Eco-Evolutionary Interactions Between Pines, Fire, and Herbivorous Insects

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Abstract Pine (*Pinus* spp.) trees worldwide are subjected to selective evolutionary pressures from both abiotic (fire) and biotic (insects) damage resulting in their extant distribution and abundance, and life-history and morphological traits. These interactions merit serious consideration in long-term pine forest conservation and sustainability plans, and hence, we provide the following elements in this chapter: (1) a synthesis of eco-evolutionary components of these tri-lateral (fire-pine-insect) interactions; (2) a framework for understanding herbivory patterns and processes as based on adaptations of pine trees to different fire regimes and whether they are fire embracers, tolerators, or avoiders; and (3) use of fire as a critical tool to directly and indirectly manage insects while enhancing forest health. Overall, pine traits that confer fire resilience (e.g., thicker bark) and/or promotion (e.g., resin in needles and bark) tend to elicit variable responses by insects. Responses of insects are dependent on fire regimes and resulting host quality (nutrition and defenses) and quantity (e.g., density and dominance). Similarly, insect life-history traits (e.g., whether they are primary or secondary colonizing species, their background density levels, and adaptations to fire) further contribute to herbivory patterns. Prescribed fire can also either indirectly or directly affect herbivorous insect populations depending on burn timing, severity, and proximity. Anthropogenic climate change and fire suppression are leading to significant changes in fire regimes that will continue to alter these ancient trilateral interactions. Future management plans to enhance forest sustainability will benefit from inclusion of these eco-evolutionary interactions in pine-dominated ecosystems.

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1 Introduction

Fire is ubiquitous, widespread, and plays a crucial evolutionary and ecological role in pine (*Pinus* spp.)-dominated ecosystems (Pausas 2015). In fact, fire is termed the "global herbivore," as it consumes vegetation in most forested and grassland biomes (Bond and Keeley 2005). Simultaneously, pine trees are also subjected to herbivory (both by invertebrates and vertebrates, but especially forest insects and their associated pathogens) that greatly varies spatially and temporally (Berryman et al. 1987; Kozlov and Zvereva 2017). Along with other natural disturbances (e.g., windstorms, ice storms, flooding, and diseases) (Irland 2000; Gandhi et al. 2007; Cobb and Metz 2017), these selective pressures have resulted in extant abiotic and biotic patterns and processes in pine forests. The interplay between these two directional selection pressures for millions of years has resulted in adaptations and traits of some pine species to thrive in fire-prone regions (Stevens et al. 2020; Jin et al. 2021), while simultaneously coevolving with herbivorous species (de la Mata et al. 2017). We argue that the successional trajectories of pine stands and landscapes are, therefore, best understood under the evolutionary framework created by both fire and herbivorous insect species. Incorporating such relationships into forest management practices may maintain and conserve pine forests for their long-term sustainability, especially under projected climate changes (Seidl et al. 2017).

Reviews of trilateral interactions (fire-pines-insects) have focused on the boreal forest, western U.S., Canada, and/or across North America (McCullough et al. 1998; Parker et al. 2006; Fettig et al. 2022), and have provided valuable frameworks in this field. Here, we synthesize the existing knowledge about direct interactions between fire and associated insects in pine-dominated landscapes around the globe as based on fire regimes. We include both naturally regenerated and planted pine forests in both the northern (the native range of pines) and southern (where pines are imported and managed in monocultures) hemispheres. We focus on Australia, Europe, and North America due to more abundant literature on pine-dominated forests. We recognize the need for more studies elsewhere, such as in Asia and Central America, where native pines represent major centers for speciation (Goldammer and Penafiel 1990). While the studies are more voluminous in some regions (e.g., western U.S.) than others, our goal is to draw general conclusions to provide a framework for future studies under eco-evolutionary patterns and processes and project into the future.

2 Historical and Contemporary Relationship of Pines with Fire

The genus *Pinus* arose ~150 million years ago in the mid-Mesozoic era (Keeley 2012; Singh et al. 2018). Due to competition from rapidly diversifying angiosperms, pines were pushed into sites that either had extreme soil and weather conditions

(subgenus *Strobus*) or were fire-prone (subgenus *Pinus*) (Millar 1993; Keeley 2012; Falcon-Lang et al. 2016; Singh et al. 2018). Molecular phylogenetic data indicate that fire-adapted traits appeared at least 126 million years ago when pines showed thicker bark and hence, resistance to low-intensity, surface fires. Pines evolved cone serotiny ~89–96 million years ago, suggesting adaptations to more intense fires (He et al. 2012). One of the oldest known fossil for pines with these fire traits is from ~133 to 140 million years ago (Falcon-Lang et al. 2016). Both of these events were coincident with increased oxygen levels in the mid-Cretaceous in the Mesozoic era (He et al. 2012). Extant pines largely arose during the Miocene, during which speciation was driven in part by fire (Jin et al. 2021). Most species within the subgenus *Pinus* radiated into fire-prone areas, and are categorized as either fire-avoider, fire-tolerator, fire-embracer, or fire-refugee with each having specific morphological and life-history traits (Keeley 2012). For example, pine species such as *P. palustris* P. Mill. (longleaf pine) and *P. pinaster* Ait. (maritime pine) are fire-tolerators that tend to have higher height to crown, thicker bark, and longer needles to allow survival from frequent surface fires. Fire-embracers such as *P. halepensis* Mill. (Aleppo pine) and *P. contorta* Dougl. ex. Loud. (lodgepole pine) retain dead branches as ladder fuels and have short needles and thin bark making them easily killed by fire, but have serotinous cones to allow post-fire regeneration. Pine trees, and their ecosystems, landscapes, and associated fauna and flora are in general, considered adapted to fire regimes—the characterization of fire frequency, intensity, season, size, and type in a region—instead of single fires (Keeley et al. 2011; Keeley 2012). More recently, five global biomes or "pyromes" with similar fire characteristics and global units of fire are recognized of which at least three are prevalent in pine ecosystems (Archibald et al. 2013). (Hood et al. 2026) further provide more details on pine traits associated with fire syndromes and regimes.

Humans have a long evolutionary history with fire, which was considered essential to the stability of communities and faster brain development due to easier absorption of cooked food (Wrangham et al. 1999; Wrangham and Carmody 2010). Indigenous communities traditionally used fire for many purposes, e.g., cooking food, opening up spaces for game wildlife and travel, keeping the fuel loads low and reducing fire hazard, and regeneration of specific plant species (Pyne 1995; Bird et al. 2008; Christianson et al. 2022). Hence, these ecosystems were largely fire-driven because of the influence of Indigenous humans. With the continued loss of Indigenous communities on almost all continents, advent of modern technology and urbanization, and higher human population pressure, use of prescribed fire in forested areas has largely diminished globally (Mistry et al. 2016; Mitsopoulos et al. 2017). In addition, wildfire suppression is common in many pine-dominated regions (Colatskie 2011; Steel et al. 2015; Fernandes et al. 2016). This decline of frequent fire in many pine ecosystems has led to major ecological issues, such as loss of pine regeneration and genetic integrity (Tauer et al. 2012) and disassembly of native communities (Nowacki and Abrams 2008; Diaz-Toribio et al. 2020). With a greater awareness of the importance of fire in pine-dominated ecosystems during the last few decades, there's been a major shift to fire inclusion as a critical tool to maintain ecosystem services along with protecting human lives and structures (Christianson

et al. 2022). This paradigm shift represents utilizing historical Indigenous ecological knowledge for restoration of pine-dominated habitats (Robinson et al. 2021) with positive consequences for extant ecological processes.

Climate change is resulting in alterations to wildfire behavior, incidence, and intensity globally. This is primarily due to increases in temperature and drier conditions that lead to greater availability of combustible fuels (Williams et al. 2019; Grünig et al. 2023), as evidenced by the recent extreme forest fires in southeastern Australia (Abram et al. 2021). Coupled with higher fuel loads due to fire suppression, this has resulted in higher fire severity, damage, and extent in many regions (Abatzoglou and Williams 2016; Littell et al. 2016). Similarly, the seasonality of wildfires has changed as the burning season has lengthened in some areas (Fill et al. 2019). Aptly termed" mega-fires," wildfires in many regions are more intense and are burning larger areas, resulting in large economic, social, and ecological costs (Kirchmeier-Young et al. 2019; Boer et al. 2020; Wunder et al. 2021). Global warming has further resulted in significant range expansion of several important pine herbivorous insects (Cullingham et al. 2011; Dodds et al. 2018; Cocos et al. 2023). As these species are coming in contact with both naïve pine hosts and novel fire regimes, their impact on ecosystems may become more pronounced. Climatic changes and ensuing shifts in fire regimes and dynamics of herbivorous insect from the historical norms have serious socio-economic implications (Wunder et al. 2021) to long-term tree health, regeneration, and productivity of pine forests (Stephens et al. 2014).

3 Historical and Contemporary Relationship of Forest Insects with Fire

Forest fires and native herbivorous insects have been interacting with each other for millions of years in pine-dominated ecosystems globally. For example, 90% of extant pine species and 70% of extant *Dendroctonus* species (Coleoptera: Curculionidae) arose in the Miocene, suggesting strong coevolutionary relationships between existing host pines and this insect genus that likely influenced speciation (Ramírez-Reyes et al. 2023). Most pine ecosystems are pyrogenic with various intervals of fire frequency (few to hundreds of years) and intensity (surface to crown fires), which—along with other factors—influences fire severity (Agee 2000; Keeley 2012). Further, amongst gymnosperms, pine trees have a rich diversity of herbivorous insects and their associated pathogens utilizing this valuable resource (Brändle and Brandl 2001). These trilateral interactions are primarily indirect as they are mediated through changes in suitable pine host quality and quantity after a fire. Direct effects of fire are on the survivorship of herbivorous species that have low dispersal abilities at certain life-stages (e.g., they are present either in the litter and duff layer or on bark on the lower bole during a fire) that could be used for management of pest species. Conversely, there may be feedback loops with

herbivorous species either contributing to or causing tree mortality which may lead to increases in fuel loads and hence, higher intensity of subsequent fires. While fire is viewed as creating a variety of habitat niches for herbivorous species, there may be opposing directional effects of fire and herbivores allowing microevolution on pines. For example, the continental variation in levels of serotiny (a heritable trait) in *P. contorta* populations is driven both by the population levels of a major seed predator, *Tamiasciurus hudsonicus* (Erxleben) (red squirrel) (positive) (Smith 1970; Talluto and Benkman 2013) and infrequent crown fire regimes (negative) (He et al. 2012; Lamont et al. 2020). Similar eco-evolutionary trends may occur for insect herbivores, but are largely undetermined.

In pine forests where fire is a large influence, the two major fire regimes include either surface or crown fires with varying characteristics and biotic responses. Surface fires, such as occur in the southeastern U.S., are low intensity and low severity (i.e., understory burning) but with high frequency (~2–3 years) (Kirkman et al. 2017). In crown or stand-replacing fires, such as in the boreal pine forests (Rowe and Scotter 1973; Bergeron et al. 2001), fire intensity and fire severity is high, but frequency is low (~80–100 years). Specific attributes of pine tree species occur within different fire regimes and are outlined by Agee (2000) and (Hood et al. 2026). As expected, the dynamics of fire with herbivorous insects vary greatly based on fire regimes, plus anthropogenic alterations, particularly due to climate change and forest management practices including fire suppression.

