beetle epidemics (Axelson et al., 2019). In 2018 and 2019, the fir engraver beetle was the most widespread biotic mortality agent in the conterminous United States, notably in California (Potter and Conkling, 2020). Between 1999 and 2016, defoliators (Fig. 4) in the western US were associated with 16.7 million ha of defoliation (Potter et al., 2020).

Barrett and Robertson (2021) summarized forest disturbance in the western US for a five- to ten-year period using USFS FIA data and found that disease damage to trees occurred on about 4 million ha compared to insect damage on about 3.2 million ha. Root diseases are the most damaging and prevalent group of forest diseases in terms of tree volume loss and forest type affected, comparable to fire and insects combined (Krist et al., 2014; Healey et al., 2016; Lockman and Kearns, 2016). *Phytophthora ramorum* has killed over 42 million trees in Oregon and California since 1990 (Cobb et al. 2020). Laminated root rot (*Coniferiporia sulphurascens* (Pilát) L.W. Shou & Y.C. Dai) disease centers occur on over 8% of the land in the Douglas-fir forests of the Pacific Northwest (Hansen and Goheen, 2000). Dwarf mistletoe is pervasive in the western US (Hawksworth and Wiens 1996; Mathiasen 2021); Dunham (2008) estimated that in Oregon the proportion of host trees infected with dwarf mistletoe was 8.9% of all conifer trees (Pinaceae), with 18% of Douglas-fir (eastern Oregon only), 33.5% of lodgepole pine, 12.2% of ponderosa pine, 10.8% of western hemlock and 31.7% of all western larch trees being infected.

Cohen et al. (2016) noted that harvesting was the primary disturbance to forests in the western US prior to the mid-1990's. Since that time, tree canopy loss not associated with fire, harvest, or other factors such as wind or land use change, and mortality has become the primary forest disturbance, which is likely caused by a combination of BDAs and drought/heat. Across the western US, wildfires and BDAs have both become more prevalent in recent decades (Raffa et al., 2008; Bentz et al., 2010; Hicke et al., 2016; Parks and Abatzoglou, 2020; Fettig et al., 2022a).

3. Principles of BDA-fuels-fire interactions

Individual BDA species are influenced by characteristics of the host and the environmental setting, which is represented by the classic disease triangle (Hennon et al. 2020, Cobb 2022)—the host must be susceptible, the BDA present, and the environment suitable for the BDA to flourish. Similarly, the classic fire behavior triangle (Agee 1993)—illustrates how fire is primarily influenced by weather, topography, and fuels. Therefore, the way BDAs interact with fire depends primarily on how significantly BDAs influence canopy, surface, and litter/duff fuels (Fig. 6). Legacies of forest management and land-use set the template for forest conditions in the western US, and BDAs and fire interact with existing conditions. Fire suppression is perhaps the most significant management impact in the western US, but historical homogenization of forest fuels conditions by uniform spacing of trees and the removal of large diameter trees has also been pervasive. Importantly, there are spatial and temporal aspects to BDA-induced changes in live and dead fuel abundance and distribution (Fig. 3), and it is critical to consider how changes in fuels related to BDAs interact with topography and weather.

BDAs influence fuel structure in live crowns by killing leaves, branches, and whole trees, they cause species-specific tree mortality, and affect competitive interactions among tree species, all of which modify canopy, surface, and litter and duff fuels, which also vary with time (Fig. 7) (Hansen and Stone, 2005; Lundquist, 2007; Shaw and Agne, 2017; Fettig et al., 2021, Cobb 2022). Dead canopy biomass eventually moves to the forest floor and understory, increasing surface and ground fuels, decreasing canopy fuels and affecting microclimate at the scale of the mortality or defoliation (Hicke et al. 2012a, Hansen et al., 2015). At landscape scales, crown mortality from BDAs can reduce crown density and connectivity of canopy cover (i.e., create gaps) across large areas (Meigs et al. 2011). The influence of BDAs on horizontal and vertical spatial patterns of fuels is complicated by the magnitude of mortality, as well as the structure and composition of the stand before and subsequent to BDA events. In general, surface fuels increase, and canopy fuels decrease, while litter and duff may increase associated with the conversion of aboveground live biomass to dead biomass. However, there is a strong time-since-event factor for episodic BDAs, while changes occur much slower in chronic disturbance agents (Fig. 7). The effects of time-since-event on fire outcomes are poorly studied for most BDA groups.

BDAs also influence fuel bulk density, packing ratio, abundance, moisture content (Jolly et al. 2012a; Page et al. 2012), and chemistry (Giunta et al. 2012, Page et al. 2012), which collectively influence fire spread rate and severity through fuel arrangement. Fuel arrangement refers to the vertical distribution of fuels (litter and duff, surface, and canopy fuels) and is a key component of fuelbeds, which are areas of relatively homogeneous organization of fuels on the landscape that are distinct combustion environments and strongly influence fire behavior and effects (Ricarrdi et al., 2007). Bulk density is the weight versus area ratio of fuels, which affects how quickly dead fuels adjust to ambient

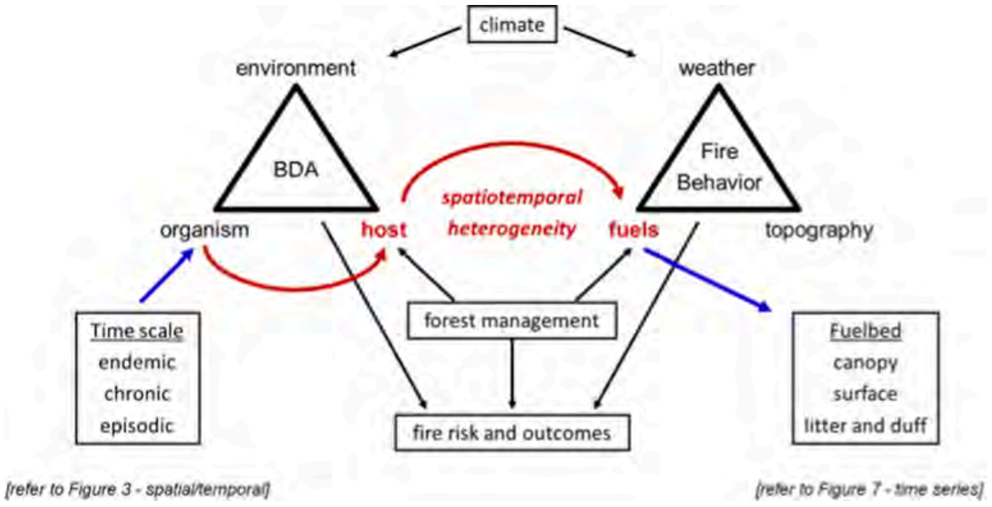

Fig. 6. A conceptual framework of the influence of BDAs on fuels and fire behavior and the relationships among associated factors. The triangle on the left is based on the forest disease triangle (Hennon et al. 2020), and the triangle on the right is the fire behavior triangle (Agee 1993). Climate and forest management influence both BDA effects and fire behavior. BDAs may occur at time scales of chronic, episodic, or endemic (Fig. 3). Fuels are organized into fuelbeds which include canopy, surface, and litter (duff) fuels (Fig. 7). Together, with forest management and weather, BDAs influence the spatial heterogeneity of fuels and associated fire risk and outcomes.

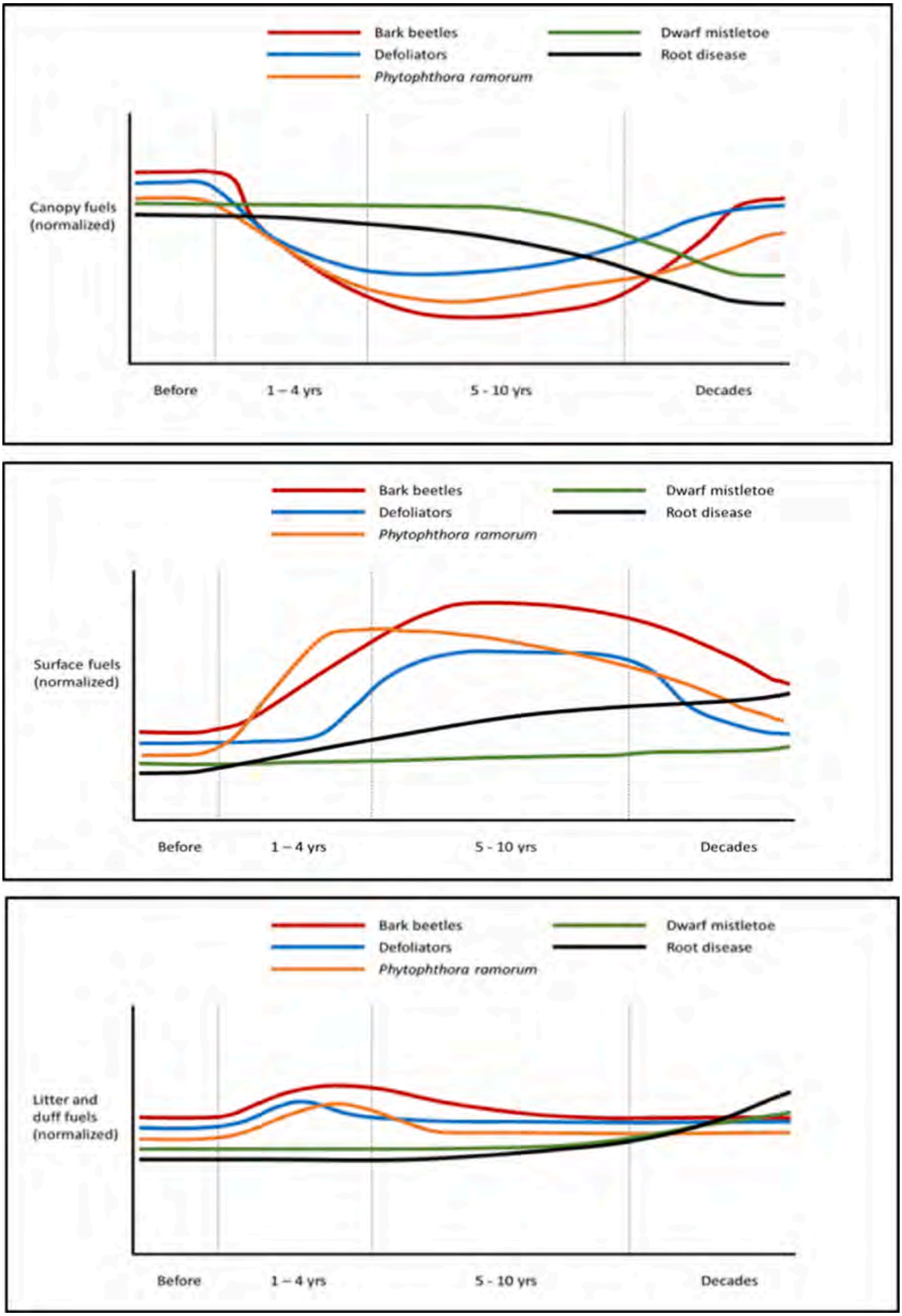

Fig. 7. Hypothetical normalized time-since-event dynamics at the stand scale for five BDA groups: bark beetles and defoliators after an outbreak, *Phytophthora ramorum* (sudden oak death) after invasion into an uninfected forest, and root diseases and dwarf mistletoes after invasion into an uninfected stand. Top panel: canopy fuels; Middle panel: surface fuels; Lower panel: litter and duff. These figures represent hypothesized trends, and more research and empirical studies are needed to evaluate these proposed relationships, although these groups do represent the BDAs with the most research to date. These relationships do not include associated understory vegetation and reproduction of trees after disturbance, which vary by site. Figure concept follows Hicke et al., (2012a).

moisture and temperature as well as the energy released through combustion—synthetically described using time-lag classes:

- 1-hour fuels: up to 1/4 in. (6.4 mm) in diameter.
- 10-hour fuels: 1/4 in. (6.4 mm) to 1 in. (2.5 cm) in diameter.
- 100-hour fuels: 1 in. (2.5 cm) to 3 in. (7.6 cm) in diameter.
- 1,000-hour fuels: 3 in. (7.6 cm) to 8 in. (20.3 cm) in diameter.
- 10,000-hour fuels: > 8 in. (20.3 cm) in diameter.

The 1- and 10-hour fuels include surface litter, leaves, grasses, shrubs, and fine branches. These fuels are critical to the ignition and spread of fire, but they have relatively low burn residence time and heat production. However, these finer fuels may be the most common fuels created and influenced by the breadth of BDAs, such as foliage, tip, and canker diseases, rusts, sap-feeders, and other shoot and tip infesting insects (Hagle et al., 2003; Wood et al. 2003, Forest Health Protection, Rocky Mt. Region 2010; Forest Health Protection, Southwest Region, 2013, Goheen and Willhite 2021), yet they also decompose relatively quickly (Hansen et al. 2015). The 100-, 1000-, and 10,000 h fuels include branches and stems of larger shrubs, trees, snags, and coarse woody debris, and medium-term increases in these fuels are associated with bark beetle and some defoliator outbreaks, as well as root disease centers (Hansen and Goheen, 2000; Hummel and Agee, 2003; Hicke et al., 2012a; Jenkins et al., 2014). These fuels take much longer to cure—have a high fuel to oxygen ratio—and thus are not as important to fire spread. However, the long residence time of burning these fuels and similarly dense duff layers in soils can result in higher tree mortality and impact soils and hydrology (Smith et al., 2016a, 2016b; Dove and Hart, 2017; Bladon, 2018, Stephens et al., 2022). The packing ratio—fuel to air mixture—of the surface fuels is also important; if fuels are tightly packed, they burn less readily but have longer residence times versus fuels that have more air space and smaller fuels, which have high flammability and flame lengths.

Fire behavior attributes are strongly associated with fuels and fuelbed characteristics, and changes in fuels amount and vertical organization can change fire behavior attributes (Van Wagtendonk, 2006). We summarize fuels changes that can increase fire behavior attributes in Table 3. For example, surface fire spread can be increased by spatial connectivity and homogeneity of fuels, as well as increased surface fuel amount, increased fuelbed depth and increased 1 hr – 100 hr fuels. The role of BDAs in causing changes in fuelbed characteristics that increase fire behavior attributes is complicated by climate and the temporal dynamics of the BDA (Figs. 3, 7), as well as fire weather and topography (Fig. 6).

Table 3
Fuels changes that increase fire behavior attributes.

Fire behavior attributes	Fuels changes that would increase fire attribute
Rate of spread	Increased spatial connectivity of surface fuels. Increases in smaller size classes of fuels, deeper fuelbeds and increased dead, dry fuel. Increases in live vegetation (shrubs, herbs, grasses) and regenerating conifers especially when mixed with large accumulations of dead surface fuels. Coarse fuels alone do not play a strong role in fire spread.
Fireline intensity	Increases with deeper fuel beds composed of all size classes of fuels.
Flame height	Increases with fuelbed depth especially of 1 – 100 h fuels.
Residence time	Can increase with more abundant standing and down dead wood in medium and large size classes.
Surface fire	Increased potential with increasing surface fuels, especially dead fuels in small and medium size classes.
Active crown fire	Increases in connectivity between forest surface and crowns, increased fuelbed depth, lower canopy base heights, higher canopy bulk density.
Passive crown fire	Increased potential with more ladder fuels and lower canopy base heights.
Spotting	Increased potential due to increases in fine materials. Torching may allow more spotting.
Smoldering	Increased potential due to increased litter/duff depth, and increased well-decayed coarse woody debris.
Torching	Increased ladder fuels

Surface fuels are critical in determining fire rate of spread, severity, and potential fire risk, and the conversion of canopy fuels to surface fuels may be one of the most important aspects of BDA influence on fuelbeds. However, the fuels complex is strongly influenced by existing conditions of the stand at the time of mortality, density of host trees vs non-host trees, understory vegetation, tree regeneration, time since mortality, and rate of decomposition. For instance, bark beetles may cause large increases in surface fuels in the short to medium term as high densities of dead trees decompose and fall together (Fig. 8). Stephens et al. (2022) have described a condition in the Sierra Nevada of California where drought and bark beetles killed a significant number of large trees, increasing surface fuels and subsequent burn severity in snagfall-phase fire, particularly where a high number of live trees had persisted. In contrast, root diseases can contribute a steady number of dying trees over the landscape, but at a much slower cadence and density (Fig. 7). The decay rate of coarse woody debris is a primary factor in determining surface fuel buildup from root diseases.

Surface fires burn through the forest immediately above the ground but below the canopy (Agee 1993, Scott and Reinhardt 2001). Surface fires transition to the canopy when there is sufficient fuel connectivity between the surface and crown, or when flame heights are sufficient to reach the canopy (often associated with wind) (Van Wagtendonk, 2006). Crown fires burn through canopy fuels, which typically consist of live and dead trees, live and dead foliage, lichen and fine live and dead branch wood, and ladder fuels and can be active, passive, or independent (Van Wagner, 1977, Scott and Reinhardt, 2001). Active crown fires burn the entire surface and canopy fuels complex of the stand (Agee, 1993, Scott and Reinhardt, 2001). Passive crown fire (torching) occurs when an individual, or small groups of trees torch, but a continuous flame is not maintained in the canopy. However, embers from torching trees may cause spotting ahead of the fire front (Van Wagtendonk, 2006). Torching is a common feature of dwarf mistletoe infection

Fig. 8. Ponderosa pine mortality (standing snag and snag fall phase) in the Sierra Nevada Mountains, California associated with drought and western pine beetle (*Dendroctonus brevicomis* LeConte). Note the removal of large ponderosa pine from the canopy, accumulation of large amounts of surface fuels, and conversion of the stand to white fir (*Abies concolor* (Gordon) Lindley ex Hildebrand) and incense-cedar (*Calocedrus decurrens* (Torr.) Florin), which increase ladder fuels and are less fire-tolerant.

centers where the canopy is more open and ladder fuels common (Parker et al., 2006; Shaw and Agne, 2017). Independent crown fires occur rarely when the canopy burns but not surface fuels.

The role of BDAs in increasing active crown fire is best described for bark beetles in lodgepole pine forests when the temporal aspect of the outbreak is at its peak of intensive tree mortality and there are many trees with dead (green foliage can be dead and dry) and red foliage. Fires in these lodgepole pine-mountain pine beetle systems in the red phase can have higher fire intensity, faster rate of spread, lower crowning thresholds, greater consumption of fine dead branches, and more crown fire than predicted by fire behavior models (Perrakis et al., 2014). However, this period of increased fire risk depends on the proportion of the overstory affected at a given point in time and is relatively brief compared to the time it takes for live canopy fuels to recover (Fig. 7). Moreover, the potential for active crown fire decreases after snags fall due to lower canopy connectivity and canopy bulk density, as well as dominance of 1,000 hr + surface fuels that do not play a large role in fire spread.

A key influence of BDAs on fuels and fire may be to increase spatial and temporal forest heterogeneity due to the wide variety of BDA agents and associated effects on forest composition and structure across space and time (Figs. 3, 6, 7). Higher heterogeneity of forest fuels moderates and regulates fire (Parsons et al., 2017; Koontz et al. 2020). Both BDAs and fire influence regeneration patterns across stands and landscape, and mosaics of disturbance create complex forest patterns that increase variability of fire effects (Kulakowski and Veblen 2007; Harvey et al., 2014a; Harvey et al., 2014b; Parsons et al., 2017; Koontz et al., 2020). Forest management and fire exclusion have increased the homogeneity of forest fuels (Graham et al., 2004; Hessburg et al., 2019; Merschel et al., 2021), and in the absence of frequent fire, we suggest that BDAs have emerged as dominant agents of forest heterogeneity creation. Although BDAs may increase fire severity in some stands during some time periods, heterogeneity in fuels created by BDAs can increase diversity in fire severity by reducing homogeneity in forest conditions and fuels that support larger patches of high-severity fire. BDAs also influence forest fuels over the long term by causing changes in species composition and structure, which can influence fuel dynamics not directly related to conversion of live to dead fuels (Holah et al., 1997; Wilson et al., 1998; Hawkins and Henkel, 2011).

3.1. *BDAs and foliar flammability*

Live foliage and branches are the principal fuel in forest canopies (Chandler et al., 1983), but despite their importance in wildland fires, relatively little emphasis has been placed on understanding what factors influence their flammability. At high enough temperatures, any organic matter will burn during a fire, but under moderate conditions some plant materials will burn while others will not (Andersen, 1970). Foliage flammability can be separated into four constituents (which are not necessarily positively correlated): ignitibility (time until ignition once exposed to heat, TTI); sustainability (the duration of burn, e.g., flame duration, FD and smolder duration, SD); combustibility (the amount and duration of heat release); and consumption (the proportion of consumed to unconsumed fuel following burning) (Anderson, 1970). Fuel moisture content (FMC, calculated as fuel mass proportions of water to dry material) is a commonly recognized factor in plant flammability (Andersen, 1970).

Outbreaks of BDAs can substantially influence the flammability of foliage, both through changes in FMC, and through changes in chemical composition (see references below). The effect of infestation on FMC can be substantial and vary depending on the stage of infestation (Jolly et al. 2012a, Page et al. 2012, Page et al. 2014). Jolly et al. (2012a) found that infestation by mountain pine beetle significantly reduced foliar FMC in lodgepole pine with an approximately threefold difference in FMC between non-infested green foliage and attacked (but still living) foliage (108.5% vs 38.6%), as well as between attacked and dead foliage (38.6% vs 11.7%). These trends correlated with substantial differences in flammability (specifically TTI) between these foliage categories. They also found significant trends in leaf chemical content such as protein, fat, carbohydrates, and ash of foliage with degree of infestation, with observed changes in foliar chemistry explaining nearly as much of the variation in TTI as FMC. Beetle infestation can also influence terpene content and isoprene emissions from host trees, both of which can significantly increase needle flammability (Giunta et al. 2012, Page et al. 2012). Leaf senescence is often associated with fungi and can result in older dead cohorts of foliage remaining attached to the tree, especially in pines such as ponderosa and lodgepole pine. The dead foliage has a much-reduced moisture content and may enhance the potential for passive crown fire (Balaguer-Romano et al., 2020).

4. Review of supporting literature

The foundation for our conceptual framework relating BDAs, fuels and fire is based on supporting literature, which we review in this section. We summarize key associations with fuels, fire, and climate for the common BDA groups in the western US (Table 4) and for bark beetles (Table 5). Bark beetles and defoliators dominate the literature because of the scale of their impacts (Kane et al., 2017; Fettig et al. 2021), and while other BDAs are important in influencing forest composition and structure, their impacts can be more subtle, and difficult to quantify. Consequently, our understanding of the influence of BDAs on fuels and fire is limited to a few major groups and taxa, including bark beetles (mountain pine beetle (e.g., Fettig et al. 2021), defoliators (western spruce budworm (e.g., Flower et al. 2014), dwarf mistletoe (Shaw and Agne 2017), and sudden oak death in California (Metz et al. 2017, Cobb 2022). Several syntheses of bark beetles, fuels, and fire (Gibson and Negrón, 2009; Hicke et al., 2012a; Jenkins et al., 2014; Stephens et al., 2018; Fettig et al., 2021) have been published as well as those focusing on insects (Fettig et al., 2022b), disease (Cobb 2022), dwarf mistletoe (Shaw and Agne, 2017) and broader BDA associations with fire (Parker et al., 2006; Kane et al., 2017) across the western US.

Lundquist (2007) is a rare example of a study that examined multiple BDAs (root rot, stem rot, stem cankers and bark beetles) and other small-scale disturbance contribution to fuels in ponderosa pine forests of the Black Hills in South Dakota. He found that root rots, stem rots, strong winds, fire exclusion, and tree cutting caused surface fuel loads to increase, bark beetles did not significantly increase fuel loads, while stem cankers, fire, ice/snow damage, failed regeneration and shallow soils were associated with decreased surface fuel loads. He concludes that root rot increased surface fuel the most.

4.1. *Bark beetles, fuels, and fire*

Research by Geiszler et al. (1980) and Gara et al. (1985) makes a strong conceptual link between bark beetles, fungi, and fire in climax lodgepole pine of South-Central Oregon. They proposed that high severity fire creates substrate for a new stand. As the regeneration cohort ages, periodic low severity fires damage the roots and create fungal infection courts (Smith et al., 2016b). Fungi invade these wounds, and over time the infected trees are preferentially attacked by mountain pine beetles due to lower vigor. Eventually the mountain pine beetle transition from endemic to epidemic stage, and the fuels created by the outbreak increase the potential for stand-replacement fire. In a unique perspective on fuels, Gara et al. (1985) consider partially decayed coarse woody debris capable of carrying a fire in this system due to its unique flammability. More recently, Heyerdahl et al., (2014), Agne et al. (2014), Shaw and Agne (2017), Woolley et al. (2019) and Hagmann et al. (2019) shed new perspectives on this system by further characterizing fire history, incorporating dwarf mistletoe into the forest and fuel dynamics, and extensively documenting forest and fuels changes over time.

The best studied system for bark beetles and fire is mountain pine

Table 4
Key BDA associations with fuels, fire, and climate. See Table 5 for more information on bark beetles and fire. Regional field guides to common and important BDAs in the western US include: Goheen and Willhite (2021), Hagle et al. (2003), Wood et al. (2003), Forest Health Protection, Southwest Region (2013), Forest Health Protection, Rocky Mt. Region (2010).

BDA group	Fuels	Fire	Climate	References
Bark beetles ● Endemic = typical phase where beetles are at lower population numbers and persist on root diseased, declining, stressed trees and fresh windthrow/slash. ● Episodic = major population eruption that allows beetles to kill healthy live trees.	● Endemic: create dead fuel but tend to kill weakened, root diseased, or declining trees, may kill treetops or partial crowns. ● Episodic: Distinct time-since-beetle outbreak changes in fuels: Fig. 7. ● Red phase or epidemic phase has higher flammability because trees are being actively killed and drier foliage and fine branches persist on the tree. ● Followed by post-epidemic phase or gray phase where canopy bulk density steeply declines, and snags occur. ● Old phase includes snag fall, regeneration, and stand development. ● Surface fuels can substantially increase associated with branch and snag fall. ● Woolly et al. 2019 for mt. pine beetle in lodgepole pine notes four distinct phases: - Overstory mortality - Standing snag and snag fall - Regeneration - Overstory recovery	● Red phase: increased canopy flammability ● Post epidemic phase: complicated by surface fuel conditions prior to outbreak, proportion of stand killed, non-host tree species density, and the time since mortality. ● Most studies note decreased fire severity after the epidemic/red phase. ● Potential for long-term persistence of high surface fuel amounts after snag fall may increase surface fire residence time and fire severity.	● Bark beetle outbreaks are associated with drought, and major windthrow events.	Table 5; Furniss and Carolin, 1977; Raffa et al., 2008; Gibson and Negron, 2009; Hicke et al., 2012a; Jenkins et al., 2014, Vega and Hofstetter, 2015; O’Connor et al., 2015; Fettig et al., 2021; Regional field guides.
Defoliators Most information on defoliators and fire is related to the western spruce budworm (WSB).	● Endemic: May be considered background herbivory. ● Episodic: Outbreaks associated with reduction of foliage amount in short term, then possible top die-back, and whole tree mortality if outbreaks persist. Understory and overstory trees can be killed. ● Stand composition and non-host amount influential in subsequent fuels composition. ● Time since outbreak influences fuels after initial canopy bulk density reductions (Fig. 7). ● Dead tops, branches and snags fall to forest floor, increasing surface fuels. ● Variablity in tree regeneration and understory vegetation amount complicates long term surface fuels dynamics.	● The potential for fire hazard to be reduced is suggested by literature. ● Fire was less likely to occur where WSB has occurred. ● Fire behavior may be influenced by reduced canopy fuels, followed by increased surface fuels if tree mortality is significant.	● WSB outbreaks may occur during the normal or above average precipitation years that succeed droughts.	Brookes et al., 1987; Hummel and Agee, 2003; Flower et al., 2014; Flower, 2016; Cohn et al., 2014;, Meigs et al. 2015; Meigs et al., 2016; Senf et al., 2016; Vane et al., 2017; Harvey et al., 2018
Wood borers	● Wood borers respond strongly to abundance of host material that is recently dead or dying. Wood borers feed and mine in bark, phloem, sapwood, and heartwood, and therefore may help aerate dead wood. ● The flatheaded fir borer is associated with Douglas-fir mortality during drought, so may increase fuel loading in some forest types. ● Most significant threat is from non-native wood borers	No information.	● Drought-caused stress increases attacks on live trees.	Regional Field Guides, Furniss and Carolin, 1977
Sap-feeders	● Native: May reduce foliage amount,	● Influence on fire behavior and severity unknown.	● BWA thought to be influenced by winter cold temperature and summer	Hain 1988, Lynch, 2002; Ragenovich and Mitchell 2006,

(continued on next page)

Table 4 (*continued*)

BDA group	Fuels	Fire	Climate	References
Balsam woolly adelgid (BWA) and Spruce aphid (SA) are non-native and invasive	cause branch tip, tree top and partial crown dieback in localized areas ● Non-Native: Can cause severe defoliation, deformation, crown decline, top-dieback and mortality of host trees	● SA in SW USA has killed large numbers of Engelmann spruce with a distinct time-since event type fuels succession may be similar to bark beetles with reduced crown fire. ● BWA kills individual trees of all sizes in *Abies* species, but subalpine fir in high elevations stands are particularly susceptible.	heat, but also September minimum temperature and cool, wet May, could be important in the western US. ● SA influenced by winter temperatures	Hrinkevich et al., 2016; Lynch, 2019.
Insect root, stem, and tip feeders	● Complex very diverse group. Various impacts and fuels structures created may include: ● Resinosis, crown thinning, tip and branch dieback, reduced leader growth or mortality, crown deformation, seedling and small tree mortality.	● Very diverse group, no real information on fire severity and behavior. ● May increase crown flammability.	● Complex	Furniss and Carolin 1977. Regional Field Guides.
Root pathogens (fungi) Root disease pathogens vary in pathogenicity, and host susceptibility complicating impacts in forests	● Chronic: Slowly colonize and kill trees. Associated with crown decline (thinning), reduced growth, dead tops, and whole tree mortality. May increase surface fuels, while reducing canopy bulk density and continuity (Fig. 7). ● Can create distinct infection centers where recent dead and dying trees occupy the margins of the center, older dead trees in the center. ● May also occur widely distributed throughout a stand. ● Some pathogens can kill trees of any vigor while others focus on stressed or damaged trees. ● Can influence forest succession and composition by selectively killing most susceptible trees.	● Effects on fire behavior and severity unknown and mostly anecdotal. ● Distinct root disease centers that create heterogeneity may reduce homogeneity of fire effects. ● One model in Armillaria and ponderosa pine suggested rate of spread and flame length were reduced in disease centers.	● Climate may increase root disease pathogen impacts, especially those that attack low vigor trees. ● Some pathogens attack trees of any vigor. ● General impacts of climate are unclear.	Dickman and Cook, 1989; Hessburg et al., 1994; Holah et al., 1997; Hansen and Goheen, 2000; Thies, 2001; Fields, 2003; Lunquist, 2007; Johnson, 2012; Lockman and Kearns, 2016; Hessburg et al., 2016; Regional Field Guides
Live wood decays	● Chronic: Heartrot and live wood decays increase with tree age and wounding history. ● Trees may have hollows and cavities, pitch streaming, and dead tops. ● Disturbance events (wind, ice storms) may significantly increase live wood decays in a forest stand.	● Unknown how heartrot and live wood decay influences fire.	● Some climate events such as windstorms, snow, and ice storms cause bole snap and create infection courts for toprots, heartrot, and sapwood rots. ● Other effects of climate uncertain, but decay rates are influenced by temperature.	Aho, 1982; Oester et al., 2018; Vasaitis, 2013; Hansen et al., 2018, Lunquist, 2007; Regional Field Guides
Foliage pathogens ● Foliage casts: foliage is dropped soon after it dies ● Foliage blights: foliage stays attached to the twig after death.	● Foliage diseases are often host or genus specific. ● Cause loss of foliage from the canopy, possible branch or top dieback, rarely mortality. ● Can be strongly associated with vertical position in the canopy, most foliage diseases kill foliage in the lower and inner crown, however some may be heavier in the upper crown. ● Endemic levels tend to be in localized microsites ● Outbreaks can occur at regional scales ● Understory vegetation (surface fuels) may increase due to thin overstory crowns.	● Relationship of foliage disease to fire behavior and severity unstudied. ● One European study in Aleppo pine suggested dead foliage in the canopy increases passive fire crowning.	● Most foliage diseases are closely tied to weather, especially precipitation during spore dispersal period because it increases dispersal and colonization success. ● Swiss needle cast disease increase is strongly linked to warmer winters and precipitation in late spring and summer.	Woods et al., 2005; Bednářová et al., 2013; Welsh et al., 2014; Hansen et al., 2018; Balaguer-Romano et al., 2020; Shaw et al., 2021; Region field guides.
Canker, branch and tip dieback fungi	● Chronic but may flare up with weather stressors such as drought or hail damage. ● Associated with tip, branch, and top dieback.	● No information on relationship to fire. ● May increase crown flammability.	● Canker, branch and tip dieback fungi appear strongly controlled by climate. May increase with climate stressors such as drought.	Lundquist, 2007; Gonthier and Nicolotti, 2013; Regional Field Guides.

(*continued on next page*)

Table 4 (*continued*)

BDA group	Fuels	Fire	Climate	References
	● May cause resinosis, deformation of branches or tips.			
Rust fungi ● Rusts may be foliage diseases, canker diseases, gall formers, or cause branch deformation and brooming. ● White pine blister rust (WPBR) is a non-native invasive rust fungus. ● Native rusts are important, particularly in managed stands.	● Chronic and episodic: Most rust fungi are strongly controlled by weather and host phenology and therefore increase and decrease with seasonal weather patterns and host management. ● Wave Years: Many rust fungi, including WPBR, will occasionally greatly increase in certain years when weather patterns and host phenology align well. ● Key fuels impacts are foliage losses, branch flagging, gall formation, resinous cankers, top dieback, whole tree death, windsnap at site of canker or gall, branch broom formation.	● Little information on influence on fire behavior and severity. ● WPBR may influence fire at high elevations/treeline by creating patches of dead trees ● Study in Sierra Nevada Mts. found no relationship between previous fires and WPBR occurrence. ● Fire may increase the alternate host (*Ribes* spp.) of WPBR.	● Strongly influenced by host, climate and microenvironmental setting. Especially areas of cold air drainage and humid air pooling.	Blenis and Li, 2005; Hamelin, 2013; Dudney et al., 2020; Regional Field Guides
***Phytophthora* spp.** *Phytophtora ramorum*, cause of sudden oak death (SOD) has the most research information about Phythophthoras and fire in the western US	● Most important *Phytophthora* spp. are non-native invasives. ● Invasion causes high mortality in susceptible hosts, becomes chronic once well established. ● Recent dead trees such as tanoak have evergreen leaves that strongly contribute to fuels. ● Pulse of snags and continued snag creation. Snags fall apart and contribute to surface fuels (Fig. 7). ● Canopy gaps increase ladder fuels.	● SOD increases fire hazard. Observations from fires in California: increased surface fuels caused longer flame lengths. ● Surface fuels were very patchy, and fire spread rate and flame height increased when burning accumulated fuels. ● A study reported greater than normal spotting from ember production and increased spotting distance. ● Increased kill of associated – non-host trees such as coast redwood due to piling of fuels at tree base and increased residence time of basal burning.	● Weather strongly influences SOD sporulation and success, with warmer - wetter periods most important (especially in spring). ● *Phytophthora* spp. are called ‘water molds’ due to the importance of moisture.	Kuljian and Varner, 2010; Lee et al., 2010; Valachovic et al., 2011; Forrestel et al, 2015; Metz et al., 2011; 2013; 2017; Shaw et al., 2017; Cobb et al., 2020; Simler-Williamson et al., 2021, Cobb 2022.
Dwarf mistletoes The distribution of dwarf mistletoes (DM) on the landscape is determined by fire history and subsequent succession and host abundance.	● Chronic impacts: DM slowly intensifies and spreads, dependent on forest composition and structure. Influence on fuels takes time (Fig. 7) ● Can occur in distinct infection centers. ● In individual trees DM causes witches’ brooms and litter accumulations in brooms, dead branches, dead tops, and resin-soaked branches. ● In forest stands DM causes: decreased canopy base height, possible greater surface fuels and increased ladder fuels. ● Canopy bulk density, tree density and stand basal area decrease with increasing DM.	● Influence of DM on fire severity and behavior are not well studied. ● Modeling is difficult as most models don’t include complex canopy of DM infested stands. ● Heavily infected trees are thought to have much higher flammability than un- or lightly infected trees. ● One model found no differences in fire rate of spread, fireline intensity, or flame length but found that lower wind speeds could transition fire into canopy. ● Observations on prescribed fire indicate increased crown scorch in heavily infected stands.	● Unusual weather can kill dwarf mistletoe aerial shoots like heat scorch or freeze damage. ● Drought may increase branch and whole tree mortality impacts of DM. ● DM prefers vigorous hosts.	Wicker and Leaphart, 1974; Alexander and Hawksworth, 1975; Alexander and Hawksworth, 1976; Koonce and Roth, 1985; Harrington and Hawksworth, 1990; Hawksworth and Wiens, 1996; Turner et al., 1999; Parker et al., 2006; Hoffman et al., 2007; Conklin and Geils, 2008; Stanton, 2009; Stanton and Hadley, 2010; Klutsch et al., 2014; Shaw and Agne, 2017; Ritter et al., 2017
Leafy mistletoes In western North America, north of Mexico, the leafy mistletoes are all in the Genus *Phoradendron* (Viscaceae)	● Bird dispersed seed. Some *Phoradendron* species may be large shrubs. ● Effect of mistletoe on the trees depends on density of mistletoe plants. *P. pauciflorum* in *Abies concolor* can increase susceptibility to bark beetle attack. As infections intensify, can lead to branch death and crown deformation and decline over many decades. ● One study in *Quercus* in California found no effect of oak	● No information. Fire controls the distribution of mistletoe by killing hosts.	● Severe drought may kill branches with leafy mistletoe. ● Extreme heat or cold may kill aerial shoots	Hawksworth and Scharpf, 1981; Geils et al., 2002; Mathiasen et al., 2008; Koenig et al., 2018