3.1 Mechanisms of Interactions Between Forest Fire and Insects

Oleoresin is a complex mixture of terpenoids (monoterpenes and sesquiterpenes) and resin acids (diterpenes) (Langenheim 1990) that are synthesized and stored in resin ducts (i.e., canals) that occur in needles, cortical tissue, and secondary xylem of all pine species (Wu and Hu 1997). Some components of oleoresin are highly volatile and in addition to other litter attributes, contributes to system flammability (Popović et al. 2021) and also pine survival through compartmentalization of fire-caused wounds (Verrall 1938). Oleoresin is also a highly co-evolved pine tree trait against herbivorous insects and pathogens, and provides formidable physical and chemical defenses (e.g., Raffa 2014; Vázquez-González et al. 2020). There are many important feeding guilds of herbivorous insects such as foliage feeders, sap suckers, bark and woodborers, seed and cone feeders, and root-feeding insects (Baker 1972)—and they invariably come in contact with oleoresin while feeding on plant tissue. Strong selection pressures from both fire and herbivorous species likely resulted in pines having the most sophisticated resin-production duct system among tree genera, and simultaneously to diversify in fire-prone areas (Wu and Hu 1997; Vázquez-González et al. 2020). The oldest known pine fossil (~133–140 million years ago) was preserved as charcoal and had resin ducts, suggesting co-occurring

adaptations to both abiotic and biotic disturbances early in their evolutionary history (Falcon-Lang et al. 2016). Consequently, several insect taxa that use pines as a habitat also arose and diversified since that time. For example, bark beetles (Coleoptera: Curculionidae: Scolytinae), of which some species are important pests of pine trees, arose at least 120 million years ago with conifers as the likely basal host (Sequeira et al. 2000; Kirkendall et al. 2015). This was around the same time pines were diversifying in fire-prone areas (He et al. 2012) and angiosperms in other areas (Sequeira et al. 2000). Many co-evolutionary relationships of herbivorous species with pine trees thus, likely developed under various fire regimes that provided a complex mosaic of spatial and temporal habitat conditions.

Fire-injured trees release volatile organic compounds (VOCs), such as many monoterpenes (e.g., alpha-pinene, beta-pinene, myrcene, and 3-carene) to varying degrees (e.g., Perrakis and Agee 2006; Perrakis et al. 2011; Powell and Raffa 2011; Davis et al. 2012). Fire-injured trees also release higher levels of ethanol, which can increase bark beetle attraction (Kelsey and Westlind 2017). As expected, these differences are present and more pronounced after wildfires (Santolamazza-Carbone et al. 2011) than in prescribed fires because of the generally higher intensity of wildfires (Cannac et al. 2009). Resin production and flow, and hence the presence of VOCs increases in recently burned trees and on the charred side of trees in wildfires (Lombardero et al. 2006; Prasetya et al. 2017) and prescribed fires (Feeney et al. 1998; Menges and Deyrup 2001; Perrakis and Agee 2006; Cannac et al. 2009; Perrakis et al. 2011). There's evidence that the resin duct area and production increases post-fire in some frequent-fire pine species (Hood et al. 2015), and there's a positive correlation between resin duct attributes and production of resin (Rodríguez-García et al. 2014; Hood and Sala 2015). Thermal warming of the tree tissue that reduces viscosity of resin along with an induced response to wounding from fire may also increase the flow and production of resin. Resin production tends to increase for a few years in burned forests, indicating elevated responses to fire (Perrakis and Agee 2006; Perrakis et al. 2011), although only immediate responses may occur (Ritger 2023). Based on the relative levels, release rates, types, and persistence of VOCs present in burned forests, insect species show differential responses post-fire.

3.2 Patterns of Interactions Between Forest Fires and Insects

Based on fire regime, and as mediated via changes in host quantity and quality, spatial and temporal patterns of insect infestations vary within and across stands. Climate-limited forests tend to support higher prevalence of coniferous species and basal area, with high fuel loads that that support higher fire intensity and severity (Wang 2002; Estes et al. 2017; Lindenmayer et al. 2021; Stephens et al. 2022). Insect attack patterns and density are largely dependent on the degree of fire injury (i.e., percent crown scorch and bark char) on the trees and the amount/depth of burned fuel. As fire injury increases, subcortical beetle on burned trees also increase

(Coleoptera: Buprestidae, Cerambycidae, Curculionidae) (e.g., Furniss 1965; Dixon et al. 1984; Rasmussen et al. 1996; McHugh et al. 2003; Sullivan et al. 2003; Wallin et al. 2003; Breece et al. 2008; Six and Skov 2009; Costello et al. 2011; Santolamazza-Carbone et al. 2011; Davis et al. 2012; Zhan et al. 2022) though they typically decrease on trees with severe fire injury (Powell et al. 2012). This unimodal response is due to reduced host tissue suitability for beetle reproduction in severely burned trees, rendering them as non-hosts beyond a certain threshold. Within high-severity burns, less severely burned snags can allow for persistence of woodboring species that have relatively long life-cycles (Nappi et al. 2010). Smaller pine trees tend to sustain greater damage than larger trees in burned areas (Santolamazza-Carbone et al. 2011; Fettig and McKelvey 2014). However, fires can also cause significant mortality of larger trees in fire-suppressed forests with high fuel loads (Kolb et al. 2007; Maloney et al. 2008; Steel et al. 2021).

In frequent fire ecosystems with fire-tolerant pine species, low-intensity fires may confer increased resistance towards insects. *Pinus ponderosa* subjected to low-intensity wildfires invested more in resin duct-based defenses and had higher survival rates against *Dendroctonus ponderosae* Hopkins (mountain pine beetle) attacks and vice versa when fire was excluded from these sites (Hood et al. 2015). Resin ducts remain functional for several years, and frequent, low-intensity can stimulate persistent induced resistance against bark beetles (Hood et al. 2015). In *P. palustris*, resin ducts were smaller in size up to 10 years after reintroduction of fire, with the greatest reduction in stem and root burns (Slack et al. 2016). However, there were no differences in resin duct size between unburned and burned trees, and resin duct responses were also influenced by climatic factors. In contrast, resin flow that may be positively linked to higher tree defense (Schroeder 1990; Strom et al. 2002), often increasing for weeks to years after fire in numerous pine species (Santoro et al. 2001; Wallin et al. 2003; Lombardero et al. 2006; Knebel and Wentworth 2007; Cannac et al. 2009; Six and Skov 2009; Perrakis et al. 2011; Davis et al. 2012; Ritger 2023). Greater activity of *D. ponderosae* occurred on *P. contorta* than on *P. ponderosa* that required greater burn damage to bole and crown for such attack-levels (Lerch et al. 2016). More detailed studies on fire-tolerant pine species are needed to better assess the presence and various attributes (size and numbers) of resin ducts under different fire regimes.

While there are few studies that directly assessed the influence of post-fire stand characteristics, such as changes in structure (e.g., density, basal area, height, and volume of woody debris) and composition (e.g., percent tree and understory plant species) on insect dynamics, fire plays a significant indirect role. *Dendroctonus frontalis* Zimmerman (southern pine beetle) primarily colonizes *P. taeda* L. (loblolly pine) and rarely *P. palustris* (Friedenberg et al. 2007), which are maintained by frequent, low-intensity prescribed burning (Mitchell et al. 2006). Stand attributes play an important role since prescribed burning creates low basal area and open savannah-like *P. palustris* stands (Gilliam and Platt 1999; Mitchell et al. 2006). Such open stand structure likely dissipates the beetle's aggregation pheromone plume and makes it much more difficult for beetles to locate the source of the attractant. This could make mass aggregation of *D. frontalis* on trees difficult and lessens

the likelihood of ensuing herbivory impacts (Thistle et al. 2004, 2011; Martinson et al. 2007). This pattern has also been seen in *P. ponderosa* forests, where stands that had either been thinned or thinned and prescribed burned had much lower mortality during a *D. ponderosae* outbreak (Hood et al. 2016).

Interactions between forest fire and subcortical insects can be broadly categorized by whether insects are primary or secondary colonizers of pine trees (Fig. 1). Most subcortical beetle species are secondary colonizers and only a few are primary colonizers on pine trees. Primary beetles are first colonizers of trees while they are still presumably healthy and can overcome the trees' defenses. Secondary beetles (plus woodwasps, Hymenoptera: Siricidae) typically colonize trees that are stressed, weakened, damaged, or dying due to other abiotic and biotic causes, although in some limited instances (e.g., post-windstorms), secondary insects can become primary colonizers (Gandhi 2005). Overall, subcortical insects function as important phloem and wood degraders (through tunneling activities). This allows other insects, fungi, and bacteria to colonize trees, enhancing forest nutrient cycling and flow. Primary subcortical beetles, mostly in the genus *Dendroctonus*, are important economically in naturally regenerated and planted native pine forests, where they can cause high levels of tree mortality and lost revenue. In some years, economic impacts by subcortical insects cost billions of dollars of lost sawtimber and pulpwood trees, along with costs associated with replanting and reforestation efforts of planted pines (Nowak et al. 2008; Grégoire et al. 2015; Six and Bracewell 2015).

3.2.1 Primary Subcortical Colonizing Insects

Several primary colonizing insects, such as *D. ponderosae* and *D. brevicomis* LeConte (western pine beetle) (Geiszler et al. 1984; Amman and Ryan 1991; Rasmussen et al. 1996; Ryan and Amman 1996; McHugh et al. 2003; Maloney et al. 2008; Six and Skov 2009; Fettig et al. 2010; Davis et al. 2012; Powell et al. 2012; Kulakowski and Jarvis 2013; Steel et al. 2021), *Ips sexdentatus* (Börner) (Valor et al. 2021), and rarely *D. frontalis* (Boyle et al. 2004) are known to attack fire-injured pines, but these insects also commonly attack unburned trees (Fig. 1). These dynamics are likely influenced by fire regime shifts that alter host tree species dominance, and fuel loads and arrangement, and are dependent on insect and host tree species (Meigs et al. 2015; Fettig et al. 2022). Tabacaru et al. (2016) reported that *D. ponderosae* readily colonized fire-damaged *P. contorta* (a fire-embracer species) after a prescribed burn, but these attacks did not lead to outbreaks. This was also found by Powell et al. (2012) after wildfire, even though that fire reduced *P. contorta* resin defenses (Powell and Raffa 2011). In a different system, infestations by *D. frontalis* were higher in young *P. taeda* stands that were prescribed burned than unburned stands (Cameron and Billings 1988). While *P. taeda* is considered fire-tolerant, it has a much lower tolerance to fire (especially in younger age classes) than other prevalent southern pine species (Pile et al. 2017). *Dendroctonus frontalis*

infestations were lower in previously prescribed burned but unthinned *P. taeda* stands (Nowak et al. 2015), suggesting that burning confers resilience to trees (even in an over-stocked stand) to subsequent bark beetle outbreaks.

These patterns are insect density-dependent, as at low density levels, *D. ponderosae* did not readily colonize trees that were fire-injured (Elkin and Reid 2004; Powell et al. 2012), and reproductive success was not affected by the level of fire-injury (Elkin and Reid 2004). At higher *D. ponderosae* densities though, trees were successfully attacked irrespective of their fire-caused injury (Elkin and Reid 2004). While burned trees provide habitats for beetle populations at endemic levels, wildfires (Powell et al. 2012) or prescribed fires (Tabacaru et al. 2016) do not typically contribute to beetle outbreaks, unless there are other suitable stand and environmental conditions. Intense competition from secondary beetle species that infest fire-injured trees earlier and have multiple generations per year may also have contributed to these patterns (Powell et al. 2012).