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Table 4 (*continued*)

BDA group	Fuels	Fire	Climate	References
	mistletoe on tree health. ● On the landscape, infections are spatially aggregated and in the largest trees.			

beetle (Fig. 9), with the mountain pine beetle - lodgepole pine system most common (Table 5). All other taxa have five or less studies. This is important because it informs our understanding of bark beetle-fuels-fire dynamics even though lodgepole pine forests are quite distinct and may not be representative of other bark beetles and forest types. For example, the bark beetle-drought-ponderosa pine forest mortality event in California (2014–2017) created large accumulations of dead biomass due to the large tree sizes, which then mixed with substantial live tree component, including hardwoods and other conifers, to increase subsequent burn severity (Stephens et al., 2022) (Compare Fig. 8 to Fig. 10).

Key to the effect of bark beetles on fuels and fire behavior and severity is the time-since-mortality event effect on fuel structure, which then influences fire behavior while interacting with fire weather and local topography (Jenkins et al., 2008; Jorgensen and Jenkins, 2011; Simard et al., 2011; Hicke et al., 2012a; Jenkins et al., 2014; Sieg et al., 2017; Woolley et al., 2019) (Table 5, Fig. 7). Some authors use a framework that includes forest structure in three phases: pre-epidemic, epidemic, and post-epidemic (Jenkins et al. 2008, Jorgensen and Jenkins, 2011, Jenkins et al. 2014), also called green (pre-epidemic or non-epidemic), red (during the epidemic when trees have died and still have red foliage attached), and gray (trees are snags which have lost all their dead leaves) phase. Hicke et al. (2012a) and Stephens et al. (2018) used time periods to describe changes in fuels and fire behavior: before, 1–4 years, 5–10 years, and decades after the epidemic. Woolley et al. (2019) categorized forest structural changes across a 32-year chronosequence of four phases from the outbreak: overstory mortality (2–4 years), standing snag and snag fall (5–13 years), regeneration (14–25 years), and overstory recovery (26–32 years). All these researchers note the clear changes in forest structure over time since the outbreak occurred (Fig. 7).

Mortality caused by bark beetles changes the structure and fuelbed of the forest in a dynamic time-since-event fashion, and fire behavior will be different in bark beetle affected stands as compared to unaffected stands due to changes in microclimate, fuel moisture content, reduction of canopy fuels, and increases in surface fuels (Jenkins et al., 2014; Hansen et al., 2015). Fire behavior involves fuels ignition, flame development and fire spread, and a significant impact of bark beetles is to increase surface fuels, which can increase the probability of fire transitioning to the canopy and also influence fire suppression difficulty and firefighter safety (Jenkins et al., 2014; Hansen et al., 2015). Fire severity, especially associated with active crown fire, increases when fire burns during the red (or epidemic or overstory mortality) phase due to lower moisture content and increased flammability of the dead foliage and fine fuels (Hicke et al., 2012a; Hoffman et al., 2012a; Jolly et al., 2012a; Perrakis et al., 2014; Sieg et al., 2017) (Table 4). After the red phase, canopy bulk density substantially decreases, reducing active crown fire potential (DeRose and Long, 2009; Simard et al., 2011; Hicke et al., 2012a; Donato et al., 2013; Hansen et al., 2015; Andrus et al., 2016; Meigs et al., 2016; Sieg et al., 2017; Woolley et al., 2019). DeRose and Long (2009) found that crown fire was reduced for over two decades following an outbreak of the spruce beetle. However, Hansen et al. (2015) found that the increase in surface and ladder fuels increased the potential for passive crown fire 15–20 years after bark beetle outbreak in ponderosa pine.

Forest composition prior to the outbreak as well as outbreak rate and severity can have a large influence on fuels in the red, gray, and regeneration phases. For example, in the Rocky Mountains and parts of the Cascade Range, Engelmann spruce and subalpine fir may be abundant in lodgepole pine stands, either as understory or co-dominant trees, which can influence fuels organization after the lodgepole pine dies (Klutsch et al., 2011). Seven years after the outbreak, non-infested forest plots were more likely to have crowning fires than infested plots, and mountain pine beetle plots that were predicted to have crown fires were composed mainly of non-host conifers (Klutsch et al., 2011). Crown fire potential in lodgepole pine systems can depend on the abundance and continuity of surface fuels prior to the mountain pine beetle mortality event in addition to the changes in fuel following mountain pine beetle outbreak (Hoffman et al., 2012a).

Most studies of fires that have occurred after bark beetle outbreaks (especially in lodgepole pine) indicate that fire severity (typically reported as proportion of trees killed by the fire) is reduced in post-bark beetle impacted stands (Harvey et al., 2013; Agne et al., 2016; Andrus et al., 2016; Meigs et al., 2016; Talucci and Krawchuk, 2019; Hart and Preston, 2020) (Table 4). Some studies do not support this observation, especially when fire burns in the red phase (Prichard and Kennedy, 2014; Wayman and Safford, 2021) or in some gray phase (McCarley et al., 2017) and snag-fall phase forests when there are abundant live trees mixed with surface fuels (Stephens et al., 2022). The variability observed in models and in the field is likely because the effect of bark beetles on fire interacts with the temporal phase of the outbreak, amount of mortality, forest composition and structure, and fire weather (particularly wind) (Andrus et al., 2016; Sieg et al., 2017). In Alaskan boreal forest, Hansen et al. (2016) described spruce beetle (*D. rufipennis* (Kirby)) interactions with landscape structure and fire and found that in some scenarios wildfire was more likely in beetle-killed stands due to increases in surface and ladder fuels after outbreaks. The authors suggest that this is different from Rocky Mountain systems due to larger accumulations of surface fuels and higher likelihood of surface fuels carrying fire.

The complexities of surface fuels, forest composition, and regeneration following bark beetle outbreaks also lead to uncertainty about how these insects influence fuels and fire behavior in the longer-term following outbreaks (Jenkins et al., 2008; Jorgensen and Jenkins, 2011; Hicke et al., 2012a; Talucci and Krawchuk, 2019; Millar and Delany, 2019). After snag fall, coarse woody debris significantly increases, which in turn could increase fire residence time, smoke generation, and suppression difficulty (Klutsch et al., 2011; Harvey et al., 2014a). If associated vegetation, regeneration, litter, and fine fuels are mixed with larger 1,000 hr fuels it could increase fire spread rate and severity after the snag fall phase (Hansen et al., 2015) (Fig. 10a and b).

4.1.1. *Modeling fire behavior after bark beetles is difficult*

The difficulty in using models to predict how bark beetles will influence fire was brought to the fore when Simard et al. (2011) published a paper contending that the potential for active crown fire was reduced in the lodgepole pine forests across a chronosequence of time-since-mt. pine beetle outbreak in the Yellowstone region (Wyoming, USA). Subsequent rebuttals from Moran and Cochrane (2012), and Jolly et al. (2012b) were critical of modeling methods and pointed out the difficulty in using some models to predict fire behavior, especially the transition from surface to canopy fire in mt. pine beetle-lodgepole pine impacted stands that have heterogenous fuels structures. In addition, they contended that foliar moisture content must be correctly estimated, especially in the red stage, that increased surface fuels must be considered, and that fire behavior models need to improve to capture these dynamics. Simard et al. (2012) responded that there is a lot of variation in

Table 5
Original published research papers on bark beetle influence on fuels and fire behavior and severity in the western US. Syntheses are not included in this list. MPB = mountain pine beetle.

Beetle and Host	Region	Measurements	Key findings	Reference
All bark beetles and hosts	Western United States	Aerial detection survey (bark beetles) and monitoring and burn severity database (fire).	Between 0.5 and 1.1% of wildfires burned in beetle killed timber indicating that fire is not burning more often in beetle killed timber.	Hicke et al. (2016)
Mountain pine beetle (MPB) and lodgepole pine	Yellowstone National Park	Ground based measurements	Severe pre-fire damage increased likelihood of crown fire although intermediate pre-fire damage reduced the likelihood of crown fire.	Turner et al., (1999)
	Greater Yellowstone	Field measurements and modeling, green, red, and gray phase chronosequence.	Surface fuels did not differ among phases, but canopy fuels decreased. Active crown fire probability reduced by mountain pine beetle.	Simard et al., (2011)
	Greater Yellowstone	Ground based data of recent fire that burned green-attack/red stage and gray-stage	Outbreak stage and burning conditions control fire severity. Red phase fire most severe, gray stage fire severity declined with increasing pre-fire mortality. Extreme burning conditions overwhelm effect of bark beetles.	Harvey et al., (2014a)
	Northern Rocky Mountains USA	Field measures of fire severity in mountain pine beetle impacted areas that burned	Outbreak severity (red and gray phases) unrelated to subsequent fire severity. In gray stage, surface fire severity increased with outbreak severity only during extreme burning conditions.	Harvey et al., (2014b)
	Northwestern Colorado	Modeled extent and severity of fire in relation to several disturbance types, including mountain pine beetle	Fire extent not related to disturbance and mountain pine beetle. Fire severity was not related to bark beetle outbreaks.	Kulakowski and Veblen, (2007)
	Northern Colorado and Southern Wyoming	Dendrochronology used to investigate pre-fire history of mountain pine beetle in 20 burned and 20 unburned stands	Burned stands not effected by outbreaks that had occurred prior to fires. Weather more important than bark beetles.	Kulakowski and Jarvis, (2011)
	North-Central Colorado	Ground based plot data 7 yr after mountain pine beetle outbreak initiation, and fire modeling	Uninfected plots had proportionally more crown fire than infested plots. Crown fire strongly influenced by non-host abundance. Surface fire intensity increased by mountain pine beetle. Tree species composition pre and post bark beetle strongly influence fire.	Klutsch et al., (2011)
	Central Oregon and Central Idaho	Numerical simulation crown fire hazard during red phase.	Preoutbreak forest structure and bark beetle morality amount influence crown fire behavior in red phase, but effect varies with spatial heterogeneity.	Hoffman et al., (2012a)
	North-Central Colorado and Western Montana	Measured fuel characteristics and ignition potential of lodgepole pine foliage in green, recently attacked, and red phase	Foliage moisture content least in red foliage compared to green and recently attacked. Changes in foliar chemistry cause red foliage to ignite quicker with less heat. Imply higher crown fire potential in red phase.	Jolly et al., (2012a)
	Central Oregon and Central Idaho	Simulation modeling, red phase, crown fire behavior across a range of surface fire intensities.	Simulated crown fire occurance increased as a function of surface fire intensity; preoutbreak surface fuels important in red phase fire behavior.	Hoffman et al., (2013)
	Montana	Modeling wind flow and fire rate-of-spread	Wind flow within canopy increases due to tree mortality. Changes in rate of spread were related to amount and continuity of mortality. Rate of spread increased in red phase but fire rate of spread declined following canopy fuels reduction (gray phase).	Hoffman et al., (2015)
	Northern Colorado	Empirical data used to predict potential fire behavior with models in pre, red phase, gray phase and older phase	Risk of active crown fire elevated in mountain pine beetle effected stands but crown fire is similar across all mountain pine beetle stages. Surface fuels increase in gray and old stage which increased surface fireline intensity. Fire weather important.	Schoennagel et al., (2012)
	British Columbia	Modeling wildfire spread from experimental fires and wildfire in red phase	Fires had faster rate of spread and more crown fire than predicted (red phase only).	Perrakis et al., (2014)
	Eastern Cascades, Central Oregon	Ground based fire severity metrics	Fire severity decreased with increasing beetle mortality in gray phase.	Agne et al., (2016)
	Eastern Cascades, Central Oregon	Lidar remote sensing of canopy loss after fire	Canopy loss from fire increased with increasing mountain pine beetle mortality in gray phase. Contrary to other studies	McCarley et al., (2017)
	South Central Oregon	Ground based metrics of fuel across a 32 year chronosequence of time since beetle outbreak initiation	Changes in fuels over time associated with basal area of live and standing dead trees, canopy bulk density, canopy base height	Woolley et al., (2019)

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Table 5 (*continued*)

Beetle and Host	Region	Measurements	Key findings	Reference
			and canopy height. Canopy bulk density declined strongly after litter fall. Surface fuels increased with snag fall.	
	Central interior British Columbia	Ground based fire severity and postfire ecological effects in three fires burned in gray phase	No evidence of relationship between outbreak severity and fire severity. Beetle killed trees had deeper char than trees killed in fire.	Talucci and Krawchuk, (2019)
MPB and all hosts (*Pinus* species)	Cascade Range, Oregon	Tree mortality and surface fuels from remote sensing, aerial detection survey and ground plots, demonstration of mapping method.	MPB demonstrated both short- and long-duration spectral declines, and variable recovery rates. Spectral changes were related to tree mortality and down coarse woody debris.	Meigs et al., (2011)
	Oregon and Washington	Aerial survey remote sensing of fire, mountain pine beetle and western spruce budworm and Landsat-based fire extent	Likelihood of fire in mountain pine beetle impacted forest not consistently different from non-mountain pine beetle impacted forests.	Meigs et al., (2015)
	Oregon and Washington	Remote sensing (LandTrendr time series analysis)	Severity of fire generally lower following MPB and western spruce budworm (WSB) outbreaks. Severity declines over time following MPB and increases over time following WSB.	Meigs et al., (2016)
	Western United States	Remote sensing, superimposed bark beetle outbreaks area with wildfire activity for 3 peak years of wildfire activity during 2002–2014	No relationship between area burned during peak wildfire years and red phase or gray phase	Hart et al., (2015)
	Three landscapes; Ochoco Mts. in eastern Oregon, Yellowstone Central Plateau in Wyoming and Elkhorn Mts. in Montana	Modeled interaction of MPB and wildland fire for future climate and management scenarios	Incorporating MPB into landscape models critical for predicting forest and fuels composition and structure. MPB had little effect on the annual percent area burned.	Keane et al., (2022)
Douglas-fir beetle and Douglas-fir	Greater Yellowstone	Ground based fuel metrics	Little effect on surface fuels except coarse woody debris 25–30 yrs. After red phase, canopy fuel load and bulk density decrease.	Donato et al., (2013)
	Eastern edge of Greater Yellowstone	Ground based fire severity metrics	No relationship of fire severity metrics with increasing bark beetle mortality except a decline in mean bole scorch. Topography and burning conditions (fire weather) were most important.	Harvey et al. (2013)
Complex of *Ips* species and Ponderosa pine	Arizona	Ground based metrics of fuel loading 5 years after bark beetle outbreak	Greater surface fuel and lower canopy fuel loading.	Hoffman et al. (2012b)
Pinyon Ips and pinyon pine	Arizona	Simulation modeling of pre outbreak, with red foliage, and post red foliage.	Fuel limited systems, sparse fuels overcome by red needles, increased wind penetration after needle fall, and increasing wind speeds.	Linn et al. (2013)
Spruce beetle and Engelmann spruce	Southern Utah	Field data and simulations (modeling)	Reduction of active crown fire for 1 or 2 decades, severity of beetle mortality and previous fire history important.	DeRose and Long (2009)
	South-central and southern Utah	Ground based fuels metrics in endemic, epidemic (red), and post epidemic (gray).	Fuels varied across the endemic, epidemic, and post epidemic phases with increased 100-hr and other fuels in epidemic phase. Post epidemic phase had less canopy fuels.	Jorgensen and Jenkins (2011)
	Colorado	Ground based fire severity metrics	Fire severity during gray phase was unrelated to pre-fire spruce beetle severity.	Andrus et al. (2016)
Western pine beetle, ponderosa pine, and drought	San Bernardino Mountains, California	Pre and post fire GIS data, red phase outbreak where fire occurred	No evidence pre fire tree mortality influenced fire severity.	Bond et al. (2009)
	California Sierra Nevada Mountains	Detailed analysis of one fire which occurred in ponderosa pine snagfall phase.	The mix of dead biomass and live tree density were associated with higher surface fuels and fire severity. The association of abundant live vegetation with the large amount of dead biomass created mass fire. The bark beetle -drought mortality event clearly had a major positive influence on the fire.	Stephens et al. (2022)
Western pine beetle and ponderosa pine. MPB and ponderosa pine, sugar pine, and lodgepole pine. Fir engraver and white and red fir. Jeffrey pine beetle and Jeffrey pine.	California Sierra Nevada Mountains	Ground based metrics measured after two fires in red phase	Fire severity increased with increasing prefire beetle mortality up to a point then plateaued.	Wayman and Safford (2021)
Ips and *Dendrotonus* species and ponderosa pine	Northern Arizona, southern Utah, and southwestern Colorado	Measured fuel parameters on long-term plots established after bark beetle outbreak across a range of severity. Modeled fire behavior in stands 15–20 years (old stage) after the outbreak.	Canopy bulk density decreased, but canopy base height was lower due to recruitment of seedlings and growth of surviving trees. Coarse fuels increased but fine fuels decomposed. Surface flame	Hansen et al. (2015)

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Table 5 (*continued*)

Beetle and Host	Region	Measurements	Key findings	Reference
			length, torching potential, and rate of spread all increased and probability of active crown fire decreased with increasing infestation severity.	
Ips and *Dendroctonus* species and ponderosa pine.	Northern Arizona	Modeled fire across range of fuel beds influence by bark beetles	Greatest fire severity in red phase. Bark beetle gray phase may buffer stand. Phase of outbreak, severity of bark beetle mortality and fire weather important.	Sieg et al. (2017)
Douglas-fir beetle and Douglas-fir, MPB and lodgepole pine, spruce beetle and Engelmann spruce	Intermountain West	Ground based fuels metrics in endemic, epidemic and post-epidemic stands. Modeled rate of spread, flame length and intensity.	Fuels changed with time and implied periods when high-severity fire would occur and when high-severity fire decreases.	Jenkins et al. (2008)
			Rate of fire spread and fireline intensity was higher in red phase stands due to increased mid-wind speed and not fuels. Post-epidemic stands had passive crown fire more common but active crown fire less likely.	
MPB and lodgepole pine, spruce beetle and Engelmann spruce	North Cascades, Washington	Used remote sensing to evaluate large fire complex for effects of silvicultural treatment and other factors including recent bark beetle outbreak on fire metrics	Red and mixed-phase bark beetle impacted stands were associated with higher burn severity.	Prichard and Kennedy, (2014)
MPB and lodgepole pine, Western pine beetle and ponderosa pine.	Idaho and Western Montana	Vegetation, surface fuels, and stand structure across post fire, post bark beetle and post bark beetle that then burned within 3–8 years.	Bark beetle outbreaks resulted in minimal differences in post-disturbance fuel complexes and vegetation succession. Disturbances are non-additive.	Stevens-Rumann et al., (2015)
MPB and whitebark pine	Eastern Sierra Nevada Mountains, California	Single fire burned from low to high elevation, including whitebark pine in gray stage after beetle outbreak. Field plots.	Fire severity was reduced due to mountain pine beetle in gray phase.	Millar and Delany, (2019)

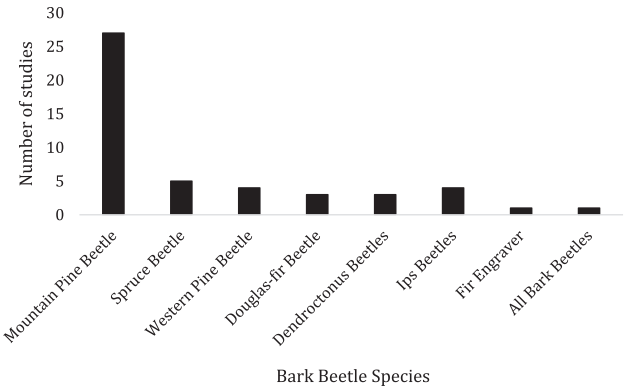

Fig. 9. Number of original studies in the western US on major bark beetle taxa and their effect on fuels and/or fire. Data based on studies in Table 5, which the authors have developed as a complete list of all original studies in western US.

the proportion of trees killed in a stand by mt. pine beetle, and therefore, one cannot assume there is a large difference in post-mt. pine beetle stands from non-attacked stands, that beetle-caused mortality is not a single-year event, but can occur in a stand for over a decade complicating canopy and surface fuels responses, and that one cannot assume fine surface fuels will increase in all cases.

Stephens et al. (2022) note that the mass fire behavior created by bark beetle/drought caused tree mortality combined with high tree density, was not predicted by operational fire behavior models in the forests of the southern Sierra Nevada Mountains, California. Mass fire is an extreme example of fire – fire interactions where strong indrafts cause the outward propagation of fire to be minimal, the fire has tall convective columns and burns for long durations so that all the fuel is consumed within the fire perimeter (Finney and McAllister, 2011). The operational fire behavior models described by Stephens et al. (2022) were not able to predict the mass fire behavior that occurred in one particular fire because they do not include post-frontal combustion, nor do they account for fire-atmosphere interactions that are particularly important for mass fire.

4.1.2. *Are fires more likely to occur after bark beetle outbreaks?*

Multiple studies have found no relationship between bark beetle outbreaks and fire occurrence and/or likelihood. Hart et al. (2015) noted that the area burned in the western US has not increased in direct response to bark beetle activity but rather is associated with climatic drivers. Meigs et al. (2015) concluded that within Oregon and Washington, fire and mountain pine beetle each occur on less than 2% of the landscape each year, and the potential for overlap is generally limited because the phenomena themselves are too rare on the landscape. Hicke et al. (2016) evaluated areas burned after bark beetle outbreaks in western United States from 1997 to 2010 and found that 1.1% of the total area of bark beetle-caused mortality subsequently burned in fire, representing 1.3% of the total area burned by fire. Keane et al., (2022) modeled the interaction of mountain pine beetle and wildfire for future climate and management scenarios in three western landscapes. They found that mountain pine beetle was not associated with increases in annual percent landscape burned.

4.2. *Defoliators, fuels, and fire*

The western spruce budworm and Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough)) (Lepidoptera: Erebidae) are particularly important in the western US due to widespread defoliation of Douglas-fir and true firs (*Abies* species) (Brookes et al., 1978; 1987). Fire suppression has caused an increase in density and predominance of susceptible host species (white fir, grand fir and Douglas-fir) across landscapes in the western US, and outbreaks have increased in duration and severity (Anderson et al., 1987; Swetnam and Lynch, 1993). A particularly large outbreak of western spruce budworm in the Pacific Northwest occurred from 1980 to 1994 and defoliated over 2 million ha (Sheehan, 1996). Key impacts to trees from defoliation include foliage removal, top dieback, whole tree mortality, and increased susceptibility to bark beetles (Brookes et al., 1987). There is a distinct time-since-defoliation event effect on forest structure (Meigs et al., 2011) as dead tops will eventually fall out of the tree, defoliation-caused mortality of host trees favors non-

Fig. 10. Differences in surface fuels complexes 21 – 28 years post-mountain pine beetle outbreak in south central Oregon lodgepole pine. Abundant regeneration and dwarf mistletoe infected trees mixed-with snag fall (a). Less regeneration and live material mixed-with snag fall material (b). Variation in long-term vegetation development leads to very different outcomes if the site burns.

host trees, and understory host trees are routinely killed (Brookes et al. 1987). Mortality from defoliation can vary from 0 to over 90% of host trees, while mortality can lag after the onset of defoliation by 3 or more years (Alfaro et al., 1982). The effect on forest structure is strongly related to the number of years of defoliation as top die-back, canopy tree mortality, and understory tree mortality increase with the increasing number of years of defoliation and severity of defoliation (Alfaro et al., 1982; Brookes et al., 1987). The greatest amount of mortality tends to be in host trees occupying the suppressed and intermediate crown positions (Filip et al., 1993).

The general conclusion of studies investigating western spruce budworm and fire is that there is potential for fire hazard to be reduced, and fire is less likely to occur in areas where western spruce budworm outbreaks have occurred (Hummel and Agee, 2003; Cohn et al., 2014; Flower et al., 2014; Meigs et al., 2015; 2016; and Vane et al., 2017), but the literature is scarce regarding other defoliators. Cohn et al. (2014) and Vane et al. (2017) used models to determine that western spruce budworm defoliation reduced the potential for torching and crowning, and the impact can last for decades. Hummel and Agee (2003) showed that canopy closure decreased following an outbreak but that surface fuels increased. Their model suggested that subsequent fire would not be stand-replacing, and although flame lengths increased, there were no major changes in torching potential and independent crown fire behavior. Meigs et al. (2016), using remote sensing data of fires in defoliated sites, concluded that fire severity was generally lower after a western spruce budworm outbreak but increased with time-since-defoliation event. Flower et al. (2014) using a dendrochronological approach and Meigs et al. (2015) using a remote sensing approach found that wildfire likelihood is generally unaffected or reduced following western spruce budworm defoliation. However, Meigs et al. (2015) do note that one fire complex (B&B Fire in Oregon, 2003) occurred where there was significant western spruce budworm activity previously in the area of the fire.

Defoliators including western spruce budworm and Douglas-fir tussock moth can temporarily influence moisture dynamics of fuels in the canopy by leaving partially eaten and dead foliage in the crown (Brookes et al, 1978; 1987). The larch casebearer (*Coleophora laricella* (Hubner) (Lepidoptera: Coleophoridae) is a non-native invasive defoliator of western larch that feeds on the interior leaf contents, hollowing out leaves (Ryan et al., 1987) (Fig. 11). A substantial portion of defoliated tree crown can consist of dead, hollow needles that are presumably drier and more flammable than healthy leaves which could influence fire behavior by increased torching in western larch stands.

4.3. *Other insect groups, fuels, and fire*

The interaction between fire and native wood boring insects, sap-feeders, and other root, bark, and tip feeding insects are poorly studied, possibly because these native BDAs do not cause widespread nor frequent mortality of trees (Furniss and Carolin 1977). However, these insects can influence tree crown fuel dynamics of trees by killing the leader, branch tips, whole branches, and cause resinosis and stem deformations (Fig. 12). In some situations, whole trees can be killed (Hagle et al., 2003; Wood et al., 2003; Forest Health Protection, Rocky Mt. Region 2010; Forest Health Protection, Southwest Region, 2013: Goheen and Willhite, 2021). Although these less-studied insects independently create a small impact on fire risk, over time they collectively contribute to the spatial heterogeneity of forests at stand and landscape scales. Depending on the season and amount of damage, there may be instances when these fuels structures increase or decrease the potential for active crown fires. For example, the flatheaded fir borer (*Phaenops drummondi* Kirby) (Coleoptera: Buprestidae) is currently associated with Douglas-fir tree mortality in northern California and southwestern Oregon at lower elevations and apparently driven by drought (Buhl et al. 2018). Non-native, invasive pests, such as balsam woolly adelgid and the spruce aphid, pose significant threats to forests in the western US, but their influence on fire is still unclear.

4.4. *Root diseases, fuels, and fire*

While not extensively studied, the relationship of root diseases to fire is likely very important because these pathogens play a major role in determining forest structure and function in the western US (Hansen and Goheen, 2000; Hansen and Stone, 2005; Hessburg et al. 1994; Lockman and Kearns, 2016; Barrett and Robertson, 2021). Lundquist (2007) found root diseases were the most important BDA contributor to surface fuels loadings in ponderosa pine forests in the Black Hills of North Dakota. Due to the spatiotemporal variability of root diseases, their effects on fuels and fire are dynamic, complex, and influenced by factors such as forest region, host distribution, stand age and history, as well as forest management. Potential interactions of root diseases with fire are further complicated by the spatial distribution of disease in a stand (dispersed versus gap-creation), the age of infection centers, and host versus non-host spatial patterns at stand and landscape scales. Root diseases can occur dispersed through a stand or in spatially distinct root disease centers (Fig. 13). Root diseases also affect forest composition by removing host species and facilitating replacement by tree species more resistant to disease (Hansen and Goheen, 2000; Hawkins and Henkel, 2011).

Although root diseases are depicted in Fig. 3 as chronic mortality

Fig. 11. Larch casebearer foliage feeding in western larch. Foliage that has been hollowed out and remains attached to the tree (a). Young stand impacted by larch casebearer defoliation (b). Note the potential for fire spread in the young stand.

Fig. 12. Branch tip mortality caused by the gouty pitch midge (*Cecidomyia piniinopis* Osten Saklen) (Diptera: Cicidomyiidae). This type of disturbance may increase crown flammability. Photo: Kenneth E. Gibson, US Forest Service, Bugwood.org.

Fig. 13. Spatially distinct root disease centers caused by *Armillaria* species in western Montana. There are three distinct circular patches on the foreground slope from bottom to top. Note the influence on canopy connectivity (reduced). Photo: Ralph Williams, USDA Forest Service, Bugwood.org.

agents that act at the tree and stand scale, they create fine-scaled heterogeneity in forest structure. In addition, although the number of trees killed per unit area is relatively low compared to episodic insect outbreaks, gaps created by chronic activity may persist for centuries (Dickman and Cook 1989) and create landscape scale heterogeneity. Spread rates are very slow, and the localized influence on mortality is chronic if host species are present. Spread rates have been estimated for root diseases that spread vegetatively from distinct infection centers: Cook, (1982, cited in Dickman and Cook 1989) estimated radial spread of *C. sulphurascens* (laminated root rot) at ca. 0.3 m/year in mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.); Hansen and Goheen (1988) estimated the radial spread of *Leptographium wageneri* (W.B. Kendrick) M.J. Wingfield) (black stain root disease) infection centers in Douglas-fir plantations at 0.9 m/year; and Ferguson et al., (2003) summarized published rates of spread for *Armillaria ostoyae* Romagn. (Armillaria root disease) at between 0.22 m/year to 1.3 m/year.

The impacts of root disease on some forests of the western US are thought to have increased over the past ~ 100 years in dry forests because fire exclusion increases the density of relatively shade-tolerant conifers such as grand/white fir and Douglas-fir (Hessburg et al., 1994; Hessburg et al., 2016; Thies, 2001; Merschel et al., 2021). These conifers are highly susceptible to root disease, while the increased tree density increases root-to-root contact, facilitating spread. In addition, stumps are inoculum refugia for many root disease fungi, and cutting of large trees left many large stumps in the western landscapes (Thies, 2001). In the long-term, root disease can persist for millennia on a site (Dickman and Cook, 1989; Ferguson et al., 2003), and any susceptible hosts that re-invade can be infected. The potential for self-limiting by root diseases is influenced by the regeneration of host vs non-host trees in disease centers. However, even conifers considered non-hosts can be infected by most conifer root diseases, and they allow the root disease fungi to persist on the site even they do not cause significant mortality (Hansen and Goheen 2000).

Fields (2003) investigated root diseases caused by *Armillaria* species and *Heterobasidion annosum* (probably *H. occidentale* Ostrosina and Garbel.) in mixed-conifer forests of the Deschutes National Forest in Oregon. The amount of coarse woody debris was positively correlated with root disease occurrence, while there was no change in the upper canopy cover, mid-canopy cover decreased, and lower canopy cover increased with increasing root disease. Johnson (2012) investigated fire and *Armillaria* root disease in ponderosa pine in eastern Washington, finding that overstory canopy cover decreased, the abundance of ladder fuels did not change, and the potential for crown fire thus decreased. However, 100-hr and 1,000-hr surface fuels increased in diseased plots, while there was no difference in 1- and 10-hr fuels. Johnson (2012) also found that models predicted lower rate of spread and flame length in the disease centers and therefore concluded that root disease may decrease fire severity.

Root disease pathogens influence forest fuels by causing tree mortality, top dieback, reduced growth, and crown decline at relatively slow rates compared to episodic BDAs like mountain pine beetle (Hansen and Goheen, 2000) (Fig. 7). Surface fuels increase due to tree mortality and tree fall because of root diseases (Fields, 2003, Johnson, 2012), especially 1000-hr fuels. However, the rate of tree mortality caused by root disease varies considerably, and surface fuels may not increase if decomposition exceeds inputs of large trees. Regeneration within gaps created by root disease is also complex, and there may be dense shrubs or regeneration within these gaps (Holah et al., 1997), which could increase vulnerability to torching.

Root diseases can form large infection centers in some forest types (Figure, 13, 14a). At high elevations of the Pacific Northwest, laminated root rot (*Coniferiporia sulphurascens* (Pilát) L.W. Shou & Y.C. Dai) is a significant disease of mountain hemlock, creating large canopy gaps along the Cascade crest where snowfall is high (Dickman and Cook, 1989) (Fig. 14a). *Armillaria* root disease is also known to form large infection centers in the western US, especially in dry mixed-conifer forests (Ferguson et al., 2003; Lockman and Kearns, 2016) (Fig. 13). Ferguson et al., (2003) described a single genet causing an infection center estimated to cover 965 ha and persisting over 2000 years old in the mixed-conifer forests of northeastern Oregon.

Over time, root diseases may cause a decrease in canopy fuels attributes, such as canopy bulk density and canopy continuity. In one anecdotal case, the 1996 Charlton Fire burned about 10,000 acres of mountain hemlock forest near Waldo Lake, Oregon, in a mostly high-severity fire. However, there were some areas of moderate-severity fire near the margins of the burn (Fig. 14b), some of which clearly align with a large patch of laminated root rot from pre-fire imagery (Fig. 14a), implying that the reduced canopy connectivity due to root disease-caused mortality may have reduced fire severity in the root disease center.