3.2.2 Secondary Subcortical Colonizing Insects

Secondary beetles, in contrast, readily colonize fire-damaged trees, and likely exert strong competitive pressure on primary beetle species, either reducing or excluding them from newly available niches. Examples of secondary beetles associated with burned forests include *Ips* spp. (pine engraver beetles), *Hylastes* spp. (root bark beetles), *Pityogenes* species (twig beetles), *D. valens* LeConte (red turpentine beetle), *D. terebrans* (Olivier) (black turpentine beetle), and many woodboring beetle species (Buprestidae and Cerambycidae: *Monochamus* spp.) (Fig. 1). These taxa are known to increase in numbers on fire-injured pine trees, and even preferably colonize fire-charred parts of the trees (e.g., Geiszler et al. 1984; Amman and Ryan 1991; Rasmussen et al. 1996; Ryan and Amman 1996; McHugh et al. 2003; Sullivan et al. 2003; Lombardero et al. 2006; Costello et al. 2011; Perrakis et al. 2011; Davis et al. 2012; Powell et al. 2012; Ray et al. 2019; Jung et al. 2020). In *P. palustris* and *P. elliotti* Engelm. (slash pine) stands (both fire tolerant), *Ips* and *D. terebrans* populations remained low and those of root-feeding beetles were higher in stands that were moderately and severely burned by a wildfire (Hanula et al. 2002), likely due to root injury. Responses of secondary insects are guild- and species-specific, likely vary across fire regimes, and dependent on the type of host injury, volume and type of available host material, and time since fire. Similar to primary species, there's little evidence that these secondary insects can build up in burned areas and start colonizing healthy or unburned green trees within and surrounding these forests (Hanula et al. 2002; Six and Skov 2009; Santolamazza-Carbone et al. 2011). However, the population spill-over effect of buildups of insects into unburned areas is still a major operational concern in many managed pine stands worldwide.

3.2.3 Variable Feedback Loops Between Insect Outbreaks and Fire

Insect-induced mortality has been hypothesized to contribute to greater probability, severity, and extent of wildfires. In the eastern and western U.S. forests where several bark beetle species outbreaks have resulted in dying and dead trees across millions of hectares (Hicke et al. 2016; McNichol et al. 2019; Audley et al. 2020), there are still numerous questions about the interactions of bark beetle outbreaks with fire. Outstanding research questions in general include (1) do insect outbreaks affect fire behavior via fuel alteration; (2) do insect outbreaks increase in number, severity, and duration with altered fire regimes; and (3) do fuel reduction treatments that are designed to reduce fire hazard also reduce insect outbreak incidence and severity? The empirical evidence for such interactions between bark beetle outbreaks and fires is mixed (Romme et al. 2006; Hicke et al. 2016). Positive interactions were observed by Turner et al. (1999) (fire severity and severe beetle damage) and Lynch et al. (2006) (probability of wildfire), and negative by Turner et al. (1999) (fire severity and intermediate beetle damage), Meigs et al. (2016) (severity), and Simard et al. (2011) (probability of crown fire). A lack of effect of beetle outbreaks on wildfires was observed by Hart et al. (2015) (area burned). Such interactions may be dependent on the conditions of the trees, such as whether standing trees have retained dead needles ("red stage") or fallen needles ("gray stage"), or post-outbreak stage with downed trees (Turner et al. 1999; Fettig et al. 2022). Various site and environmental conditions also likely play a role in these dynamics (Lynch et al. 2006; Black et al. 2013). However, in a rare study on foliage feeding insects about 20-times higher frequency of wildfire occurred in areas of *Dendrolimus sibiricus* (Tschetv.) (Siberian silkmoth) outbreaks that affected multiple conifer species in Siberia (Kharuk and Antamoshkina 2017).

At any given time, pine species are impacted either by stand-replacing wildfire or beetle species. These events may be thought of as operating in near exclusion of one other, although bark beetles are always present in low numbers in these stands. However, fire and/or beetle driven changes in forest composition (tree species and diversity) and structure (age and density) can have feedback loops. Post-burned forests may result in greater regeneration of tree species (e.g., hardwoods, shrubs, or other pine species) that are more tolerant of fire and/or beetles (Retana et al. 2002; Coleman et al. 2008; Perovich and Sibold 2016; Pelz and Smith 2012), particularly at the trailing edge of a tree species range (Renwick et al. 2016). Differential mortality of tree species from wildfires and beetles may negate impacts from the two disturbances. For example, recruitment of *P. pungens* lamb. (Table Mountain pine) was severely limited due to mortality by *D. frontalis* and ice-storms, but promoted by wildfire, as fire killed competitive hardwood species (Lafon and Kutac 2003).

The timing of either disturbance agent may be important for pine recruitment dynamics, both at the individual and population levels. Within a period of 6 years, serotinous *P. contorta* stands killed by *D. ponderosae* lost an estimated 45% more cones than stands unimpacted by beetles (Teste et al. 2011). After a *D. ponderosae* outbreak in *P. contorta* gray-phase forests, heterogeneous burn severities, coupled

with areas of unburned fire refugia, fostered subsequent heterogeneity of *P. contorta* regeneration (Talucci et al. 2019). In the gray-phase, unburned patches, canopy seed stored in serotinous cones were reduced via squirrel predation, branch breakage, and cones opening, resulting in reduced regeneration relative to areas that burned at higher intensity. While *P. contorta* cones may germinate from both beetle-killed and live trees (Aoki et al. 2011), germination rates were reduced over time on beetle-killed trees (Rhoades et al. 2022), and short-return interval fires that occurred before serotiny develops can also reduce regeneration (Turner et al. 2019).

Insect outbreaks before prescribed fire can also alter regeneration dynamics of pine stands. In *P. echinata* Mill. (shortleaf pine) stands that were mostly killed by *D. frontalis* and were subsequently prescribed burned, natural regeneration was much higher and more vigorous than in unburned sites (Land and Rieske 2006). Regeneration-attacking insects on younger-aged pines showed a variable response where pine weevils [*Hylobius pales* (Herbst) (Pales weevil) and *Pissodes nemorensis* Germar (pitch-eating weevil)] and *Rhyacionia frustrana* (Comstock) (Nantucket pine tip moth) did not differ between burned and unburned sites (Land and Rieske 2006). However, *Tetralopha robustella* Zeller (pine webworm) infestations were greater on seedlings in burned areas. Conifer sawfly numbers were much lower in burned areas, likely because the fires consumed the duff layer where sawflies overwinter (Land and Rieske 2006). Prescribed fire after *Ips* beetle outbreaks may enhance the health of residual *P. taeda* trees making them more resilient to future beetle colonization activities (McNichol et al. 2019).

3.3 Interactions Between Prescribed Burning and Insects

3.3.1 Indirect Management of Insects Using Prescribed Fire

Prescribed burning is a frequently used tool in managed pine forests for multiple desired outcomes including removing hardwood competition, reducing tree density, improving wildlife habitats dependent on fire, reducing surface and canopy fuel loads, and enhancing tree health in general (Van Lear and Waldrop 1991; Fernandes and Botelho 2004; Ryan et al. 2013; Hunter and Robles 2020; Agbeshie et al. 2022). Low-intensity fire also enhances nutrient cycling and provides a pulse of nutrients that stimulate understory plants and other taxa (Carter and Foster 2004; Agbeshie et al. 2022), and higher intensity fires can cause sufficient injuries to pine trees. Trees stressed during prescribed burning may be attacked by secondary insect species that colonize injured and stressed trees (e.g., Bradley and Tueller 2001; Menges and Deyrup 2001; Sullivan et al. 2003; Campbell et al. 2008; Six and Skov 2009; Davis et al. 2012).

Based on whether the pine species are fire-tolerators [e.g., *P. nigra* Arn. (European black pine), *P. ponderosae*, and *P. palustris*] or fire-embracers (e.g., *P. contorta, P. halepensis*, and *P. pinaster*) (Agee 2000; Tapias et al. 2004), the dynamics of including low-intensity prescribed burning are different and elicit different responses

by forest insects. Fire-tolerators have thicker bark and are less prone to fire-caused injury; and may have higher resin duct area and thus, be better defended against insects than fire-embracers (Valor et al. 2021). Insects encounter a more formidable defense system and have a harder time colonizing fire-tolerators than fire-embracers after a prescribed fire. For example, *I. sexdentatus* (Boern) readily colonized *P. sylvestris* L. (Scots pine), which is less tolerant of fire than *P. nigra,* after a prescribed burn (Valor et al. 2021). Most *P. nigra* trees that were attacked were of smaller diameter size that likely experienced greater stem injury (Valor et al. 2021).

Fire-excluded pine stands are more vulnerable to basal injury from prescribed burning due to long-term smoldering of basal duff accumulations (Hood 2010), as reported for *P. ponderosa* (e.g., Perrakis and Agee 2006; Fule et al. 2007; Six and Skov 2009; Perrakis et al. 2011), *P. palustris* (O'Brien et al. 2010), and mixed pine forests (Maloney et al. 2008), particularly under drier conditions (Varner et al. 2007; Ritger et al. 2023). After reintroduction of fire to *P. palustris*, trees with stem and root burns had smaller resin ducts which were correlated with lower precipitation levels, suggesting that climate change is an important consideration in restoration activities (Slack et al. 2016). Fire-suppressed (~15 years) *P. palustris* had higher trap catches of *Ips* beetles and higher resin flows on xeric than mesic sites (Ritger et al. 2023). However, exactly how climate change will affect these dynamics is unknown. In fire-suppressed forests, deep litter and duff can accumulate at the bases of trees, which if burned can lead to long-duration, low-intensity smoldering of the duff and basal cambial kill. In some pine species (e.g., *P. palustris*), when stands are not regularly burned, fine roots grow into developing forest floor layers and may be killed during burning, causing tree stress and mortality (Swezy and Agee 1991; O'Brien et al. 2010). In these cases, tree mortality may occur a few years post-fire, indicating a lag phase (Sullivan et al. 2003; Fettig and McKelvey 2014) where interactions with climate (e.g., drought) can further impact tree health and cause additional mortality (Steel et al. 2021). Hence, longer-term monitoring of stands where prescribed fire is reintroduced is recommended. Slowly reintroducing fire through a series of low-intensity prescribed fires to gradually reduce duff accumulations after long periods of fire exclusion or thinning of smaller diameter trees will reduce tree injury and mortality (Pollet and Omi 2002; Perrakis et al. 2011). This may also increase their resilience to drought (Vilà-Vilardell et al. 2023) and reduce activity of herbivorous insects (Ritger et al. 2023). If gradual consumption of deep duff layers is difficult to achieve due to duff moisture, other mitigation treatments such as raking of basal duff may be warranted (Hood 2010).

Cessation of frequent prescribed burning cycles may have implications for bark beetle outbreaks. During 2016–2017, many states in the southeastern U.S. experienced higher numbers of, and damage by, *Ips* beetles, presumably under water deficit conditions (Georgia Forestry Commission 2017). Deferred prescribed burning was recommended for *P. taeda* stands (under 2–3 year fire frequency cycle) that had *Ips* beetle outbreaks until the drought alleviated. However, these fire-deferred pine stands had greater infestation of, and higher mortality caused by *Ips* beetles than stands kept on their regular burn cycle (McNichol et al. 2019). Further, in some sites, these *Ips* beetle outbreaks were immediately followed by *D. frontalis*

outbreaks in unburned pine stands (*personal observations*) as fire suppression altered relationships between pine trees and subcortical beetles.