4.5. Other pathogen groups, fuels, and fire

Native live wood decays, foliage pathogens, canker, branch and tip dieback fungi, and rust fungi and leafy mistletoe (Hagle et al., 2003; Wood et al., 2003; Forest Health Protection, Rocky Mt. Region 2010; Forest Health Protection, Southwest Region, 2013: Goheen and Willhite, 2021) are not well studied for their relationships to fuels and fire in the

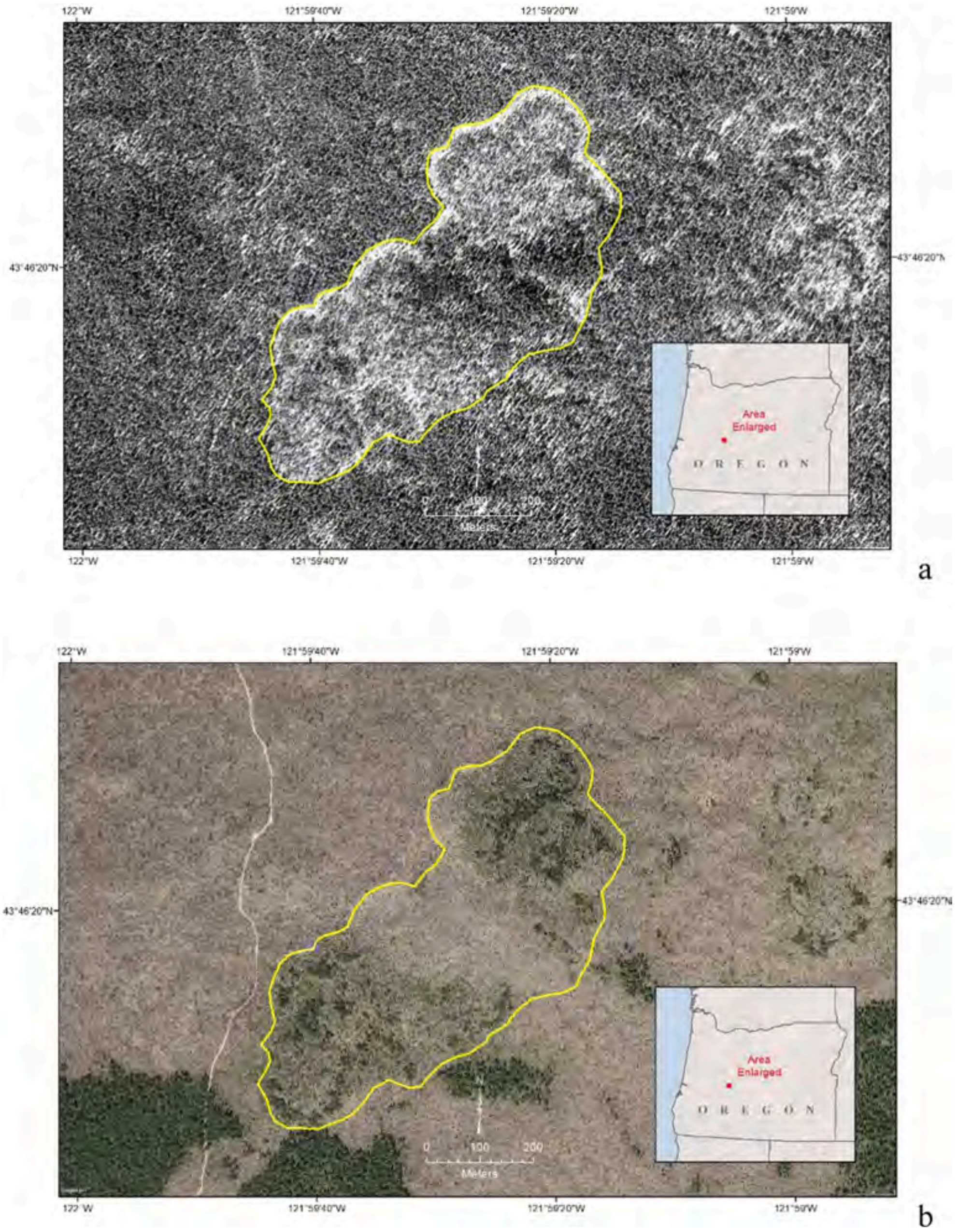

Fig. 14. A laminated root rot disease center in mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) forests in 1994. Google Earth image from 2012 (a). The same location in 2012 after the 1996 Charlton Fire (b). Note the moderate-severity fire patterns near the margin of the 1996 Charlton Fire. The yellow outline delineates the infection center in 1994 and after the fire in 2012. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

western US, likely because they do not cause widespread whole-stand mortality except under exceptional conditions. Foliage diseases of conifers, however, can manifest as outbreaks across wide regions (Woods et al., 2005; Lee et al., 2017; Shaw et al., 2021) and reduce canopy bulk density by causing needle loss, top dieback, and whole tree mortality. The severe loss of canopy foliage may cause an increase in the abundance of understory vegetation (Bladon et al., 2019) that could influence surface fire. Fuels structures such as resin-soaked stems and branches, and witches' brooms caused by rusts, or abundant dead branches and branch tips caused by canker fungi, may increase flammability of tree crowns under some conditions where fresh-dead material is abundant with a tree crown (Rocca et al, 2020, Balaguer-Romano et al., 2020). While live tree wood decay fungi can decompose wood in live trees, this tends to be in the form of root, butt, trunk, and top rots. How these decays might influence flammability of stems is not well documented, but severely decayed trees are more prone to wind-snap and may contribute to surface fuels in this way (Lundquist, 2007).

4.6. *Dwarf mistletoes, fuels, and fire*

Fire is a major control on the local distribution and persistence of dwarf mistletoes in the western US (Wicker and Leaphart, 1974; Alexander and Hawksworth, 1975; 1976; Parker et al., 2006; Shaw and Agne, 2017). Both active and passive crown fire kills dwarf mistletoe either directly or indirectly by killing the host tree, while surface fire can kill trees too. Surface fire that does not kill the tree and partial crown scorching may also reduce dwarf mistletoe infections by killing branches in the lower crown and heating aerial shoots. Fire is the key determinant of dwarf mistletoe distribution on the landscape, with time-since-fire interacting with host abundance and succession to control local abundance and infection severity (Wicker and Leaphart, 1974; Alexander and Hawksworth, 1976; Shaw and Agne, 2017). Fire suppression is thought to have increased the abundance of dwarf mistletoes, although changes in forest succession to non-hosts could decrease abundance (Alexander and Hawksworth, 1976). Tree growth may be slowed by dwarf mistletoe, while branch dieback and top dieback, as well as tree mortality of heavily infected trees are common (Hawksworth and Wiens, 1996, Mathiasen 1996). Dwarf mistletoe spreads by explosive discharge of the seed, which can be up to about 16 m, although most seed are intercepted within 2 – 4 m (Robinson and Geils, 2006).

Dwarf mistletoe can interrupt plant hormones and cause formation of profusely branched structures called witches' brooms, creating dense masses of distorted host branches (Hawksworth and Wiens, 1996) that elevate crown fuels. Brooms are significant fuels structures due to the density of branching, resin exudates, and accumulation of litter in the brooms (Shaw and Agne, 2017) (Fig. 15). Dwarf mistletoe tends to infect branches in the lower crowns more abundantly, where it persists longer than uninfected branches and increases torching and crown consumption due to ladder fuels (Parker et al. 2006. Shaw and Agne, 2017) (Fig. 15). Parker et al. (2006) contend that dwarf mistletoe infested stands are at generally greater risk of high-intensity fire because of increased surface fuels and increased flammability of heavily infested tree crowns.

In ponderosa pine, fuel loadings were not strongly influenced by dwarf mistletoe (Hoffman et al., 2007; Stanton, 2009). However, Koonce and Roth (1985) found an increase in fine surface fuels and brooming, and Stanton and Hadley (2010) documented a decrease in canopy base height in ponderosa pine. Shaw and Agne (2017) noted a decrease in tree density and size, as well as canopy base height in lodgepole pine of south-central Oregon with increasing stand-level dwarf mistletoe infection, while surface fuels and ladder fuels were not significantly influenced. However, Ritter et al. (2017) documented an increase in surface fuel loadings in Central Colorado lodgepole pine, but also found that live basal area, average tree size, canopy base height, canopy fuel load, and canopy bulk density were negatively correlated with increasing dwarf mistletoe stand-level severity. Ritter et al. (2017) concluded that although surface fuels increased, infested stands have lower canopy fuel abundance, which may influence fire behavior.

Fig. 15. Douglas-fir dwarf mistletoe (*Arceuthobium douglasii* Engelm.) causing brooming of branches in Douglas-fir. Brooms can also be seen in background, left also. Note how brooms may persist in the lower crown with the potential to influence ladder fuels and torching of crowns.

Hoffman et al. (2007) modeled fire rate of spread, fireline intensity, and flame length, and found no relationship with dwarf mistletoe infections in ponderosa pine. However, they found that lower wind speeds were required to transition from surface to canopy fire. Agne (2013) modeled active crown fire in lodgepole pine in south-central Oregon. She found that at low to moderate wind speeds, torching can increase as the abundance of dwarf mistletoe infections increased in the stand, but there was no effect with high wind speeds, and the potential for active crown fires was low across all severity classes. Stanton (2009) compared infected and uninfected ponderosa pine stands and found that fire behavior was similar in both stand types, although there were differences in burning temperature and duration. Turner et al. (1999) studied lodgepole pine fire in stands influenced by bark beetle and dwarf mistletoe, finding that stands severely influenced by either mountain pine beetle or dwarf mistletoe had a higher likelihood of crown fire, while stands with moderate damage were less likely to have crown fire. Crown scorch has been found to be more likely in heavily infected ponderosa pine during prescribed fire than in uninfected or lightly infected stands (Harrington and Hawksworth 1990, Conklin and Geils 2008).

4.7. *Invasive species including Phytophthoras*

Invasive species that cause mortality in host trees, such as sudden oak death, Port Orford cedar root disease, white pine blister rust, and balsam woolly adelgid, typically move into an area, cause significant mortality, and then become chronic mortality agents once naturalized. The larch casebearer and spruce aphid invade and then become cyclic defoliators once naturalized and may cause some mortality. There are concerns that white pine blister rust in high elevation whitebark pine (*Pinus albicaulis* Engelm.), and balsam woolly adelgid in high elevation subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall), which both are associated with tree decline and mortality, will increase fire severity at treeline, however data are limited; white pine blister rust was not associated with previous fires in the Sierra Nevada Range (Dudney et al., 2020). At this time, it appears that sudden oak death in California has been the primary invasive species studied regarding influence on fuels, fire behavior, and fire severity in the western US (Kuljian and Varner 2010; Metz et al., 2011; 2013; 2017; Valachovic et al. 2011, Forrestel et al., 2015, Cobb 2022).

Phytophthora ramorum kills hardwoods that grow intermixed with conifers, but does not kill California coastal conifers typically (Cobb 2020). The accumulation of dead fuels around the conifers appears to be a major fuels consequence of mortality, but the effect can be ephemeral after all available hosts are killed (Fig. 7). The stage of the invasion by *P. ramorum* influenced fire outcomes, with recently invaded forests showing increased overstory burn severity, but not in areas with longer term disease presence, which showed increased substrate burn severity (Metz et al. 2011). Dead leaves and litter of tanoak (*Notholithocarpus densiflorus* (Hook. & Am.) Manos. Cann & S.H. Oh) killed by *P. ramorum* had low moisture content reducing the canopy base height needed to transfer from surface to crown fire (Kuljian and Varner, 2010). Shaw et al. (2017), working in coast live oak (*Quercus agrifolia* Née) forests, found that within distinct mortality patches, surface and ladder fuels were greatly increased. Modeled fire behavior in sudden oak death impacted Douglas-fir-tanoak forests demonstrated that rates of spread, flame lengths, fire line intensities and surface fire intensities may significantly increase over the uninfected baseline (Valachovic et al., 2011; Forrestel et al., 2015). In addition, there was unexpected coast redwood (*Sequoia sempervirens* (D. Don) Endl.) mortality in coastal California fires from the synergistic effect of wildfire and increased surface fuel loading from sudden oak death caused mortality (Metz et al., 2013). Hardwood mortality was associated with increased burn residence time which overwhelmed the usual ability of coast redwood (thick bark) to withstand fire.

5. BDAs, fire, and climate change

Changing climate and drought are affecting both wildfire and BDAs across the western US due to increased growing season temperature, decreased growing season precipitation, increased length of the growing season, warmer winters, reduced snow accumulation, increasing extreme events, and the influence of drier fuel conditions occurring for a longer duration and earlier in the season (McKenzie et al., 2009; Bentz et al., 2010; O'Connor et al., 2015: Abatzoglou and Williams, 2016; Kolb et al., 2016; Agne et al., 2018; Stephens et al., 2018; Littell, 2018; Cassell et al., 2019; Voelker et al., 2019; Hennon et al., 2021). In a modeling study of future climate and management interactions with mountain pine beetle and wildland fire in pine dominated forest systems, Keane et al., (2022) contend that it is necessary to incorporate mountain pine beetle into landscape models because of their ubiquitous influence on pine forest composition and structure. In addition, they don't predict that area burned by fire will increase due to mountain pine beetle activity.

Drought stress can exacerbate the effects of BDAs on tree primary productivity and survival (Bell et al., 2019), resulting in increased risk of tree mortality, wildfire, and erosion and sedimentation, most notably in the Pacific Southwest (Clark et al., 2016). However, the influence of BDAs on wildfire may be diminished as severe fire weather becomes increasingly common and widespread in the western US (Hart and Preston, 2020), as evidenced by the very extensive fire events associated with extreme weather that burned in eastern Washington during 2015 (Engel et al., 2019), western Oregon in 2020 (Abatzoglou et al., 2021), and California since 2017 (e.g., Williams et al., 2019).

Severe fire weather, which is occurring more often, can overwhelm the influence of BDAs on fuels during a fire (Harvey et al., 2014a; Sieg et al., 2017). Drought, either alone or in combination with BDAs, has a strong influence on fuel moisture condition, increasing the flammability of both live and dead fuels (Abatzoglou and Williams, 2016). At large spatial scales, wildfires in the western US are driven more by weather and topography than by BDA-induced changes in fuels (Hart and Preston 2020). At the stand level, the reverse may be true, but the time-since-event effects on fuels, flammability, and fire severity remain widely applicable (Hart et al. 2015; Meigs et al. 2016). Bark beetles have caused tree mortality across 7% of forested area in the western US over the past three decades (Hart and Preston 2020), yet the annual area burned has not increased in direct response to bark beetle outbreaks (Hart et al. 2015).

The 1990–2020 drought period in the western US has generally corresponded with larger fires and greater area burned (Wing and Long, 2015; Westerling, 2016; Littell, 2018; Engel et al., 2019), short interval reburns (Halofsky et al., 2020), and increased forest mortality and stress complexes (McKenzie et al., 2009; Halofsky et al., 2020). Climate projections suggest that hotter droughts such as those in recent decades will become more intense and prolonged due to hotter, drier summers and decreased snowpacks (Mote et al., 2019), and the fire regimes and area burned are projected to increase substantially in the western U.S. due to anthropogenic climate change (Abatzoglou and Williams, 2016; Kitzberger et al., 2017; McKenzie and Littell, 2017).

Future risks of drought- and insect-related tree mortality are also projected to increase substantially during the 21st century in California and the southwest but decrease in the PNW based on climate model projections using historical data records from forest inventories (Anderegg et al., 2021). An emerging theme of the influence of climate change on BDAs is the "rise of the secondaries", i.e., the pathogens and insects previously considered unimportant in tree mortality may become increasingly important as climate changes and tree stress increases (Cohen et al., 2016; Hennon et al., 2020). However, a recent assessment suggests that one reason predicting tree mortality from drought is so difficult is because BDA effects on tree mortality can confuse the predicted effects based on stress physiology (Trugman et al. 2021). Therefore, understanding both the proximate and ultimate causes of tree mortality during drought requires an understanding of BDAs and their specific host interactions in addition to organismal-level physiology and local site factors.

6. Conclusions

BDAs are pervasive across most landscapes in the western US, where they influence forest composition and structure (Table 2). Regional variation across the western US in how BDAs influence fuels and fire is significant due to the complexity of interactions, including the wide variability of BDA types and dynamics, changing climate, historic fire regimes, variation in the effects of land management and fire suppression, regional forest type differences, and abiotic disturbances (Hessburg et al. 2019). Our review found little evidence to support the common belief that BDAs predominantly increase the likelihood and severity of wildfire. In fact, native BDAs can act to mitigate negative fire outcomes by contributing to the structural diversity of fuels and increasing landscape heterogeneity. Although BDAs may increase fire severity in some instances or on some components of forest ecosystems, it is not possible to generalize that BDAs increase or decrease fire severity and risk.

We propose a framework to conceptualize these interactions by focusing on whether the BDA manifests as an outbreak or episode of tree defoliation and mortality, or whether the BDA acts as a chronic tree decline and mortality agent (Figs. 3, 6). This defines the rate and abundance of dead vs live fuels that are created and how the fuel strata will be influenced in the short- and long-term time scales (Fig. 7). BDAs shift live fuels to dead fuels with decreased moisture content and changes in chemistry and therefore may increase flammability of the canopy. As the dead material falls to the forest floor, canopy fuels decrease and surface fuels increase, but the rate of decomposition of surface fuels, especially finer fuels that are influential in fire spread, can ameliorate the effect. An increase in surface fuels can increase the potential for surface fires to transition to the canopy, increase fire rate of spread and flame height, and can increase fire residence time and therefore increase fire severity. However, the influence of BDAs on fuels and fires depends on initial forest composition, structure, and pattern, the specific BDA or BDAs modifying fuels, and the spatial and temporal variation in how fuels were modified. These complex interactions make it impossible to categorically state that BDAs increase or decrease fire likelihood, severity, or negative social-ecological outcomes. Finally, there is a need for more research concerning all BDA and their influence on fuels and fire as well as fire behavior models that take into account of the complexities of BDA created fuels.

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.

Data availability

Data will be made available on request.

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References

Abatzoglou, J.T., Williams, A.P., 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proc. Natl. Acad. Sci. 113 (42), 11770–11775.

Abatzoglou, J.T., Rupp, D.E., O'Neill, L.W., Sadegh, M., 2021. Compound extremes drive the western Oregon wildfires of September 2020. Geophys. Res. Lett. https://doi.org/10.1029/2021GL092520.

Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington D. C.

Agne, M.C., 2013. Influence of Dwarf Mistletoe (*Arceuthobium americanum*) on Stand Structure, Canopy Fuels, and Fire Behavior in Lodgepole Pine (*Pinus contorta*) Forests 21–28 Years Post-Mountain Pine Beetle (*Dendroctonus ponderosae*) Epidemic in Central Oregon. Oregon State University. Master's Thesis.

Agne, M.C., Shaw, D.C., Woolley, T.J., Queijeiro-Bolaños, M.E., 2014. Effects of dwarf mistletoe on stand structure of lodgepole pine forests 21–28 years post-mountain pine beetle mortality in central Oregon. PLoS ONE 9, e107532.

Agne, M.C., Woolley, T., Fitzgerald, S., 2016. Fire severity and cumulative disturbance effects in the post-mountain pine beetle lodgepole pine forests of the Pole Creek Fire. For. Ecol. Manage. 366, 73–86. https://doi.org/10.1016/j.foreco.2016.02.004.

Agne, M.C., Beedlow, P.A., Shaw, D.C., Woodruff, D.R., Lee, E.H., Cline, S.P., Comeleo, R. L., 2018. Interactions of predominant insects and diseases with climate change in Douglas-fir forests of western Oregon and Washington. For. Ecol. Manage. 409, 371–1332.

Aho, P.E. 1982. Indicators of Cull in Western Oregon Conifers. USDA Forest Service, General Technical Report PNW-144. Pacific Northwest Range and Experiment Station, Portland, OR.

Alexander, M.E., Hawksworth, F.G., 1975. Wildland fires and dwarf mistletoes: a literature review of ecology and prescribed burning. USDA For. Serv. Gen. Tech. Rep. RM-14.

Alexander, M.E., Hawksworth, F.G., 1976. Fire and dwarf mistletoes in North American coniferous forests. J. Forest. 74, 446–449. https://doi.org/10.1093/jof/74.7.446.

Alfaro, R.I., Van Sickle, G.A., Thomson, A.J., Wegwitz, E., 1982. Tree mortality and radial growth losses caused by the western spruce budworm in a Douglas-fir stand in British Columbia. Can. J. For. Res. 12, 780–787.

Anderegg, W.R.L, O.S. Chegwidden, G. Badgley, A. T. Trugman, D. Cullenward, J. T. Abatzoglou, J. A. Hicke, J. Freeman, and J. J. Hamman. 2021. Climate risks to carbon sequestration in US forests. bioRxiv (2021) doi: 10.1101/2021.05.11.443688.

Anderson, L., C.E. Carlson, and R.H. Wakimoto. 1987. Forest fire frequency and western spruce budworm outbreaks in western Montana. Forest Ecology and Management 22: 251-260. doi: 10.1016/0378-1127(87)90109-5.

Anderson, H. 1970. Forest fuel ignitibility. Fire Technology, 6, 312–319. https://doi.org/10.1007/BF025 88932.

Andrus, R.A., Veblen, T.T., Harvey, B.J., Hart, S.J., 2016. Fire severity unaffected by spruce beetle outbreak in spruce-fir forests in southwestern Colorado. Ecol. Appl. 26, 700–711.

Axelson, J., Battles, J., Bulaon, B., Cluck, D., Cousins, S., Cox, L., Estes, B., Fettig, C., Hefty, A., Hishinuma, S., Hood, S., 2019. The California Tree Mortality Data Collection Network—Enhanced communication and collaboration among scientists and stakeholders. Calif. Agric. 73 (2), 55–62.

Balaguer-Romano, R., Díaz-Sierra, R., Madrigal, J., Voltas, J., Resco de Dios, V., 2020. Needle senescence affects fire behavior in Aleppo pine (*Pinus halepensis* Mill.) stands: a simulation study. Forests 11:1054. https://doi.org/10.3390/f11101054.

Barrett, T.M., and G.C. Robertson (eds.). 2021. Disturbance and Sustainability in Forests of the Western United States. General Technical Report PNW-GTR-992., USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Bednářová, M., M. Dvořásk, J. Janoušek, and L. Jankovsky. 2013. Other Foliar Diseases of Coniferous Trees. Chapter 23, In; P. Gonthier and G. Nicolotti. Infectious Forest Diseases. Cabi, UK.

Bell, D.M., Pabst, R.J., Shaw, D.C., 2019. Tree growth declines and mortality were associated with a parasitic plant during warm and dry climatic conditions in a temperate coniferous forest ecosystem. Glob. Change Biol. https://doi.org/10.1111/gcb.14834.

Bentz, B.J., Régnière, J.R., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R. G., Negrón, J.F., Seybold, S.J., 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. Bioscience 60, 602–613. https://doi.org/10.1525/bio.2010.60.8.6.

Berryman, A.A., 1982. Biological control, thresholds, and pest outbreaks. Environ. Entomol. 11, 544–549.

Bladon, K.D., 2018. Rethinking wildfire and forest watershed management. Science 359 (6379), 1001–1002.

Bladon, K.D., Bywater-Reyes, S., LeBoldus, J.M., Keriö, S., Segura, C., Ritóková, G., Shaw, D.C., 2019. Increased streamflow in catchments affected by a forest disease epidemic. Sci. Total Environ. 691, 112–123. https://doi.org/10.1016/j.scitotenv.2019.07.127.

Blenis, P.V., Li, W., 2005. Incidence of main stem infections of lodgepole pine by western gall rust decreases with tree age. Can. J. For. Res. 35, 1314–1318. https://doi.org/10.1139/x05-059.

Bond, M.L., Lee, D.E., Bradley, C.M., Hanson, C.T., 2009. Influence of pre-fire tree mortality on fire severity in conifer forests of the San Bernardino Mountains, California. Open For. Sci. J. 2, 41–47.

Brookes, M.H., R.W. Stark, R.W. Campbell. 1978. The Douglas-fir Tussock Moth: A Synthesis. USDA Forest Service Technical Bulletin 1585, Washington D.C.

Brookes, M.H., Colbert, J.J., Mitchell, R.G., Stark, R.W., 1987.Western Spruce Budworm. USDA For. Serv. Tech. Bull. 1694. Washington, D.C.

Buhl, C. and others. 2018. Forest Health Highlights in Oregon 2017. USDA Forest Service, Pacific Northwest Region, Forest Health Protection and Oregon Department of Forestry. Available at; https://digital.osl.state.or.us/islandora/object/osl:506514.

Cassell, B.A., Scheller, R.M., Lucash, M.S., Hurteau, M.D., Loudermilk, E.L., 2019. Widespread severe wildfires under climate change lead to increased forest homogeneity in dry mixed-conifer forests. Ecosphere 10 (11), e02934.

Castello, J.D., and S.A. Teale (eds.). 2011. Forest Health: An Integrated Perspective. Cambridge University Press, NY.

Castello, J.D., Leopold, D.J., Smallidge, P.J., 1995. Pathogens, patterns, and processes in forest ecosystems. Bioscience 45, 16–24.

Chandler C, P. Cheney, P. Thomas, L. Trabaud, D. Williams. 1983. Fire in forestry. Volume I: Forest Fire Behavior and Effects. Wiley: New York.

Clark, J. S., L. Iverson, C. W., Woodall, C. D. Allen, D. M. Bell, D. C. Bragg, A. W. D'Amato, F. W. Davis, M. H. Hersh, I. Ibanez, and S. T. Jackson. 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. Global Change Biology 22(7): 2329-2352.

Cobb, R.C., 2022. The intertwined problems of wildfire, forest disease, and climate change interactions. Curr. For. Reports. https://doi.org/10.1007/s40725-022-00161-2.

Cobb, R.C., Haas, S.E., Kruskamp, N., Dillon, W.W., Swiecki, T.J., Rizzo, D.M., Frankel, S. J., Meentemeyer, R.K., 2020. The Magnitude of Regional-Scale Tree Mortality Caused by the Invasive Pathogen *Phytophthora ramorum*. Earth's. Future 8 (7). https://doi.org/10.1029/2020EF001500.

Cohen, W.B., Yang, Z., Stehman, S.V., Schroeder, T.A., Bell, D.M., Masek, J.G., Huang, C., Meigs, G.W., 2016. Forest disturbance across the conterminous United States from 1985–2012: The emerging dominance of forest decline. For. Ecol. Manage. 360, 242–252.

Cohn, G.M., Parsons, R.A., Heyerdahl, E.K., Gavin, D.G., Flower, A., 2014. Simulated western spruce budworm defoliation reduces torching and crowning potential: A sensitivity analysis using a physics-based fire model. Int. J. Wildland Fire 23, 709–720. https://doi.org/10.1071/WF13074.

Coleman, T.W., Graves, A.D., Heath, Z., Flowers, R.W., Hanavan, R.P., Cluck, D.R., Ryerson, D., 2018. Accuracy of aerial detection surveys for mapping insect and disease disturbances in the United States. For. Ecol. Manage. 430, 321–336. https://doi.org/10.1016/j.foreco.2018.08.020.

Conklin, D.A., Geils, B.W., 2008. Survival and sanitation of dwarf mistletoe-infected ponderosa pine following prescribed underburning. W. J. Appl. For. 23 (4), 216–222.

Cook, S.A. 1982. Stand development in the presence of a pathogen, *Phellinus weirii*. In Forest succession and stand development research in the Northwest. Edited by J. E. Means. Forest Research Laboratory, Oregon State University, Corvallis, OR. pp. 159–163.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Wotton, B.M., 2001. Climate Change and Forest Disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslide. Bioscience 51, 723–734. https://doi.org/10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2.

DeRose, R.J., Long, J.N., 2009. Wildfire and spruce beetle outbreak: Simulation of interacting disturbances in the central Rocky Mountains. Ecoscience 16, 28–38. https://doi.org/10.2980/16-1-3160.

Dickman, A., Cook, S., 1989. Fire and fungus in a mountain hemlock forest. Can. J. Bot. 67, 2005–2016.

Donato, D.C., Harvey, B.J., Romme, W.H., Simard, M., Turner, M.G., 2013. Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. Ecol. Appl. 23, 3–20.

Dove, N.C., Hart, S.C., 2017. Fire Reduces Fungal Species Richness and In Situ Mycorrhizal Colonization: A Meta-Analysis. Fire Ecol. 13, 37–65. https://doi.org/10.4996/fireecology.130237746.

Dudney, J.C., Nesmith, J.C.B., Cahill, M.C., Cribbs, J.E., Duriscoe, D.M., Das, A.J., Stephenson, N.L., Battles, J.J., 2020. Compounding effects of white pine blister rust, mountain pine beetle, and fire threaten four white pine species. Ecosphere 11 (10). https://doi.org/10.1002/ecs2.3263.

Dunham, P. 2008. Incidence of Insects, Diseases, and Other Damaging Agents in Oregon Forests. Resource Bulletin PNW-RB-257. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Edmonds, R.L., Agee, J.K., Gara, R.I., 2000. Forest Health and Protection. McGraw-Hill, New York.

Engel, R.A., Marlier, M.E., Lettenmaier, D.P., 2019. On the causes of the summer 2015 Eastern Washington wildfires. Environ. Res. Commun. 1 (1), 011009.

Ferguson, B.A., Dreisbach, T.A., Parks, C.G., Filip, G.M., Schmitt, C.L., 2003. Coarse-scale population structure of pathogenic Armillaria species in a mixed-conifer forest in the Blue Mountains of northeast Oregon. Can. J. For. Res. 33, 612–623. https://doi.org/10.1139/X03-065.

Fettig, C.J., Hood, S.M., Runyon, J.B., Stalling, C.M., 2021. Bark beetle and fire interactions in western coniferous forests: Research findings. Fire Manage. Today 79 (1), 14–23.

Fettig, C.J., Asaro, C., Nowak, J.T., Dodds, K.J., Gandhi, K.J.K., Moan, J.E., Robert, J., 2022a. Trends in bark beetle impacts in North America during a period (2000–2020) of rapid environmental change. J. Forest. 2022, 1–21. https://doi.org/10.1093/jofore/fvac021.

Fettig, C.J., Runyon, J.B., Homicz, C.S., James, P.M.A., Ulyshen, M.D., 2022b. Fire and insect interactions in North American Forests. Current Forestry Reports. https://doi.org/10.1007/s40725-022-00170-1.

Fields, K.N. 2003. Impact of Armillaria and Annosus Root Diseases on Stand and Canopy Structure, Species Diversity, and Down Woody Material in a Central Oregon Mixed-Conifer Forest. Oregon State University MS Thesis.

Filip, G.M., Colbert, J.J., Shaw III, C.G., Hessburg, P.F., Hosman, K.P., 1993. Influence of dwarf mistletoe and western spruce budworm on growth and mortality of Douglas-fir in unmanaged stands. For. Sci. 39, 465–477. https://doi.org/10.1093/forestscience/39.3.465.

Finney, M.A., McAllister, S.S., 2011. A review of fire interactions and mass fires. J. Combust. https://doi.org/10.1155/2011/548328.

Flower, A., 2016. Three centuries of synchronous forest defoliator outbreaks in western North America. PLoS ONE 11 (10). https://doi.org/10.1371/journal.pone.0164737.

Flower, A., Gavin, D.G., Heyerdahl, E.K., Parsons, R.A., Cohn, G.M., 2014. Western spruce budworm outbreaks did not increase fire risk over the last three centuries: A dendrochronological analysis of inter-disturbance synergism. PLoS ONE 9 (12). https://doi.org/10.1371/journal.pone.0114282.

Forest Health Protection, Rocky Mountain Region. 2010. Field Guide to Diseases and Insects of the Rocky Mountain Region. Gen. Tech. Rep. RMRS-GTR-241. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 10.2737/RMRS-GTR-241.

Forest Health Protection, Southwest Region. 2013. Field Guide to Insects and Diseases of Arizona and New Mexico Forests. MR-R3-16-3. Southwestern Region, USDA Forest Service, Albuquerque, New Mexico. (https://www.fs.fed.us/r3/resources/health/field-guide/pdf/FieldGuide_AZ_NM.pdf, last checked Dec. 15, 2021).

Forrestel, A.B., Ramage, B.S., Moody, T., Moritz, M.A., Stephens, S.L., 2015. Disease, fuels and potential fire behavior: Impacts of Sudden Oak Death in two coastal California forest types. For. Ecol. Manage. 348, 23–30. https://doi.org/10.1016/j.foreco.2015.03.024.

Furniss, R.L. and V.M. Carolin. 1977. Western Forest Insects. USDA Forest Service, Misc. Publication No. 1339. Washington, D.C.

Gara, R.I., W.R. Littke, J.K. Agee, D.R. Geiszler, J.D. Stuart, C.H. Driver. 1985. Influence of fires, fungi, and mountain pine beetles on development of a lodgepole pine forest in South-Central Oregon. Pages 153-162, in; D.M. Baumgartner et al., (eds.). Lodgepole Pine: The Species and it's Management, Symposium Proceedings. Washington State University, Pullman.

Geils, B.W., Cibrian-Tovar, J., Moody, B., 2002. Mistletoes of North American Conifers. Gen. Tech. Rep. RMRS-GTR-98. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT. 10.2737/RMRS-GTR-98.

Geiszler, D. R., Gara, R.I., Driver, C.H., Gallucci, V.F., Martin, R.E., 1980. Fire, Fungi, and Beetle Influences on a Lodgepole Pine Ecosystem of South-Central Oregon. Oecologia 46: 239–243.

Gibson, K., Negrón, J.F., 2009. Fire and Bark Beetle Interactions. Pg. 51-69, in; General Technical Report PNW-GTR-784, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Giunta, A.D., Runyon, J.B., Jenkins, M.J., Teich, M., 2012. Volatile and within-needle terpene changes to Douglas-fir trees associated with Douglas-fir beetle (Coleoptera: Curculionidae) attack. Environ. Entomol., 45(4), 2016, 920–929.

Goheen, E.M., Willhite, E.A., 2021. Field Guide to Common Diseases and Insect Pests of Oregon and Washington Conifers. Rev. ed. R6-FHP-RO-2021-01. Portland, OR: USDA Forest Service, Pacific Northwest Region.

Gonthier, P., and G. Nicolotti (Ed.). 2013. Infectious Forest Diseases. Cabi Press, Oxfordshire, UK.

Graham, R.T. S. McCaffrey, and T.B. Jain. 2004. Science basis for changing forest structure to modify wildfire behavior and severity. General Technical Report; RMRS-GTR-120. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins CO.

Hagle, S.K., K.E. Gibson, and S. Tunnock. 2003. Field Guide to Diseases and Insect Pests of Northern and Central Rocky Mountain Conifers. Report number R1-03-08. Missoula, Montana and Ogden, Utah: USDA Forest Service, Northern Region and Intermountain Region. https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5188654.pdf (checked Dec 15, 2021).

Hagmann, R.K., Merschel, A.G., Reilly, M.J., 2019. Historical patterns of fire severity and forest structure and composition in a landscape structured by frequent large fires: Pumice Plateau ecoregion, Oregon, USA. Landscape Ecol. 34, 551–568.

Hain, F.P. 1988. The Balsam Woolly Adelgid in North America. Chapter 5, in; A.A. Berryman (ed.). Dynamics of Forest Insect Populations. Springer, New York.

Halofsky, J.E., Peterson, D.L., Harvey, B.J., 2020. Changing wildfire, changing forests: the effects of climate change on fire regimes and vegetation in the Pacific Northwest, USA. Fire Ecology 16. https://doi.org/10.1186/s42408-019-0062-8.

Hamelin, R.C., 2013. Tree Rusts. Chapter 26, In; Infectious Forest Diseases. Cabi Press, Oxfordshire, UK.

Hansen, W.D., Chapin III, F.S., Naughton, H.T., Rupp, T.S., Verbyla, D., 2016. Forest-landscape structure mediates effects of a spruce bark beetle (*Dendroctonus rufipennis*) outbreak on subsequent likelihood of burning in Alaskan boreal forest. For. Ecol. Manage. 369, 38–46. https://doi.org/10.1016/j.foreco.2016.03.036.

Hansen, E.M., Goheen, D.J., 1988. Rate of increase of black-stain root disease in Douglas-fir plantations in Oregon and Washington. Can. J. For. Res. 18, 942–946.

Hansen, E.M., Goheen, E.M., 2000. *Phellinus weirii* and other native root pathogens as determinants of forest structure and process in Western North America. Annu. Rev. Phytopathol. 38, 515–539.