Pine tree mortality and associated insect activity vary based on the season of prescribed burning. Fall burning of *P. ponderosa* stands may result in greater tree injury than spring burning due to generally wetter and cooler conditions in the spring (Perrakis and Agee 2006; Perrakis et al. 2011). In other studies, no differences in tree mortality or beetle infestations were observed after prescribed burning in different seasons (Ganz et al. 2003; Schwilk et al. 2006; Fettig et al. 2010), or the highest tree mortality occurred in spring burns and lowest in fall burns (McHugh et al. 2003). In *P. ponderosa* stands burned at 5- and 15-year intervals in spring and fall, the lowest mortality of pines and the highest activity of *Neophasia menapia* Felder (pine butterfly) and *D. brevicomis* were found in stands burned in the fall at 5-year intervals (Westlind and Kerns 2021). Phenological responses of trees and insects to fire may also be attributed to stand, fuel, weather conditions, and ignition patterns in prescribed burned forests, and may explain this variation in herbivore responses across studies.

Trapping studies report increased numbers of bark beetle species (mostly secondary colonizers) in recently prescribed burned areas (e.g., Santoro et al. 2001; Sullivan et al. 2003; Ritger et al. 2023; Palmer et al. 2024), suggesting immigration of insects from surrounding areas. However, after low-intensity prescribed fires in fire-tolerator ecosystems, little insect activity on trees was observed, as there were fewer trees that were sufficiently fire-injured (Cannac et al. 2009; Ritger et al. 2023). Burned areas may provide beetles with a short-term refuge from their natural enemies that are not responding positively to fire, and that have similar population sizes in burned and unburned areas (Six and Skov 2009; Powell et al. 2012). If trees are well or even better defended (Hood et al. 2015), then insects would have used their valuable energy reserves to find suitable hosts (Kinn et al. 1994; Evenden et al. 2014), particularly during the spring-time when both the burning and first insect dispersal activity occurs. Fire can influence constitutive and induced defenses, and post-fire, bark beetle attack success may be more influenced by induced defenses of pine trees (Howe et al. 2020). Stands that are well maintained by prescribed fire likely have stronger constitutive and induced defenses post-fire, and thus may be acting as an ecological trap for these insects. In landscapes where multiple stands are regularly burned on a rotating basis in spring and fall of each year (e.g., in many *P. palustris* stands in Florida and Georgia), subsequent generations of beetles may be dispersing from one burn to the next in attempts to find suitable hosts, yet prescribed burned sites may still yield a greater number of suitable hosts than unburned sites, where stressed and damaged hosts are a rare and ephemeral resource at the landscape-level. Trees that have lower crown vigor, growth rates, and smaller diameter, along with greater degree of bark charring, provide more suitable hosts for colonizing insects in burned (Menges and Deyrup 2001; Wallin et al. 2003; Perrakis et al. 2011; Valor et al. 2021) than in unburned areas.

Prescribed burning after catastrophic storms (wind and ice) has been used as a fuel reduction treatment to reduce woody debris on the landscape (Emery et al. 2020), prevent insect outbreaks and accelerate pine regeneration (Gilmore et al.

2002; Gandhi et al. 2009). Burning these forests also presumably counteracts the effects of fire suppression in fire embracer species, although that remains untested. Subcortical beetles and their associated predators can increase in numbers after windstorms and in post-storm-prescribed burned *P. banksiana* Lamb. (jack pine) stands (Gandhi et al. 2009). Their populations decrease after a few years as natural enemies build up and host resources degrade.

3.3.2 Direct Management of Insects Using Prescribed Fire

While the concept of "thermosanitation" is decades-old, the alternate use of chemicals and the logistical and legal challenges of conducting prescribed burning have taken precedence in modern silviculture (Miller 1979; Schmid and Parker 1990). It is well recognized that prescribed fire can be used as a tool to directly kill and reduce populations of several herbivorous insects in pine stands, although this management tactic is rarely applied in many pine ecosystems (McCullough et al. 1998; Fettig et al. 2022). Insects that have specific life-stages that overwinter on the forest floor and in fallen woody material are especially appropriate targets for prescribed burning, as they are in a vulnerable stage (McCullough et al. 1998). Rarely is fire used to control foliage-feeding insects (Parker et al. 2006), although those utilizing younger age classes of trees are more vulnerable. Prescribed fire has been recommended to reduce populations of seed predators such as *Conophthorus resinosae* Hopkins (red pine cone beetle), and *Eucosma monitorana* (Heinrich) (red pinecone borer moth) in *P. resinosa* Ait. (red pine) seed production areas (and when cones are on the forest floor) (Miller 1978), *Coloradia pandora* Blake (Pandora moth), in *P. ponderosa* stands (when moths are pupating in the soil) (Miller and Wagner 1984; Gerson and Kelsey 1997), and sawflies in *P. echinata* stands (on smaller trees) (Land and Rieske 2006). Burning of slash piles from logging and thinning is also conducted to reduce infestations by subcortical beetles (Dahl 1971; Schmid and Parker 1990; DeGomez et al. 2008) and likelihood of beetles colonizing trees near slash piles. Interestingly, both the load of non-native pinewood nematodes [*Bursaphelenchus xylophilus* (Steiner & Buhrer)] that causes pine wilt disease and its vector the Japanese pine sawyer (*Monochamus alternatus* Hope) were reduced greatly in *Pinus massoniana* Lambert (Masson pine) stands after prescribed burning (Chen and Liu 2020). This was attributed to greater mortality and/or disruption of life-cycle of cerambycid beetles and nematodes in the lower part of tree boles due to fire-injury (Chen and Liu 2020).

Prescribed fire may be used as a preventative management tool to reduce the probability of insect outbreaks (Miller 1979), but this has rarely been implemented. *Dendroctonus ponderosae* brood density was reduced by 50% in prescribed burned than unburned *P. contorta* forests (Safranyik et al. 2001). On the burned trees, the incidence of attacks, average attacks, and brood production per tree were lower than on unburned trees (Safranyik et al. 2001). Beetles preferentially attacked uncharred areas on burned trees. The following year, *D. ponderosae* tended to attack trees in unburned rather than burned sites, as previously reported by Elkin and Reid (2004).

Similar studies need to be conducted on other primary subcortical insect species under various fire regimes, especially some of them have expanded their distribution range into novel habitats due to climate change.

3.4 Adaptations of Insects to Fire

Like many other animal species, herbivorous insects have developed behavioral, morphological, or physiological adaptations to fire in pine ecosystems (Pausas and Parr 2018). These adaptations are advantageous to insects in that fire creates empty niches for a host of insects and other organisms to colonize—and the first colonizers experience the lowest competitive and predation pressures. Only a few forest herbivorous insects on pines are known to be attracted to post-burned pine stands, although other pyrophilous genera and species of insects are attracted to burned trees (e.g., the carabid beetle, *Sericoda* species) (Wikars 1997; Koivula et al. 2006) in pine-dominated and pine-hardwood ecosystems. A few species (e.g., *Calosoma frigidum* Kirby) have behavioral adaptations where they construct underground burrows, and after low-intensity fire, start foraging aboveground *en masse* (Jacobs et al. 2011). Pyrophilous species have been well studied in Canadian and European pine forests, and several of them are threatened with extinction due to fire-suppression and habitat changes in European forests (e.g., Gongalsky et al. 2003; Süda et al. 2009; Milberg et al. 2015; Heikkala et al. 2017). These insects have even been discovered in fossil records of burned wetland pine forests in Europe (Whitehouse 2000) indicating their long evolutionary history with fire. Smoke can also be both an attractant and deterrent to other species in pine forests that are not necessarily using pine trees directly as a resource (Liu et al. 2022). For example, *Exyra* spp. (pitcher plant moth) lives in pitcher plants (*Sarracenia* spp.) in frequently burned southern U.S. pine forests, and when exposed only to smoke, exits the plant (Lee et al. 2016), indicating strong behavioral adaptations to fire. Many other vertebrate and invertebrate species in pine forests also escape from fire either by running or burrowing deeper into the soil (Certini et al. 2021).

Several insect species cue into forest fires rapidly. Beetles in the genus *Melanophila* (Buprestidae) have sensors on their thorax to detect infrared radiation (Evans 1966) and their antennae can also detect smoke (Schütz et al. 1999). They were reported to find forest fires >95 km away from the nearest conifers in California and can even pick up anthropogenic fire sources (e.g., sugar refineries, smelting plants, and trash fires) (Hart 1998). Many buprestid beetles in the genera *Dicerca* and *Melanophila* have colors and reflective patterns resembling burnt wood which allow them to blend well when they land on burnt trees (*personal observations*). The cerambycid beetle, *Monochamus galloprovincialis* (Olivier), also has antennal sensillae that detect smoke-related compounds and is frequently found on burnt pine wood (Álvarez et al. 2015). Interestingly, *C. pandora* (Pandora moth) is attracted to night-burning prescribed fires, causing ~2%–17% mortality of its local populations; therefore, night burning may be a better management tool for that pest species

(Gerson and Kelsey 1997). It's quite possible that other pine herbivorous insects have various adaptations to fire, but they have been vastly under documented.

4 Fire and Insects in Non-native Planted Pines

Pine species [e.g., *P. caribaea* Morelet (Caribbean pine), *P. elliottii*, *P. patula* Schldl. et Cham. (Patula pine), *P. pinaster*, *P. radiata* D. Don (Monterey pine), and *P. taeda*] planted in the Southern Hemisphere are all non-native and imported from Europe, Mexico, and North America (Pryor 1991; Richardson 1998; Richardson and Nsikani 2021). There is a positive feedback loop where fire promotes invasion of these pine species into novel habitats, and pines also alter stand attributes to promote persistence of fire in these ecosystems (Zalba et al. 2008; Franzese and Raffaele 2017; Taylor et al. 2017; Davis et al. 2019). This has led to major changes in invaded habitats with adverse consequences for their native biodiversity and ecological processes (García et al. 2018; Cifuentes-Croquevielle et al. 2020).

Many insect species are introduced to these non-native planted pines and can cause damage irrespective of their colonizing status in their native range (Neumann 1987; Zhang et al. 1993; Yan et al. 2005; Carnegie et al. 2018; Estay 2020; Graziosi et al. 2020). This is due to planting off-site that stresses trees, and release from host defenses, natural enemies, and inter-species competitive pressures. Similar to their native ranges, bark and woodboring insects positively interact with wildfires due to highly available scorched and burnt host material in the non-native ranges (Bradbury 1998; Wylie et al. 1999; Zhan et al. 2022). *Dendroctonus valens* was introduced to China and also readily attacks pine trees after burning (Zhan et al. 2022). Females of *Arhopalus tristi* (F.) (burnt pine longhorn beetle), a cerambycid beetle introduced to planted pines in New Zealand, orient positively towards odors from burnt pine on which they lay eggs (Suckling et al. 2001), and colonize trees within days after a wildfire (Bradbury 1998). Wildfires can interfere with integrated pest management strategies in non-native pine stands. For example, mega-wildfires have resulted in catastrophic pine timber losses in southeastern Australia (Keeves and Douglas 1983; Bousfield et al. 2023). This led to increases in populations of *I. grandicollis* Eichhoff, a North American bark beetle, and interference with biocontrol of *Sirex noctilio* F., a Eurasian woodwasp, due to competitive pressure on trap logs (Gitau et al. 2013; Hayes and Nahrung 2022) (Fig. 1).

5 Conclusions

The long-evolved, complex, and co-occurring nature of fire and herbivorous insects as natural disturbance agents from individual pine trees to stand and landscape levels contributes to extant forest patterns and processes. Fire may positively or negatively affect pine tree and stand health, herbivorous insects, and their interactions as

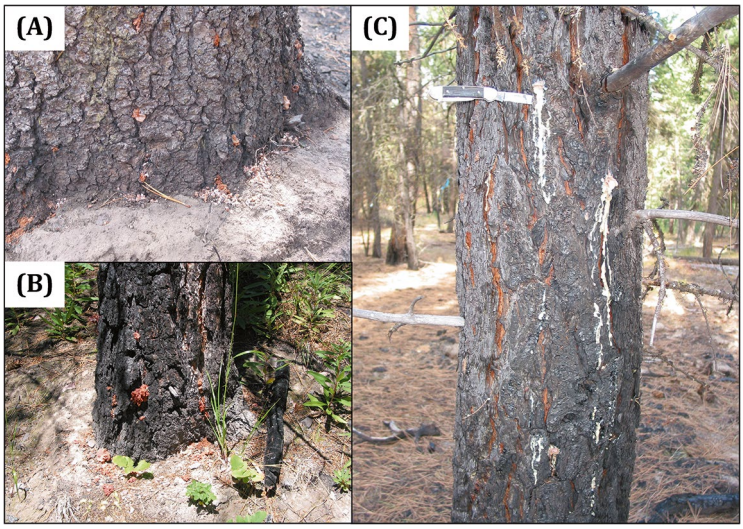

Fig. 1 Examples of activity (as evidenced by resin pitch tubes) of herbivorous insects on pine trees after fires: (**a**) *Dendroctonus valens* on *Pinus contorta* after a low intensity prescribe fire; (**b**) *Dendroctonus valens* on *Pinus ponderosa* after a wildfire; (**c**) *Dendroctonus ponderosae* on *Pinus ponderosa* after a wildfire

based on its frequency and intensity, and hence severity (Figs. 2 and 3). Hence, an understanding of historical fire regimes is critical to restoring ecosystem services in pinelands. A mechanistic model of these trilateral interactions indicates that attributes of pine trees and stands that are adapted to fire provide a positive feedback loop to fire's persistence in the ecosystem (Fig. 3). Similarly, fires affect insect herbivores either indirectly through alterations in host quality/quantity or directly through mortality. There is mixed evidence for feedback loops from insects to pine tree-insect interactions to persistence of fires, and these patterns remain unknown for many outbreaking species (Fig. 3). Pine trees and herbivorous insects may positively or negatively affect each other. From an ecological perspective, insects act as a disturbance agent retriggering or augmenting forest succession and thus, are an integral positive component of forested ecosystems. From an economic perspective, herbivorous insects are capturing the mortality of pine trees instead of foresters, hence causing economic damage particularly in planted pine stands. Interestingly, fire and insects as abiotic and biotic disturbance agents, respectively, contribute to similar altered pine dynamics such as stand composition and structure, and tree nutrition, defenses, morphology, and various life history strategies including reproduction (Fig. 3). This lends greater support towards simultaneously including their evolutionary history in forest pine management plans with a focus on their differential impacts.

In managed pine stands, interventions against herbivorous insect pests may result in variable forestry responses depending on population levels and responses to fire (Fig. 4). In pre-fire conditions and low insect population levels, prevention is the

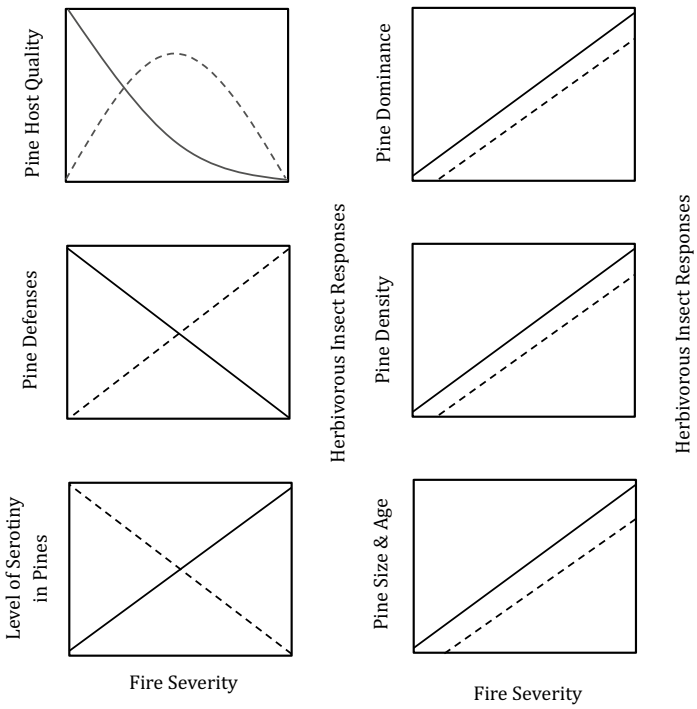

Fig. 2 Examples of potential effects of fire severity on pine trees and stand attributes (solid line) and resulting herbivorous pine insect responses (dashed line) levels

best option and may include reduction in fuel loads (e.g., inclusion of appropriate fire regimes and optimal silvicultural practices such as thinning) to avoid high-severity fires. At higher insect population levels (i.e., outbreak phase) pre-fire, management techniques such as removal and treatment of infested trees to reduce insect levels are warranted. Post-fire, increased insect activity (higher population levels) may trigger management activities such as pest reduction (e.g., removal of infested trees) and pest prevention (e.g., thinning) practices. Moderate responses by insects post-fire may be managed via prevention activities, while little to no responses from insects to fire won't trigger any management interventions. Interestingly, these strategies may be used in pine stands irrespective of their fire regimes, and can be refined based on insect and tree attributes.

We recognize several gaps and areas for future research on these trilateral interactions in pine-dominated ecosystems: (1) little is known about these interactions in Mesoamerica, which is the epicenter for pine diversity, and in Asia, where many species of pines occur at high elevation and latitude sites; (2) a better understanding of morphological, physiological, and other adaptations of herbivorous insects to fire regimes is warranted; (3) a greater focus on insect guilds other than bark beetles,

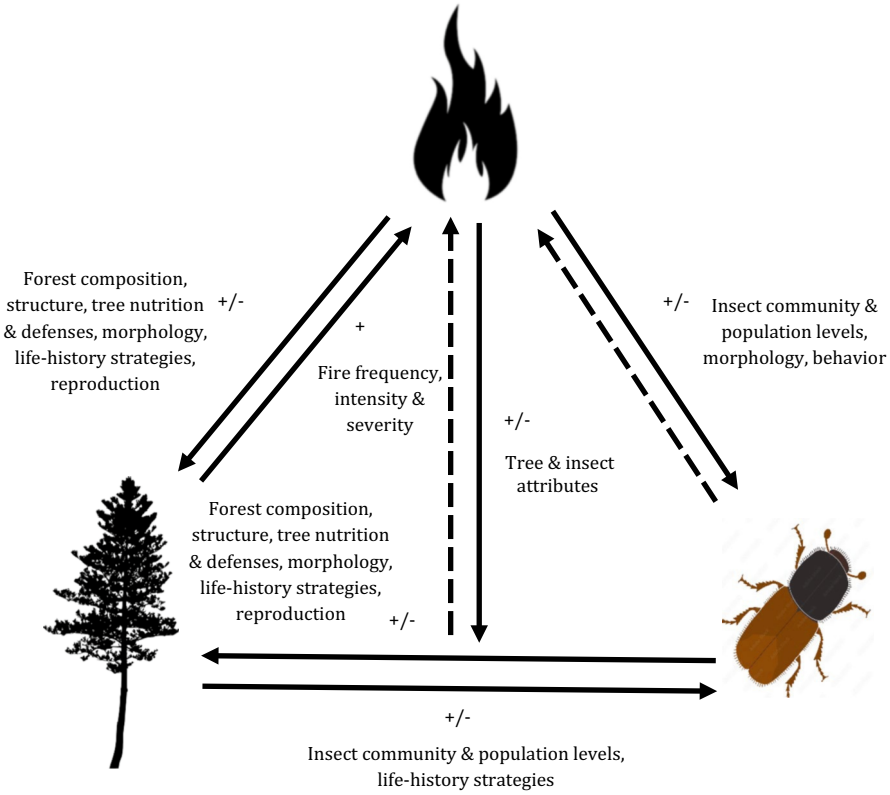

Fig. 3 Proposed interactions [positive (+) or negative (−)] between fire, pine trees, and herbivorous insects. Solid lines indicate established interactions and dashed lines indicate mixed or hypothesized evidence for interactions

insect-associated pathogens, and vertebrates will be useful; (4) many feedback loops from pine tree-insect interactions and those of insects to fire regimes are largely unknown (Fig. 3); and (5) a thorough underpinning of the relative selection pressures by the abiotic and biotic agents on pine tree and stand attributes are critical to restoring pinelands under continuing fire regime and climatic changes worldwide.

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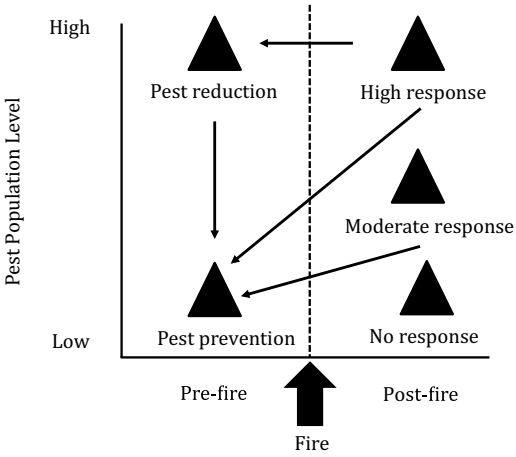

Fig. 4 Various management interventions for herbivorous insects (pests) as based on their population levels and responses after pre- and post-fire

References

Abatzoglou JT, Williams AP (2016) Impact of anthropogenic climate change on wildfire across western US forests. Proc Natl Acad Sci USA 113(42):11770–11775

Abram NJ, Henley BJ, Sen Gupta A et al (2021) Connections of climate change and variability to large and extreme forest fires in southeast Australia. Commun Earth Environ 2(1):8

Agbeshie AA, Abugre S, Atta-Darkwa T et al (2022) A review of the effects of forest fire on soil properties. J For Res 33:1419–1441

Agee JK (2000) Fire and pine ecosystems. In: Richardson DM (ed) Ecology and biogeography of *Pinus*. Cambridge University Press

Álvarez G, Ammagarahalli B, Hall DR et al (2015) Smoke, pheromone and kairomone olfactory receptor neurons in males and females of the pine sawyer *Monochamus galloprovincialis* (Olivier) (Coleoptera: Cerambycidae). J Insect Physiol 82:46–55

Amman GD, Ryan KC (1991) Insect infestation of fire-injured trees in the Greater Yellowstone Area. USDA Forest Service, Intermountain Research Station, Research Note INT-398, p 9

Aoki CF, Romme WH, Rocca ME (2011) Lodgepole pine seed germination following tree death from mountain pine beetle attack in Colorado, USA. Am Midl Nat 165(2):446–451