Hansen, E.M., Stone, J.K., 2005. Impacts of Plant Pathogenic Fungi on Plant Communities. Chapter 23, In; The Fungal Community. CRC Press, Boca Raton, FL.

Hansen, E.M., Johnson, M.C., Bentz, B.J., Vandygriff, J.C., Munson, A.S., 2015. Fuel loads and simulated fire behavior in 'old-stage' beetle infested ponderosa pine of the Colorado Plateau. For. Sci. 61, 644–664. https://doi.org/10.5849/forsci.14-081.

Hansen, E.M., Lewis, K.J., Chastagner, G.A., 2018. Compendium of Conifer Diseases, 2nd Edition. APS Press, St. Paul, Minnesota, USA.

Harrington, M.G., Hawksworth, F.G., 1990. Interactions of fire and dwarf mistletoe on mortality of southwestern ponderosa pine. USDA For. Serv. Gen. Tech. Rep. RM-191, 234–240.

Hart, S.J., Preston, D.L., 2020. Fire weather drives daily area burned and observations of fire behavior in mountain pine beetle affected landscapes. Environ. Res. Lett. 15 (5) https://doi.org/10.1088/1748-9326/ab7953.

Hart, S.J., Schoennagel, T., Veblen, T.T., Chapman, T.B., Franklin, J., 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. PNAS 112 (14), 4375–4380. https://doi.org/10.1073/pnas.1424037112.

Harvey, J.E., Axelson, J.N., Smith, D.J., 2018. Disturbance-climate relationships between wildfire and western spruce budworm in interior British Columbia. Ecosphere 9 (3), e02126.

Harvey, B.J., Donato, D.C., Romme, W.H., Turner, M.G., 2013. Influence of recent bark beetle outbreak on fire severity and postfire tree regeneration in montane Douglas-fir forests. Ecology 94, 2475–2486.

Harvey, B.J., Donato, D.C., Romme, W.H., Turner, M.G., 2014a. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. Ecol. Appl. 24, 1608–1625.

Harvey, B.J., Donato, D.C., Turner, M.G., 2014b. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proc. Natl. Acad. Sci. 111 https://doi.org/10.1073/pnas.1411346111.

Hawkins, A.E., Henkel, T.W., 2011. Native forest pathogens facilitate persistence of Douglas-fir in old-growth forests of Northwestern California. Can. J. For. Res. 41 (6), 1256–1266. https://doi.org/10.1139/x11-053.

Hawksworth, F.G., and R.G. Scharpf. 1981. *Phoradendron* on Conifers. Forest Insect and Disease Leaflet 164, USDA Forest Service, Washington D.C.

Hawksworth, F.G., and D. Wiens. 1996. Dwarf Mistletoes: Biology, Pathology, and Systematics. Agriculture Handbook 709. USDA Forest Service, Washington D.C.

Healey, S.P., Raymond, C.L., Lockman, I.B., Hernandez, A.J., Garrard, C., Huang, C., 2016. Root disease can rival fire and harvest in reducing forest carbon storage. Ecosphere 7 (11). https://doi.org/10.1002/ecs2.1569.

Hennon, P.E., Frankel, S.J., Woods, A.J., Worrall, J.J., Norlander, D., Zambino, P.J., Warwell, M.V., Shaw, C.G., 2020. A framework to evaluate climate effects on forest tree diseases. For. Pathol. 50 (6) https://doi.org/10.1111/efp.12649.

Hennon, P.E., Frankel, S.J., Woods, A.J., Worrall, J.J., Ramsfield, T.D., Zambino, P.J., Shaw, D.C., Ritokova, G., Warwell, M.V., Norlander, D., Mulvey, R.L., Shaw III, C.G., 2021. Applications of a conceptual framework to assess climate controls of forest tree diseases. For. Pathol. 51 https://doi.org/10.1111/efp.12719.

Hessburg, P.F., Agee, J.K., Franklin, J.F., 2005. Dry forests and wildland fires of the inland Northwest USA: Contrasting the landscape ecology of the pre-settlement and modern eras. For. Ecol. Manage. 211, 117–139.

Hessburg, P.F., Mitchell, R.G., Filip, G.M., 1994. Historical and Current Roles of Insects and Pathogens in Eastern Oregon and Washington Forested Landscapes. Gen. Tech. Report PNW-GTR-327, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Hessburg, P.F., Spies, T.A., Perry, D.A., Skinner, C.N., Taylor, A.H., Brown, P.M., Stephens, S.L., Larson, A.J., Churchill, D.J., Povak, N.A., Singleton, P.H., McComb, B., Zielinski, W.J., Collins, B.M., Salter, R.B., Keane, J.J., Franklin, J.F., Riegel, G., 2016. Tamm Review: Management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. For. Ecol. Manage. 366, 221–250. https://doi.org/10.1016/j.foreco.2016.01.034.

Hessburg, P.F., Miller, C.L., Parks, S.A., Povak, N.A., Taylor, A.H., Higuera, P.E., Prichard, S.J., North, M.P., Collins, B.M., Hurteau, M.D., Larson, A.J., Allen, C.D., Stephens, S.L., Rivera-Huerta, H., Stevens-Rumann, C.S., Daniels, L.D., Gedalof, Z., Gray, R.W., Kane, V., Churchill, D., Haggmann, R., Spies, T., Cansler, C., Delote, R., Veblen, T., Battaglia, M., Hoffman, C., Skinner, C., Safford, H., Salter, R.B., 2019. Climate, Environment, and Disturbance History Govern Resilience of Western North American Forests. Front. Ecol. Evol. 7 https://doi.org/10.3389/fevo.2019.00239.

Heyerdahl, E.K., Loehman, R.A., Falk, D.A., 2014. Mixed-severity fire in lodgepole pine dominated forests: are historical regimes sustainable on Oregon's Pumice Plateau, USA? Can. J. For. Res. 44, 593–603.

Hicke, J.A., Johnson, M.C., Hayes, J.L., Preisler, H.K., 2012a. Effects of bark beetle-caused tree mortality on wildfire. For. Ecol. Manage. 271, 81–90. https://doi.org/10.1016/j.foreco.2012.02.005.

Hicke, J.A., Allen, C.D., Desai, A.R., Dietze, M.C., Hall, R.J., Hogg, E.H., Kashian, D.M., Moore, D., Raffa, K.F., Sturrock, R.N., Vogelmann, J., 2012b. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. Glob. Change Biol. 18 (1), 7–34. https://doi.org/10.1111/j.1365-2486.2011.02543.x.

Hicke, J.A., Meddens, A.J.H., Kolden, C.A., 2016. Recent tree mortality in the Western United States from bark beetles and forest fires. Forest Science 62, 141–153. https://doi.org/10.5849/forsci.15-086.

Hicke, J.A., Xu, B., Meddens, A.J.H., Egan, J.M., 2020. Characterizing recent bark beetle-caused tree mortality in the western United States from aerial surveys. For. Ecol. Manage. 475 https://doi.org/10.1016/j.foreco.2020.118402.

Hoffman, C.M., Sieg, C.H., McMillin, J.D., FuÍe, P.Z., 2012b. Fuel loadings 5 years after a bark beetle outbreak in south-western USA ponderosa pine forests. Int. J. Wildland Fire 21 (3), 306–312. https://doi.org/10.1071/WF11019.

Hoffman, C.M., Linn, R., Parsons, R., Sieg, C., Winterkamp, J., 2015. Modeling spatial and temporal dynamics of wind flow and potential fire behavior following a mountain pine beetle outbreak in a lodgepole pine forest. Agric. For. Meteorol. 204, 79–93. https://doi.org/10.1016/j.agrformet.2015.01.018.

Hoffman, C., Mathiasen, R., Sieg, C.H., 2007. Dwarf mistletoe effects on fuel loadings in ponderosa pine forests in northern Arizona. Can. J. For. Res. 37 (3), 662–670. https://doi.org/10.1139/X06-259.

Hoffman, C., Morgan, P., Mell, W., Parsons, R., Strand, E.K., Cook, S., 2012a. Numerical simulation of crown fire hazard immediately after bark beetle-caused mortality in lodgepole pine forests. For. Sci. 58 (2), 178–188. https://doi.org/10.5849/forsci.10-137.

Hoffman, C.M., Morgan, P., Mell, W., Parsons, R., Strand, E., Cook, S., 2013. Surface fire intensity influences simulated crown fire behavior in lodgepole pine forests with recent mountain pine beetle-caused tree mortality. For. Sci. 59 (4), 390–399. https://doi.org/10.5849/forsci.11-114.

Holah, J.C., Wilson, M.V., Hansen, E.M., 1997. Impacts of a native root-rotting pathogen on successional development of old-growth Douglas-fir forests. Oecologia 111, 429–433.

Hrinkevich, K.H., Progar, R.A., Shaw, D.C., 2016. Climate risk modelling of balsam woolly adelgid damage severity in subalpine fir stands of Western North America. PLoS ONE 11 (10). https://doi.org/10.1371/journal.pone.0165094.

Hummel, S., and J.K. Agee. 2003. Western spruce budworm defoliation effects on forest structure and potential fire behavior. Northwest Sci. 77, 159–169-.

Jenkins, M.J., Hebertson, E., Page, W., Jorgensen, C.A., 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. For. Ecol. Manage. 254, 16–34. https://doi.org/10.1016/j.foreco.2007.09.045.

Jenkins, M.J., Runyon, J.B., Fettig, C.J., Page, W.G., Bentz, B.J., 2014. Interactions among the mountain pine beetle, fires, and fuels. For. Sci. 60, 489–501. https://doi.org/10.5849/forsci.13-017.

Johnson, N., 2012. Effect of Armillaria Root Disease on Stand Structure, Composition, and Potential Fire Behavior in a Managed Ponderosa Pine Forest near Glenwood, WA. University of Washington, MS. Thesis.

Jolly, W.M., Parsons, R.A., Hadlow, A.M., Cohn, G., McAllister, S., Popp, J.B., Hubbard, R.M., Negrón, J.F., 2012a. Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack. For. Ecol. Manage. 269, 52–59.

Jolly, W.M., Parsons, R., Varner, J.M., Butler, B.W., Ryan, K.C., Gucker, C.L., 2012b. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Comment. Ecology 93, 941–946.

Jorgensen, C.A., Jenkins, M.J., 2011. Fuel complex alterations associated with spruce beetle-induced tree mortality in Intermountain spruce/fir forests. For. Sci. 57, 232–240.

Kane, J.M., Varner, J.M., Metz, M.R., van Mantgem, P.J., 2017. Characterizing interactions between fire and other disturbances and their impacts on tree mortality in western U.S. Forests. For. Ecol. Manage. 405, 188–199. https://doi.org/10.1016/j.foreco.2017.09.037.

Keane, R.E., Bentz, B., Holsinger, L.M., Saab, V.A., Loehman, R., 2022. Modeled interactions of mountain pine beetle and wildland fire under future climate and management scenarios for three western US landscapes. Fire Ecol. 2022, 18–112. https://doi.org/10.1186/s42408-022-00137-4.

Kitzberger, T., Falk, D.A., Westerling, A.L., Swetnam, T.W., 2017. Direct and indirect climate controls predict heterogeneous early-mid 21st century wildfire burned area across western and boreal North America. PLoS ONE 12, e0188486.

Klutsch, J.G., Battaglia, M.A., West, D.R., Costello, S.L., Negrón, J.F., 2011. Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in North-Central Colorado. West. J. Appl. For. 26, 101–109.

Klutsch, J.G., Beam, R.D., Jacobi, W.R., Negrón, J.F., 2014. Bark beetles and dwarf mistletoe interact to alter downed woody material, canopy structure, and stand characteristics in northern Colorado ponderosa pine. For. Ecol. Manage. 315, 63–71. https://doi.org/10.1016/j.foreco.2013.12.024.

Koenig, W.D., Knops, J.M.H., Carmen, W.J., Pesendorfer, M.B., Dickinson, J.L., 2018. Effects of mistletoe (*Phoradendron villosum*) on California Oaks. Biol. Lett. 14, 20180240. https://doi.org/10.1098/rsbl.2018.0240.

Kolb, T.E., Wagner, M.R., Covington, W.W., 1994. Concepts of forest health - utilitarian and ecosystem perspectives. J. For. 92, 10–15.

Kolb, T.E., Fettig, C.J., Ayres, M.P., Bentz, B.J., Hicke, J.A., Mathiasen, R., Stewart, J.E., Weed, A.S., 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. For. Ecol. Manage. 380, 321–334. https://doi.org/10.1016/j.foreco.2016.04.051.

Koonce, A.L., Roth, L.F., 1985. In: The Effects of Dwarf Mistletoe on Fuel in Precommercial Ponderosa Pine Stands. Society of American Foresters, Bethesda, Md, pp. 66–72.

Koontz, M.J., North, M.P., Werner, C.M., Pick, S.E., Latimer, A.M., 2020. Local forest structure variability increases resilience to wildfire in dry western U.S. coniferous forests. Ecol. Lett. 23, 483–494. https://doi.org/10.1111/ele.13447.

Krist Jr, F.J., Ellenwood, J.R., Woods, M.E., McMahan, A.J., Cowardin, J.P., Ryerson, D. E., Sapio, F.J., Zweifler, M.O., Romero, S.A., 2014. National Insect and Disease Forest Risk Assessment; 2013–2027/ FHTET-14-01. USDA Forest Service, Forest Health Technology Enterprise Team, Fort Collins CO.

Kulakowski, D., and D. Jarvis. 2011. The influence of mountain pine beetle outbreaks and drought on severe wildfires in northwestern Colorado and southern Wyoming: a look at the past century. For. Ecol. Manage. 262, 1686–1696. http://dx.doi.org/10.1016/j.foreco.2011.07.016.

Kulakowski, D., Veblen, T.T., 2007. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. Ecology 88, 759–769. https://doi.org/10.1890/06-0124.

Kuljian, H., Varner, J.M., 2010. The effects of sudden oak death on foliar moisture content and crown fire potential in tanoak. For. Ecol. Manage. 259 (10), 2103–2110.

Lee, E.H., Beedlow, P.A., Waschmann, R.S., Tingey, D.T., Cline, S., Bollman, M., Wickham, C., Carlile, C., 2017. Regional patterns of increasing Swiss needle cast impacts on Douglas-fir growth with warming temperatures. Ecol. Evol. 7 (24), 11167–11196.

Lee, C., Y. Valachovic, S. Frankel, and K. Palmieri. 2010. Sudden oak death mortality and fire: lessons from the Basin Complex. Pages 271-279, in; Proceedings of the Sudden Oak Death Fourth Science Symposium. General Technical Report PSW-GTR-229, USDA Forest Service, Pacific Southwest Research Station, Albany, CA.

Linn, R.R., Sieg, C.H., Hoffman, C.M., Winterkamp, J.L., McMillin, J.D., 2013. Modeling wind fields and fire propagation following bark beetle outbreaks in spatially-heterogeneous pinyon-juniper woodland fuel complexes. Agric. For. Meteorol. 173, 139–153. https://doi.org/10.1016/j.agrformet.2012.11.007.

Littell, J.S., 2018. Drought and Fire in the Western USA: Is Climate Attribution Enough? Curr. Clim. Change Reports 4 (4), 396–406.

Lockman, I.B., and H.S.J. Kearns (eds.). 2016. Forest Root Diseases Across the United States. Gen. Tech. Rep. RMRS-GTR-342, USDA Forest Service, Rocky Mountain Research Station, Ogden, UT.

Lundquist, J.E., 2007. The relative influence of diseases and other small-scale disturbances on fuel loading in the Black Hills. Plant Dis. 91 (2), 147–152. https://doi.org/10.1094/PDIS-91-2-0147.

Lynch, A.M., 2019. Socioecological impacts of multiple forest insect outbreaks in the Pinaleño spruce-fir forest, Arizona. J. For. 117 (2), 164–170. https://doi.org/10.1093/jofore/fvy039.

Lynch, A.M. 2002. Spruce aphid in high elevation habitats in the Southwest. Pg 60-63 in; Gen. Tech. Report GTR-NE-300, Proceedings: 2002 U.S. Department of Agriculture Interagency Research Forum. Washington D.C.

Manion, P.D., 1981. Tree Disease Concepts. Prentice Hall, Hoboken, N.J., USA.

Mathiasen, R.L., 1996. Dwarf mistletoe in forest canopies. Northwest Sci. 70 (Special Issue), 61–70.

Mathiasen, R.L., 2021. Mistletoes of the Continental United States and Canada. BRIT Press, Fort Worth, TX, USA.

Mathiasen, R.L., Nickrent, D.L., Shaw, D.C., Watson, D.M., 2008. Mistletoes: Systematics, Pathology, Ecology, and Management. Plant Dis. 92, 988–1006.

McCarley, T.R., Kolden, C.A., Vaillant, N.M., Hudak, A.T., Smith, A.M.S., Kreitler, J., 2017. Landscape-scale quantification of fire-induced change in canopy cover following mountain pine beetle outbreak and timber harvest. For. Ecol. Manage. 391, 164–175. https://doi.org/10.1016/j.foreco.2017.02.015.

McKenzie, D., Littell, J.S., 2017. Climate change and the eco-hydrology of fire: will area burned increase in a warming western USA. Ecol Appl. 27, 26–36. https://doi.org/10.1002/eap.1420.

McKenzie, D. D.L. Peterson, and J.J. Littell. 2009. Global warming and stress complexes in forests of western North America. Chapter 15, in; Bytnerowicz, A., M. Arbaugh, A. Riebau, and C. Andersen (eds). Developments in Environmental Science, 8. Elsevier. http://doi.org/10.1016/S1474-8177(08)00015-6.

Meigs, G.W., Kennedy, R.E., Cohen, W.B., 2011. A Landsat time series approach to characterize bark beetle and defoliator impacts on tree mortality and surface fuels in conifer forests. Remote Sens. Environ. 115 (12), 3707–3718.

Meigs, G.W., Campbell, J.L., Zald, H.S.J., Bailey, J.D., Shaw, D.C., Kennedy, R.E., 2015. Does wildfire likelihood increase following insect outbreaks in conifer forests? Ecosphere 6 (7). https://doi.org/10.1890/es15-00037.1.