Archibald S, Lehmann CE, Gómez-Dans JL et al (2013) Defining pyromes and global syndromes of fire regimes. Proc Natl Acad Sci 110(16):6442–6447

Audley JP, Fettig CJ, Munson AS et al (2020) Impacts of mountain pine beetle outbreaks on lodgepole pine forests in the Intermountain West, US, 2004–2019. For Ecol Manag 475:118403

Baker WL (1972) Eastern forest insects, vol 1166. US Department of Agriculture, Forest Service

Bergeron Y, Gauthier S, Kafka V et al (2001) Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can J For Res 31(3):384–391

Berryman AA, Stenseth NC, Isaev AS (1987) Natural regulation of herbivorous forest insect populations. Oecologia 71:174–184

Bird RB, Bird DW, Codding BF et al (2008) The "fire stick farming". Hypothesis: Australian Aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics. Proc Natl Acad Sci 105(39):14796–14,801

Black SH, Kulakowski D, Noon BR et al (2013) Do bark beetle outbreaks increase wildfire risks in the central US Rocky Mountains? Implications from recent research. N Areas J 33(1):59–65

Boer MM, Resco de Dios V, Bradstock R (2020) Unprecedented burn area of Australian mega forest fires. Nat Clim Change 10:171–172
Bond WJ, Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol Evol 20:387–394
Bousfield CG, Lindenmayer DB, Edwards DP (2023) Substantial and increasing global losses of timber-producing forest due to wildfires. Nat Geosci 16(12):1145–1150
Boyle MF, Hedden RL, Waldrop TA (2004) Impact of prescribed fire and thinning on host resistance to the southern pine beetle: preliminary results of the National Fire and Fire Surrogate Study. In: Proceedings, 12th biennial southern silvicultural research conference. General Technical Report SRS-71. US Department of Agriculture, Forest Service, Southern Research Station, Asheville, pp 60–64
Bradbury PM (1998) The effects of the burnt pine longhorn beetle and wood-staining fungi on fire damaged *Pinus radiata* in Canterbury. N Z For 43:28–31
Bradley T, Tueller P (2001) Effects of fire on bark beetle presence on Jeffrey pine in the Lake Tahoe Basin. For Ecol Manag 142(1–3):205–214
Brändle M, Brandl R (2001) Species richness of insects and mites on trees: expanding Southwood. J Anim Ecol 70(3):491–450
Breece CR, Kolb TE, Dickson BG et al (2008) Prescribed fire effects on bark beetle activity and tree mortality in southwestern ponderosa pine forests. For Ecol Manag 255(1):119–128
Cameron RS, Billings RF (1988) Southern pine beetle: factors associated with spot occurrence and spread in young plantations. South J Appl For 12(3):208–214
Campbell JW, Hanula JL, Waldrop TA (2008) Effects of prescribed fire and fire surrogates on saproxylic Coleoptera in the southern Appalachians of North Carolina. J Entomol Sci 43:57–75
Cannac M, Barboni T, Ferrat L et al (2009) Oleoresin flow and chemical composition of Corsican pine (*Pinus nigra* subsp. *laricio*) in response to prescribed burnings. For Ecol Manag 257(4):1247–1254
Carnegie AJ, Venn T, Lawson S et al (2018) An analysis of pest risk and potential economic impact of pine wilt disease to *Pinus* plantations in Australia. Aust For 81(1):24–36
Carter MC, Foster CD (2004) Prescribed burning and productivity in southern pine forests: a review. For Ecol Manag 191(1–3):93–109
Certini G, Moya D, Lucas-Borja ME et al (2021) The impact of fire on soil-dwelling biota: a review. For Ecol Mang 488:118989
Chen XW, Liu FL (2020) Effects of prescribed burning on pine wood nematode (*Bursaphelenchus xylophilus*). Appl Ecol Environ Res 18(5):1–14
Christianson AC, Sutherland CR, Moola F et al (2022) Centering Indigenous voices: the role of fire in the boreal forest of North America. Curr For Rep 8(3):257–276
Cifuentes-Croquevielle C, Stanton DE, Armesto JJ (2020) Soil invertebrate diversity loss and functional changes in temperate forest soils replaced by exotic pine plantations. Sci Rep 10(1):7762
Cobb RC, Metz MR (2017) Tree diseases as a cause and consequence of interacting forest disturbances. Forests 8(5):147
Cocos D, Klapwijk MJ, Schroeder M (2023) Tree species preference and impact on native species community by the bark beetle *Ips amitinus* in a recently invaded region. NeoBiota 84:349–367
Colatskie R (2011) Fuel management considerations in Caribbean pine forests of the Mountain Pine Ridge of Belize, Central America. Dissertation, University of Missouri-Columbia
Coleman TW, Clarke SR, Meeker JR et al (2008) Forest composition following overstory mortality from southern pine beetle and associated treatments. Can J For Res 38(6):1406–1418
Costello SL, Negrón JF, Jacobi WR (2011) Wood-boring insect abundance in fire-injured ponderosa pine. Agric For Entomol 13(4):373–381
Cullingham CI, Cooke JE, Dang S et al (2011) Mountain pine beetle host-range expansion threatens the boreal forest. Mol Ecol 20(10):2157–2171
Dahl BM (1971) Mortality of *Monochamus* larvae in slash fires. Environ Can For Ser Bimon Res Notes 27(2):12

Davis RS, Hood S, Bentz BJ et al (2012) Fire-injured ponderosa pine provide a pulsed resource for bark beetles. Can J For Res 42(12):2022–2036
Davis KT, Maxwell BD, Caplat P et al (2019) Simulation model suggests that fire promotes lodgepole pine (*Pinus contorta*) invasion in Patagonia. Biol Invasions 21:2287–2300
de la Mata R, Hood S, Sala A (2017) Insect outbreak shifts the direction of selection from fast to slow growth rates in the long-lived conifer *Pinus ponderosa*. Proc Natl Acad Sci 114(28):7391–7396
DeGomez T, Fettig CJ, McMillin JD et al (2008) Managing slash to minimize colonization of residual leave trees by *Ips* and other bark beetle species following thinning in southwestern ponderosa pine. University of Arizona, College of Agriculture and Life Sciences Bulletin, AZ1448, Tucson, pp 1–12
Diaz-Toribio MH, Carr S, Putz FE (2020) Pine savanna plant community disassembly after fire suppression. J Veg Sci 31(2):245–254
Dixon WN, Corneil JA, Wilkinson RC et al (1984) Using stem char to predict mortality and insect infestation of fire-damaged slash pines. South J Appl For 8(2):85–88
Dodds KJ, Aoki CF, Arango-Velez A et al (2018) Expansion of southern pine beetle into northeastern forests: management and impact of a primary bark beetle in a new region. J For 116(2):178–191
Elkin CM, Reid ML (2004) Attack and reproductive success of mountain pine beetles (Coleoptera: Scolytidae) in fire-damaged lodgepole pines. Environ Entomol 33(4):1070–1080
Emery RK, Kleinman JS, Goode JD (2020) Effects of catastrophic wind disturbance, salvage logging, and prescribed fire on fuel loading and composition in a *Pinus palustris* woodland. For Ecol Manag 478:118515
Estay SA (2020) Insect pests affecting exotic trees in Chile and their management. In: Estay S (ed) Forest Pest and Disease Management in Latin America. Springer, Cham, pp 185–195
Estes BL, Knapp EE, Skinner CN et al (2017) Factors influencing fire severity under moderate burning conditions in the Klamath Mountains, northern California, USA. Ecosphere 8(5):e01794
Evans WG (1966) Perception of infrared radiation from forest fires by *Melanophila acuminata* De Geer (Buprestidae, Coleoptera). Ecology 47(6):1061–1065
Evenden ML, Whitehouse CM, Sykes J (2014) Factors influencing flight capacity of the mountain pine beetle (Coleoptera: Curculionidae: Scolytinae). Environ Entomol 43(1):187–196
Falcon-Lang HJ, Mages V, Collinson M (2016) The oldest *Pinus* and its preservation by fire. Geology 44(4):303–306
Feeney SR, Kolb TE, Covington WW (1998) Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson Natural Area. Can J For Res 28(9):1295–1306
Fernandes P, Botelho H (2004) Analysis of the prescribed burning practice in the pine forest of northwestern Portugal. J Environ Manage 70(1):15–26
Fernandes PM, Pacheco AP, Almeida R et al (2016) The role of fire-suppression force in limiting the spread of extremely large forest fires in Portugal. Eur J For Res 135:253–262
Fettig CJ, McKelvey SR (2014) Resiliency of an interior ponderosa pine forest to bark beetle infestations following fuel-reduction and forest-restoration treatments. Forests 5(1):153–176
Fettig CJ, McKelvey SR, Cluck DR et al (2010) Effects of prescribed fire and season of burn on direct and indirect levels of tree mortality in ponderosa and Jeffrey pine forests in California, USA. For Ecol Manag 260(2):207–218
Fettig CJ, Runyon JB, Homicz CS et al (2022) Fire and insect interactions in North American forests. Curr For Rep 8(4):301–316
Fill JM, Davis CN, Crandall RM (2019) Climate change lengthens southeastern USA lightning-ignited fire seasons. Glob Chang Biol 25(10):3562–3356
Franzese J, Raffaele E (2017) Fire as a driver of pine invasions in the Southern Hemisphere: a review. Biol Invasions 19:2237–2246
Friedenberg NA, Whited BM, Slone DH (2007) Differential impacts of the southern pine beetle, *Dendroctonus frontalis*, on *Pinus palustris* and *Pinus taeda*. Can J For Res 37(8):1427–1437

Fule PZ, Roccaforte JP, Covington WW (2007) Posttreatment tree mortality after forest ecological restoration, Arizona, United States. Environ Manage 40:623–634
Furniss MM (1965) Susceptibility of fire-injured Douglas-fir to bark beetle attack in southern Idaho. J For 63(1):8–11
Gandhi KJK (2005) The responses of sub-boreal forest insects to a catastrophic wind-disturbance event and subsequent fuel-reduction practices in northeastern Minnesota. Dissertation, University of Minnesota
Gandhi KJK, Gilmore DW, Katovich SA et al (2007) Physical effects of weather events on the abundance and diversity of insects in North American forests. Environ Rev 15:113–152
Gandhi KJK, Gilmore DW, Haack RA et al (2009) Application of semiochemicals to assess the biodiversity of subcortical insects following an ecosystem disturbance in a sub-boreal forest. J Chem Ecol 35:1384–1410
Ganz DJ, Dahlsten DL, Shea PJ (2003) The post-burning response of bark beetles to prescribed burning treatments. In: Fire, fuel treatments, and ecological restoration. US Forest Service, p 143
García RA, Franzese J, Policelli N et al (2018) Non-native pines are homogenizing the ecosystems of South America. In: Biocultural homogenization to biocultural conservation. Springer, pp 245–263
Geiszler DR, Gara RI, Littke WR (1984) Bark beetle infestations of Lodgepole pine following a fire in South Central Oregon. Z Angew Entomol 98(1–5):389–394
Georgia Forestry Commission (2017) *Ips* engraver beetle outbreak update, 30 January 2017. Georgia Forestry Commission, Forest Health Program
Gerson EA, Kelsey RG (1997) Attraction and direct mortality of pandora moths, *Coloradia pandora* (Lepidoptera: Saturniidae), by nocturnal fire. For Ecol Manag 98(1):71–75
Gilliam FS, Platt WJ (1999) Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. Plant Ecol 140:15–26
Gilmore DW, Seybold SJ, Zasada JC et al (2002) Cumulative effects of a severe windstorm and subsequent silvicultural treatments on plant and arthropod diversity in the Gunflint Corridor of the Superior National Forest in northern Minnesota: project design. In: Forestry at the Great Divide, Proceedings: Society of American Foresters 2001 National Convention. Denver, CO, pp 364–337
Gitau CW, Carnegie AJ, Nicol HI et al (2013) Incidence of *Ips grandicollis* (Coleoptera: Scolytinae) in trap trees prepared for biological control of *Sirex noctilio* (Hymenoptera: Siricidae) in Australia: influence of environment and silviculture. For Ecol Manag 310:865–874
Goldammer JG, Penafiel SR (1990) Fire in the pine-grassland biomes of tropical and subtropical Asia. In: Fire in the tropical biota: ecosystem processes and global challenges. Springer, Berlin/Heidelberg, pp 45–62
Gongalsky KB, Wikars LO, Persson T (2003) Dynamics of pyrophilous carabids in a burned pine forest in Central Sweden. Balt J Coleopterol 3(2):107–111
Graziosi I, Tembo M, Kuate J et al (2020) Pests and diseases of trees in Africa: a growing continental emergency. Plants People Planet 2(1):14–28
Grégoire JC, Raffa KF, Lindgren BS (2015) Economics and politics of bark beetles. In: Bark beetles. Academic Press, pp 585–613
Grünig M, Seidl R, Senf C (2023) Increasing aridity causes larger and more severe forest fires across Europe. Glob Chang Biol 29(6):1648–1659
Hanula JL, Meeker JR, Miller DR et al (2002) Association of wildfire with tree health and numbers of pine bark beetles, reproduction weevils and their associates in Florida. For Ecol Manag 170(1–3):233–247
Hart S (1998) Beetle mania: an attraction to fire. BioScience 48(1):3–5
Hart SJ, Schoennagel T, Veblen TT et al (2015) Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proc Natl Acad Sci USA 112(14):4375–4380
Hayes A, Nahrung H (2022) An a-luring solution for bark beetles. The Forester 2022:44–45
He T, Pausas JG, Belcher CM et al (2012) Fire-adapted traits of *Pinus* arose in the fiery Cretaceous. New Phytol 194(3):751–759

Heikkala O, Martikainen P, Kouki J (2017) Prescribed burning is an effective and quick method to conserve rare pyrophilous forest-dwelling flat bugs. Insect Conserv Divers 10(1):32–41
Hicke JA, Meddens AJ, Kolden CA (2016) Recent tree mortality in the western United States from bark beetles and forest fires. For Sci 62(2):141–115
Hood SM (2010) Mitigating old tree mortality in long-unburned, fire-dependent forests: a synthesis. RMRS-GTR-238. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins
Hood S, Sala A (2015) Ponderosa pine resin defenses and growth: metrics matter. Tree Physiol 35(11):1223–1235
Hood S, Sala A, Heyerdahl EK et al (2015) Low-severity fire increases tree defense against bark beetle attacks. Ecology 96(7):1846–1855
Hood SM, Baker S, Sala A (2016) Fortifying the forest: thinning and burning increase resistance to a bark beetle outbreak and promote forest resilience. Ecol Appl 26(7):1984–2000
Howe M, Mason CJ, Gratton C et al (2020) Relationships between conifer constitutive and inducible defenses against bark beetles change across levels of biological and ecological scale. Oikos 129(7):1093–1107
Hunter ME, Robles MD (2020) Tamm review: The effects of prescribed fire on wildfire regimes and impacts: a framework for comparison. For Ecol Manag 475:118435
Irland LC (2000) Ice storms and forest impacts. Sci Total Environ 262(3):231–242
Jacobs JM, Bergeron JC, Work TT et al (2011) Low intensity surface fire instigates movement by adults of *Calosoma frigidum* (Coleoptera, Carabidae). ZooKeys 147:641
Jin WT, Gernandt DS, Wehenkel C et al (2021) Phylogenomic and ecological analyses reveal the spatiotemporal evolution of global pines. Proc Natl Acad Sci USA 118(20):e2022302118
Jung JK, Kim M, Nam Y et al (2020) Changes in spatial and temporal distributions of *Monochamus* beetles along the fire severity in burned *Pinus densiflora* forests. J Asia Pac Entomol 23(2):404–410
Keeley JE (2012) Ecology and evolution of pine life histories. Ann For Sci 69(4):445–453
Keeley JE, Pausas JG, Rundel PW (2011) Fire as an evolutionary pressure shaping plant traits. Trends Plant Sci 16(8):406–411
Keeves A, Douglas DR (1983) Forest fires in South Australia on 16 February 1983 and consequent future forest management aims. Aust For 46(3):148–162
Kelsey RG, Westlind DJ (2017) Ethanol and primary attraction of red turpentine beetle in fire stressed ponderosa pine. For Ecol Manage 396:44–54
Kharuk VI, Antamoshkina OA (2017) Impact of silkmoth outbreak on taiga wildfires. Contemp Probl Ecol 10:556–562
Kinn DN, Perry TJ, Guinn FH et al (1994) Energy reserves of individual southern pine beetles (Coleoptera: Scolytidae) as determined by a modified phosphovanillin spectrophotometry method. J Entomol Sci 29(1):152–163
Kirchmeier-Young MC, Gillett NP et al (2019) Attribution of the influence of human-induced climate change on an extreme fire season. Earth's Future 7(1):2–10
Kirkendall LR, Biedermann P, Jordal BH (2015) Evolution and diversity of bark and Ambrosia beetles. In: Vega FE, Hofstetter RW (eds) Bark Beetles: biology and ecology of native and invasive species. Elsevier, pp 85–156
Kirkman LK, Jack SB, McIntyre RK (2017) The fire forest of the past and present. In: Ecological Restoration and Management of Longleaf Pine Forests. CRC Press, pp 3–16
Knebel L, Wentworth TR (2007) Influence of fire and southern pine beetle on pine-dominated forests in the Linville Gorge Wilderness, North Carolina. Castanea 72(4):214–225
Koivula M, Cobb T, Déchêne A et al (2006) Responses of two *Sericoda* Kirby, 1837 (Coleoptera: Carabidae) species to forest harvesting, wildfire, and burn severity. Entomol Fenn 17(3):315–324
Kolb TE, Agee JK, Fule PZ et al (2007) Perpetuating old ponderosa pine. For Ecol Manag 249(3):141–157
Kozlov MV, Zvereva EL (2017) Background insect herbivory: impacts, patterns and methodology. Prog Bot 79:313–355

Kulakowski D, Jarvis D (2013) Low-severity fires increase susceptibility of lodgepole pine to mountain pine beetle outbreaks in Colorado. For Ecol Manag 289:544–550
Lafon CW, Kutac MJ (2003) Effects of ice storms, southern pine beetle infestation, and fire on Table Mountain pine forests of southwestern Virginia. Phys Geogr 24(6):502–519
Lamont, B. B., P. J. G., H. Tianhua, W. E. T. F., and M. E. and Hanley. 2020. Fire as a selective agent for both serotiny and nonserotiny over space and time. Crit Rev Plant Sci 39:140–172.
Land AD, Rieske LK (2006) Interactions among prescribed fire, herbivore pressure and shortleaf pine (*Pinus echinata*) regeneration following southern pine beetle (*Dendroctonus frontalis*) mortality. For Ecol Manage 235(1–3):260–269
Langenheim JH (1990) Plant resins. Am Sci 78(1):16–24
Lee J, Brumley J, Ryckeley M et al (2016) Pitcher plant moths (*Exyra*) fly from pitchers in response to smoke. J Lepid Soc 70(4):268–270
Lerch AP, Pfammatter JA, Bentz BJ et al (2016) Mountain pine beetle dynamics and reproductive success in post-fire lodgepole and ponderosa pine forests in northeastern Utah. PLoS One 11(10):e0164738
Lindenmayer D, Taylor C, Blanchard W (2021) Empirical analyses of the factors influencing fire severity in southeastern Australia. Ecosphere 12(8):e03721
Littell JS, Peterson DL, Riley KL et al (2016) A review of the relationships between drought and forest fire in the United States. Glob Chang Biol 22:2353–2369
Liu Y, Francis RA, Wooster MJ et al (2022) Systematic mapping and review of Landscape Fire Smoke (LFS) exposure impacts on insects. Environ Entomol 51(5):871–884
Lombardero MJ, Ayres MP, Ayres BD (2006) Effects of fire and mechanical wounding on *Pinus resinosa* resin defenses, beetle attacks, and pathogens. For Ecol Manag 225(1–3):349–358
Lynch HJ, Renkin RA, Crabtree RL et al (2006) The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. Ecosystems 9:1318–1327
Maloney PE, Smith TF, Jensen CE et al (2008) Initial tree mortality and insect and pathogen response to fire and thinning restoration treatments in an old-growth mixed-conifer forest of the Sierra Nevada, California. Can J For Res 38(12):3011–3020
Martinson S, Hofstetter RW, Ayres MP (2007) Why does longleaf pine have low susceptibility to southern pine beetle? Can J For Res 37(10):1966–1977
McCullough DG, Werner RA, Neumann D (1998) Fire and insects in northern and boreal forest ecosystems of North America. Annu Rev Entomol 43(1):107–127
McHugh CW, Kolb TE, Wilson JL (2003) Bark beetle attacks on ponderosa pine following fire in northern Arizona. Environ Entomol 32(3):510–522
McNichol BH, Montes CR, Barnes BF et al (2019) Interactions between southern *Ips* bark beetle outbreaks, prescribed fire, and loblolly pine (*Pinus taeda* L.) mortality. For Ecol Manag 446:164–174
Meigs GW, Campbell JL, Zald HSJ et al (2015) Does wildfire likelihood increase following insect outbreaks in conifer forests? Ecosphere 6(7):art118
Meigs GW, Zald HS, Campbell JL et al (2016) Do insect outbreaks reduce the severity of subsequent forest fires? Environ Res Lett 11(4):045008
Menges ES, Deyrup MA (2001) Postfire survival in south Florida slash pine: interacting effects of fire intensity, fire season, vegetation, burn size, and bark beetles. Int J Wildland Fire 10(1):53–63
Milberg P, Bergman KO, Norman H et al (2015) A burning desire for smoke? Sampling insects favoured by forest fire in the absence of fire. J Insect Conserv 19:55–65
Millar CI (1993) Impact of the Eocene on the evolution of *Pinus* L. Ann Mo Bot Gard 80:471–498
Miller WE (1978) Use of prescribed burning in seed production areas to control red pine cone beetle. Environ Entomol 7(5):698–702
Miller WE (1979) Fire as an insect management tool. Bull ESA 25(2):137–140
Miller KK, Wagner MR (1984) Factors influencing pupal distribution of the pandora moth (Lepidoptera: Saturniidae) and their relationship to prescribed burning. Environ Entomol 13(2):430–431

Mistry J, Bilbao BA, Berardi A (2016) Community owned solutions for fire management in tropical ecosystems: case studies from Indigenous communities of South America. Philos Trans R Soc B Biol Sci 371(1696):20150174

Mitchell RJ, Hiers JK, O'Brien JJ (2006) Silviculture that sustains: the nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in longleaf pine forests of the southeastern United States. Can J For Res 36(11):2724–2736