Meigs, G.W., Zald, H.S.J., Campbell, J.L., Keeton, W.S., Kennedy, R.E., 2016. Do insect outbreaks reduce the severity of subsequent forest fires? Environ. Res. Lett. 11 (4) https://doi.org/10.1088/1748-9326/11/4/045008.

Merschel, A.G., Beedlow, P.A., Shaw, D.C., Woodruff, D.R., Lee, E.H., Cline, S.P., Comeleo, R.L., Hagmann, R.K., Reilly, M.J., 2021. An ecological perspective on living with fire in ponderosa pine forests of Oregon and Washington: Resistance, gone but not forgotten. Trees, Forests, and People. https://doi.org/10.1016/j.tfp.2021.100074.

Metz, M. R., M. Varner, J. Frangioso, K. M., R. K. Meentemeyer, and D. M. Rizzo. 2013. Unexpected redwood mortality from synergies between wildfire and an emerging infectious disease. Ecology 94, 2152–2159.

Metz, M.R., Frangioso, K.M., Meentemeyer, R.K., Rizzo, D.M., 2011. Interacting disturbances: wildfire severity affected by stage of forest disease invasion. Ecol. Appl. 21, 313–320.

Metz, M., Varner, J.M., Simler, A., Frangioso, K., Rizzo, D., 2017. Implications of sudden oak death for wildland fire management. For. Phytophthoras 7 (1). https://doi.org/10.5399/osu/fp.7.1.4027.

Michel, A.K., Winter, S., 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A. For. Ecol. Manage. 257, 1453–1464.

Millar, C.I., Delany, D.L., 2019. Interaction between mountain pine beetle-caused tree mortality and fire behavior in subalpine whitebark pine forests, eastern Sierra Nevada, CA; retrospective observations. For. Ecol. Manage. 447, 195–202. https://doi.org/10.1016/j.foreco.2019.05.052.

Moran, C.J., Cochrane, M.A., 2012. Do mountain pine beetle outbreaks change the probability of crown fire in lodgepole pine forests? Comment. Ecology 93, 939–941.

Mote, P.W., Abatzoglou, J., Dello, K.D., Hegewisch, K., Rupp, D.E., 2019. Fourth Oregon Climate Assessment Report. Oregon Climate Change Research Institute. occri.net/ocar4.

O'Connor, C.D., Lynch, A.M., Falk, D.A., Swetnam, T.W., 2015. Post-fire forest dynamics and climate variability affect spatial and temporal properties of spruce beetle outbreaks on a Sky Island mountain range. For. Ecol. Manage. 336, 148–162.

Oester, P.T., D.C. Shaw, and G.M. Filip. 2018. Managing Insects and Diseases of Oregon Conifers. Extension Manual EM 8980, Oregon State University Extension Service, Corvallis, Oregon.

Page, W.G., Jenkins, M.J., Runyon, J.B., 2012. Mountain pine beetle attack alters the chemistry and flammability of lodgepole pine foliage. Can. J. For. Res. 42, 1631–1647.

Page, W.G., Jenkins, M.J., Runyon, J.B., 2014. Spruce Beetle-Induced Changes to Engelmann Spruce Foliage Flammability. For. Sci. 60 (4), 691–702.

Parker, T.J., Clancy, K.M., Mathiasen, R.L., 2006. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. Agric. For. Entomol. 8, 167–189.

Parks, S.A., Abatzoglou, J.T., 2020. Warmer and drier fire seasons contribute to increases in area burned at high severity in western US Forests from 1985–2017. Geophys. Res. Lett. 47 https://doi.org/10.1029/2020GL089858.

Parsons, R.A., Linn, R.R., Pimont, F., Hoffman, C., Sauer, J., Winterkamp, J., Sieg, C.H., Jolly, W.M., 2017. Numerical investigation of aggregated fuel spatial pattern impacts on fire behavior. Land 6 (2). https://doi.org/10.3390/land6020043.

Perrakis, D.D.B., Lanoville, R.A., Taylor, S.W., Hicks, D., 2014. Modeling wildfire spread in mountain pine beetle-affected forest stands, British Columbia. Canada. Fire Ecology 10 (2), 10–35. https://doi.org/10.4996/fireecology.1002010.

Potter, K.M., Canavin, J.C., Koch, F.H., 2020. A forest health retrospective: National and regional results from 20 years of insect and disease survey data. Chapter 6. In: Potter, K.M., Conkling, B.L. (Eds.), Forest Health Monitoring: National Status, Trends, and Analysis 2019. USDA Forest Service; Gen. Tech. Rep. SRS-250. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station, 2020. DOI: 10.2737/SRS-GTR-250.

Potter, K.M., Conkling, B.L., 2020. Forest Health Monitoring: National Status, Trends, and Analysis 2019. USDA Forest Service; Gen. Tech. Rep. SRS-250. Asheville, NC: U. S. Department of Agriculture, Forest Service, Southern Research Station. doi: 10.2737/SRS-GTR-250.

Prichard, S.J., and M.C., Kennedy. 2014. Fuel treatments and landform modify landscape patterns of burn severity in an extreme fire event. Ecol. Appl. 24, 571–590. http://dx.doi.org/10.1890/13-0343.1.

Pritchard, K.R., Hagar, J.C., Shaw, D.C., 2017. Avian abundance and diversity are associated with oak mistletoe (*Phoradendron villousm*) in Willamette Valley *Quercus* Woodlands. Botany 95 (3), 283–294. https://doi.org/10.1139/cjb-2016-0249.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58, 501–517. https://doi.org/10.1641/B580607.

Raffa, K.F., Aukema, B., Bentz, B.J., Carroll, A., Erbilgin, N., Herms, D.A., Hicke, J.A., Hofstetter, R.W., Katovich, S., Lindgren, B.S., 2009. A literal use of "forest health" safeguards against misuse and misapplication. J. For. 5, 276–277. https://doi.org/10.1093/jof/107.5.276.

Ragenovich, I.R., and R.G. Mitchell. 2006. Balsam Woolly Adelgid. Forest Insect and Disease Leaflet 118, R6-NR-FID-PR-04-2006. USDA Forest Service, Portland, OR.

Regnery, B., Couvet, D., Kubarek, L., Julien, J.-F., Kerbiriou, C., 2013. Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. Ecol. Ind. 34, 221–230.

Ricarrdi, C.L., Ottmar, R.D., Sandberg, D.V., Andreu, A., Elman, E., Kopper, K., Long, J., 2007. The fuelbed: a key element of the Fuel Characteristic Classification System. Can. J. For. Res. 37, 2394–2412.

Ritter, S.M., Hoffman, C.M., Ex, S.A., Stewart, J.E., 2017. Impacts of lodgepole pine dwarf mistletoe (*Arceuthobium americanum*) infestation on stand structure and fuel load in lodgepole pine dominated forests in central Colorado. Botany 95 (3), 307–321. https://doi.org/10.1139/cjb-2016-0255.

Robinson, D.C.E., Geils, B.W., 2006. Modelling dwarf mistletoe at three scales: life history, ballistics, and contagion. Ecol. Model. 199, 23–38.

Rocca, G.D., R. Danti, C. Hernando, M. Guijarro, Michelozzi, C. Carrillo, and J. Madrigal. 2020. Terpenoid accumulation links plant health and flammability in the Cypress-bark canker pathosystem. Forests 2020, 11, 651; http://doi.org/10.3390/f11060651.

Ryan, R.B., Tunnock, S., Ebel, F.W., 1987. The larch casebearer in North America. J. Forest. 85, 33–39. https://doi.org/10.1093/jof/85.7.33.

Schoennagel, T., T. T. Veblen, J. F. Negron, and J. M. Smith. 2012. Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. PLoS ONE 7(1). 10.1371/journal.pone.0030002.

Scott, J.H., and E.D. Reinhardt. 2001. Assessing Crown Fire Potential by Linking Models of Surface and Crown Fire Behavior. Research Paper RMRS-RP-29, USDA Forest Service, Rocky Mountain Region, Fort Collins, CO, USA. (website: https://www.fs.fed.us/rm/pubs/rmrs_rp029.pdf, last checked Dec. 29, 2021).

Senf, C., Wulder, M.A., Campbell, E.M., Hostert, P., 2016. Using Landsat to assess the relationship between spatiotemporal patterns of western spruce budworm outbreaks and regional-scale weather variability. Can. J. Remote Sens. 42, 706–718. https://doi.org/10.1080/07038992.2016.1220828.

Shaw, D.C., Agne, M.C., 2017. Fire and Dwarf Mistletoe (Viscaceae: Arceuthobium species) in Western North America: Contrasting Arceuthobium tsugense and Arceuthobium americanum. Botany 95 (3), 231–246. https://doi.org/10.1139/cjb-2016-0245.

Shaw, D.C., Woolley, T., Kelsey, R.G., McPherson, B.A., Westlind, D., Wood, D.L., Peterson, E.K., 2017. Surface fuels in recent *Phytophthora ramorum* created gaps and adjacent intact *Quercus agrifolia* forests, East Bay Regional Parks, California, USA. For. Ecol. Manage. 384, 331–338.

Shaw, D.C., Ritóková, G., Lan, Y.-H., Mainwaring, D.B., Russo, A., Comeleo, R., Navarro, S., Norlander, D., Smith, B., 2021. Persistence of the Swiss Needle Cast Outbreak in Oregon Coastal Douglas-fir, and New Insights from Research and Monitoring. J. Forest. https://doi.org/10.1093/jofore/fvab011.

Sheehan, K.A. 1996. Defoliation by western spruce budworm in Oregon and Washington from 1980- through 1994. USDA Forest Service, PNW Region. Tech. Publ. R6-NR-TP-04-96, Portland, Oregon.

Sieg, C.H., Linn, R.R., Pimont, F., Hoffman, C.M., McMillin, J.D., Winterkamp, J., Baggett, L.S., 2017. Fires following bark beetles: Factors controlling severity and disturbance interactions in ponderosa pine. Fire Ecol. 13 (3), 1–23. https://doi.org/10.4996/fireecology.130300123.

Simard, M., Romme, W.H., Griffin, J.M., Turner, M.G., 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecol. Monogr. 81, 3–24.

Simard, M., Romme, W.H., Griffin, J.M., Turner, M.G., 2012. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Reply. Ecology 93, 946–950.

Simler-Williamson, A.B., Metz, M.R., Frangioso, K.M., Rizzo, D.M., 2021. Wildfire alters the disturbance impacts of an emerging forest disease via changes to host occurrence and demographic structure. J. Ecol. 109 (2), 676–691. https://doi.org/10.1111/1365-2745.13495.

Smith, K.T., Arbellay, E., Falk, D.A., Sutherland, E.K., 2016b. Macroanatomy and compartmentalization of recent fire scars in three North American conifers. Can. J. For. Res. 46, 535–542.

Smith, G.D., Carroll, A.L., Lindgren, B.S., 2011. Facilitation in bark beetles: endemic mountain pine beetle gets a helping hand. Agric. For. Entomol. 13, 37–43. https://doi.org/10.1111/j.1461-9563.2010.00499.x.

Smith, J.E., Cowan, A.D., Fitzgerald, S.A., 2016a. Soil heating during the complete combustion of mega-logs and broadcast burning in central Oregon USA pumice soils. Int. J. Wildland Fire. 25 (11), 1202–1207.

Stanton, S., 2009. Western dwarf mistletoe and prescribed fire behavior — a case study from Crater Lake National Park. Northw. Sci. 83 (3), 189–199. https://doi.org/10.3955/046.083.0303.

Stanton, S., Hadley, K.S., 2010. Influence of western dwarf mistletoe (*Arceuthobium campylopodum* Engelm.) on surface fuels and snag abundance in mature ponderosa pine mixed conifer stands in central Oregon. Nat. Areas J. 30 (3), 261–270. https://doi.org/10.3375/043.030.0302.

Stephens, S.L., Collins, B.M., Fettig, C.J., Finney, M.A., Hoffman, C.M., Knapp, E.E., North, M.P., Safford, H., Wayman, R.B., 2018. Drought, tree mortality, and wildfire in forests adapted to frequent fire. Bioscience 68, 77–88.

Stephens, S.L., Bernal, A.A., Collins, B.M., Finney, M.A., Lautenberger, C., Saah, D., 2022. Mass fire behavior created by extensive tree mortality and high tree density not predicted by operational fire behavior models in the southern Sierra Nevada. For. Ecol. Manage. 518, 15. https://doi.org/10.1016/j.foreco.2022.120258.

Stevens-Rumann, C., Morgan, P., Hoffman, C., 2015. Bark beetles and wildfires: How does forest recovery change with repeated disturbances in mixed conifer forests? Ecosphere 6 (6). https://doi.org/10.1890/ES14-00443.1.

Swetnam, T.W., Lynch, A.M., 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. Ecol. Monogr. 63, 399–424. https://doi.org/10.2307/2937153.

Talucci, A.C., Krawchuk, M.A., 2019. Dead forests burning: the influence of beetle outbreaks on fire severity and legacy structure in sub-boreal forests. Ecosphere 10 (5). https://doi.org/10.1002/ecs2.2744.

Thies, W.G., 2001. Root diseases in eastern Oregon and Washington. Northwest Science75. 38–45, Special Issue.

Trugman, A.T., Anderegg, L.D.L., Anderegg, W.R.L., Das, A.J., Stephenson, N.L., 2021. Why is tree drought mortality so hard to predict? Trends Ecol. Evol. 36 https://doi.org/10.1016/j.tree.2021.02.001.

Trumbore, S., Brando, P., Hartmann, H., 2015. Forest health and global change. Science 349, 814–818. https://doi.org/10.1126/science.aac6759.

Turner, M.G., Romme, W.H., Gardner, R.H., 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. Int. J. Wildl. Fire 9, 21–36. https://doi.org/10.1071/WF99003.

Valachovic, Y.S., Lee, C.A., Scanlon, H., Varner, J.M., Glebocki, R., Graham, B.D., Rizzo, D.M., 2011. Sudden oak death-caused changes to surface fuel loading and potential fire behavior in Douglas-fir-tanoak forests. For. Ecol. Manage. 261 (11), 1973–1986. https://doi.org/10.1016/j.foreco.2011.02.024.

Van Wagner, C.E., 1977. Conditions for the start and spread of crown fire. Can. J. For. Res. 7, 23–34.

Van Wagtendonk, J.W. 2006. Fire as a physical process. Chapter 3, in; Fire in California's Ecosystems. Edited by; N.G. Sugihara, J.W. Van Wagtendonk, K. E. Shaffer, J. Fites-Kauffman, and A.E. Thode. University of California Press, Berkeley.

Vane, E., Waring, K., Polinko, A., 2017. The influence of western spruce budworm on fire in spruce-fir forests. Fire Ecol. 13 (1), 16–33. https://doi.org/10.4996/fireecology.1301016.

Vasaitis, R., 2013. Heart Rots, Sap Rots and Canker Rots. Chapter 10, In; Infectious Forest Diseases. Cabi Press, Oxfordshire, UK.

Vega, F.E., Hofstetter, R.W., 2015. Bark Beetles. Academic Press, UK, Biology and Ecology of Native and Invasive Species.

Voelker, S.L., Merschel, A.G., Meinzer, F.C., Ulrich, D.E.M., Spies, T.A., Still, C.J., 2019. Fire deficits have increased drought sensitivity in dry conifer forests: Fire frequency and tree-ring carbon isotope evidence from Central Oregon. Glob. Change Biol. 25, 1247–1262. https://doi.org/10.1111/gcb.1454.

Wayman, R.B., Safford, H.D., 2021. Recent bark beetle outbreaks influence wildfire severity in mixed-conifer forests of the Sierra Nevada, California, USA. Ecol. Appl. 31 (3), e02287.

Welsh, C., Lewis, K.J., Woods, A.J., 2014. Regional outbreak dynamics of Dothistroma needle blight linked to weather patterns in British Columbia, Canada. Can. J. For. Res. 44, 212–219. https://doi.org/10.1139/cjfr-2013-0387.

Westerling, A.L.R., 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Phil. Trans. R. Soc. B 371, 20150178. https://doi.org/10.1098/rstb.2015.0178.

Wicker, E.F., and C.D. Leaphart. 1974. Fire and dwarf mistletoe (*Arceuthobium* spp.) relationships in the Northern Rocky Mountains. In Proceedings, Tall Timbers Fire Ecology Conference, Fire and Land Management Symposium, Missoula, Mont., Tallahassee, Fla., 8–10 October 1974. pp. 279–298.

Wickman, B.E. 1992. Forest Health in the Blue Mountains: The influence of Insects and Diseases. General Technical Report PNW-GTR-295, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Williams, A.P., Abatzoglou, J.T., Gershunov, A., Guzman-Morales, J., Bishop, D.A., Balch, J.K., Lettenmaier, D.P., 2019. Observed impacts of anthropogenic climate change on wildfire in California. Earth's Future. https://doi.org/10.1029/2019EF001210.

Wilson, J., Isaac, E., Gara, R., 1998. Impacts of mountain pine beetle (Dendroctonus ponderosae) (Coleoptera: Scolytidae) infestation on future landscape susceptibility to western spruce budworm (*Choristoneura occidentalis*) (Lepidoptera: Trotricidae) in north central Washington. J. Appl. Ent. 122, 239–245.

Wing, M.G., Long, J., 2015. A 25-year history of spatial and temporal trends in wildfire activity in Oregon and Washington, USA. Modern Appl. Sci. 9 (3), 117.

Wood, D.L., Koerber, T.W., Sharpf, R.F., Storer, A.J., 2003. Pests of the Native California Conifers. University of California Press, Berkeley.

Woods, A., Coates, K.D., Hamann, A., 2005. Is an unprecedented Dothistroma needle blight epidemic related to climate change? Bioscience 55, 761–769.

Woolley, T., Shaw, D.C., Hollingsworth, L.T., Agne, M.C., Fitzgerald, S., Eglitis, A., Kurth, L., 2019. Beyond red crowns: complex changes in surface and crown fuels and their interactions 32 years following mountain pine beetle epidemics in south-central Oregon, USA. Fire Ecol. 15, 4. https://doi.org/10.1186/s42408-018-0010-.