Mitsopoulos I, Mallinis G, Zibtsev S et al (2017) An integrated approach for mapping fire suppression difficulty in three different ecosystems of Eastern Europe. J Spat Sci 62(1):139–155

Nappi A, Drapeau P, Saint-Germain M et al (2010) Effect of fire severity on long-term occupancy of burned boreal conifer forests by saproxylic insects and wood-foraging birds. Int J Wildland Fire 19(4):500–511

Neumann FG (1987) Introduced bark beetles on exotic trees in Australia with special reference to infestations of *Ips grandicollis* in pine plantations. Aust For 50(3):166–178

Nowacki GJ, Abrams MD (2008) The demise of fire and "mesophication" of forests in the eastern United States. BioScience 58(2):123–138

Nowak J, Asaro C, Klepzig K et al (2008) The southern pine beetle prevention initiative: working for healthier forests. J For 106(5):261–267

Nowak JT, Meeker JR, Coyle DR et al (2015) Southern pine beetle infestations in relation to forest stand conditions, previous thinning, and prescribed burning: evaluation of the southern pine beetle prevention program. J For 113(5):454–462

O'Brien JJ, Kevin Hiers J, Mitchell RJ et al (2010) Acute physiological stress and mortality following fire in a long-unburned longleaf pine ecosystem. Fire Ecol 6(2):1–12

Palmer JF, Coyle DR, Heaton WC et al (2024) Response of *Ips* bark beetles (Coleoptera: Curculionidae: Scolytinae) to prescribed fire in South Carolina. For Ecol Manag 561:121870

Parker TJ, Clancy KM, Mathiasen RL (2006) Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. Agric For Entomol 8(3):167–189

Pausas JG (2015) Evolutionary fire ecology: lessons learned from pines. Trends Plant Sci 20(5):318–324

Pausas JG, Parr CL (2018) Towards an understanding of the evolutionary role of fire in animals. Evol Ecol 32(2–3):113–125

Pelz KA, Smith FW (2012) Thirty year change in lodgepole and lodgepole/mixed conifer forest structure following 1980s mountain pine beetle outbreak in western Colorado, USA. For Ecol Manag 280:93–102

Perovich C, Sibold JS (2016) Forest composition change after a mountain pine beetle outbreak, Rocky Mountain National Park, CO, USA. For Ecol Manag 366:184–192

Perrakis DD, Agee JK (2006) Seasonal fire effects on mixed-conifer forest structure and ponderosa pine resin properties. Can J For Res 36(1):238–254

Perrakis DD, Agee JK, Eglitis A (2011) Effects of prescribed burning on mortality and resin defenses in old growth ponderosa pine (Crater Lake, Oregon): four years of post-fire monitoring. Nat Areas J 31(1):14–25

Pile LS, Wang GG, Knapp BO et al (2017) Comparing morphology and physiology of southeastern US *Pinus* seedlings: implications for adaptation to surface fire regimes. Ann For Sci 74:1–12

Pollet J, Omi PN (2002) Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. Int J Wildland Fire 11(1):1–10

Popović Z, Bojović S, Marković M et al (2021) Tree species flammability based on plant traits: a synthesis. Sci Total Environ 800:149625

Powell EN, Raffa KF (2011) Fire injury reduces inducible defenses of lodgepole pine against mountain pine beetle. J Chem Ecol 37:1184–1192

Powell EN, Townsend PA, Raffa KF (2012) Wildfire provides refuge from local extinction but is an unlikely driver of outbreaks by mountain pine beetle. Ecol Monogr 82(1):69–84

Prasetya CD, Syaufina L, Santosa G (2017) The effect of various types of forest fires on pine resin productivity in Gunung Walat University Forest, Sukabumi, Indonesia. Biodiversitas 18(1):476–482

Pryor LD (1991) Forest plantations and invasions in the Mediterranean zones of Australia and South Africa. In: Biogeography of Mediterranean Invasions. Cambridge University Press, pp 405–412

Pyne SJ (1995) World fire: the culture of fire on earth. Henry Holt

Raffa KF (2014) Terpenes tell different tales at different scales: glimpses into the chemical ecology of conifer-bark beetle-microbial interactions. J Chem Ecol 40:1–20

Ramírez-Reyes T, Armendáriz-Toledano F, Rodríguez LGC (2023) Rearranging and completing the puzzle: phylogenomic analysis of bark beetles *Dendroctonus* reveals new hypotheses about genus diversification. Mol Phylogenet Evol 187:107885

Rasmussen LA, Amman G, Vandygriff JC et al (1996) Bark beetle and wood borer infestation in the Greater Yellowstone Area during four postfire years. USDA Forest Service, Intermountain Research Station, Research Paper INT-RP-487, p 9

Ray C, Cluck DR, Wilkerson RL et al (2019) Patterns of woodboring beetle activity following fires and bark beetle outbreaks in montane forests of California, USA. Fire Ecol 15:21

Renwick KM, Rocce ME, Stohlgren TJ (2016) Biotic disturbance facilitates range shift at the trailing but not the leading edge of lodgepole pine's altitudinal distribution. J Veg Sci 27(4):780–788

Retana J, Maria Espelta J, Habrouk A et al (2002) Regeneration patterns of three Mediterranean pines and forest changes after a large wildfire in northeastern Spain. Ecoscience 9(1):89–97

Rhoades CC, Fegel TS, Hubbard RM et al (2022) Limited seed viability in long-dead serotinous lodgepole pine trees in the Southern Rockies, USA. For Ecol Manag 526:120565

Richardson DM (1998) Forestry trees as invasive aliens. Conserv Biol 12(1):18–26

Richardson DM, Nsikani MM (2021) Mediterranean pines as invasive species in the Southern Hemisphere. In: Pines and their mixed forest ecosystems in the Mediterranean Basin. Springer, pp 83–99

Ritger HMW (2023) Forest Health implications of restoring longleaf pine (*Pinus palustris* Mill.) ecosystems with prescribed fire. Ph.D. Dissertation, University of Georgia

Ritger HW, Brantley ST, Klepzig KD et al (2023) Differential effects of fire regime and site conditions on bark beetle (Coleoptera: Curculionidae) activity in longleaf pine (*Pinus palustris* Mill.) ecosystem. For Ecol Manag 549:121488

Robinson JM, Gellie N, MacCarthy D et al (2021) Traditional ecological knowledge in restoration ecology: a call to listen deeply, to engage with, and respect Indigenous voices. Rest Ecol 29(4):e13381

Rodríguez-García A, López R, Martín JA et al (2014) Resin yield in *Pinus pinaster* is related to tree dendrometry, stand density and tapping-induced systemic changes in xylem anatomy. For Ecol Manag 313:47–54

Romme WH, Clement J, Hicke J et al (2006) Recent forest insect outbreaks and fire risk in Colorado forests: a brief synthesis of relevant research. Colorado Forest Restoration Institute, p 24

Rowe JS, Scotter GW (1973) Fire in the boreal forest. Quat Res 3(3):444–464

Ryan KC, Amman GD (1996) Bark beetle activity and delayed tree mortality in the Greater Yellowstone Area following the 1988 fires. In: The Bark Beetles, fuels, and fire bibliography, vol 15. Utah State University

Ryan KC, Knapp EE, Varner JM (2013) Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Front Ecol Environ 11(s1):e15–e24

Safranyik L, Linton DA, Shore TL et al (2001) The effects of prescribed burning on mountain pine beetle in lodgepole pine. Pacific Forestry Center, Information Report BC-X-391

Santolamazza-Carbone S, Pestana M, Vega JA (2011) Post-fire attractiveness of maritime pines (*Pinus pinaster* Ait.) to xylophagous insects. J Pest Sci 84(3):343

Santoro AE, Lombardero MJ, Ayres MP, Ruel JJ (2001) Interactions between fire and bark beetles in an old growth pine forest. For Ecol Manag 144(1–3):245–254

Schmid JM, Parker DL (1990) Fire and forest insect pests. Paper presented at Effect of fire management of southwestern natural resources, Tucson, AZ, Nov 15–17
Schroeder LM (1990) Duct resin flow in Scots pine in relation to the attack of the bark beetle *Tomicus piniperda* (L.) (Col., Scolytidae). J Appl Entomol 109(1–5):105–112
Schütz S, Weissbecker B, Hummel HE et al (1999) Insect antenna as a smoke detector. Nature 398(6725):298–299
Schwilk DW, Knapp EE, Ferrenberg SM et al (2006) Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. For Ecol Manag 232(1–3):36–45
Seidl R, Thom D, Kautz M et al (2017) Forest disturbances under climate change. Nat Clim Change 7(6):395–402
Sequeira AS, Normark BB, Farrell BD (2000) Evolutionary assembly of the conifer fauna: distinguishing ancient from recent associations in bark beetles. Proc R Soc Lond Ser B: Biol Sci 267(1460):2359–2366
Simard M, Romme WH, Griffin JM et al (2011) Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecol Monogr 81(1):3–24
Singh SP, Inderjit Singh JS, Majumdar S et al (2018) Insights on the persistence of pines (*Pinus* species) in the Late Cretaceous and their increasing dominance in the Anthropocene. Ecol Evol 8(20):10345–10359
Six DL, Bracewell R (2015) *Dendroctonus*. In: Bark beetles. Academic Press, pp 305–350
Six DL, Skov K (2009) Response of bark beetles and their natural enemies to fire and fire surrogate treatments in mixed-conifer forests in western Montana. For Ecol Manag 258(5):761–772
Slack AW, Zeibig-Kichas NE, Kane JM et al (2016) Contingent resistance in longleaf pine (*Pinus palustris*) growth and defense 10 years following smoldering fires. For Ecol Manag 364:130–138
Smith CC (1970) The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecol Monogr 40(3):349–371
Steel ZL, Safford HD, Viers JH (2015) The fire frequency-severity relationship and the legacy of fire suppression in California forests. Ecosphere 6(1):1–23
Steel ZL, Goodwin MJ, Meyer MD et al (2021) Do forest fuel reduction treatments confer resistance to beetle infestation and drought mortality? Ecosphere 12(1):e03344
Stephens SL, Burrows N, Buyantuyev A et al (2014) Temperate and boreal forest mega-fires: characteristics and challenges. Front Ecol Environ 12(2):115–122
Stephens SL, Bernal AA, Collins BM et al (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 Manag 518:120258
Stevens JT, Kling MM, Schwilk DW et al (2020) Biogeography of fire regimes in western US conifer forests: a trait-based approach. Glob Ecol Biogeogr 29(5):944–955
Strom BL, Goyer RA, Ingram LL Jr et al (2002) Oleoresin characteristics of progeny of loblolly pines that escaped attack by the southern pine beetle. For Ecol Manag 158(1–3):169–178
Suckling DM, Gibb AR, Daly JM et al (2001) Behavioral and electrophysiological responses of *Arhopalus tristis* to burnt pine and other stimuli. J Chem Ecol 27:1091–1104
Süda I, Voolma K, Õunap H (2009) Short-term monitoring of fire-adapted Coleoptera in burnt pine forest of northern Estonia. Acta Biol Univ Daugavpiliensis 9(1):43–48
Sullivan BT, Fettig CJ, Otrosina WJ et al (2003) Association between severity of prescribed burns and subsequent activity of conifer-infesting beetles in stands of longleaf pine. For Ecol Manag 185(3):327–340
Swezy DM, Agee JK (1991) Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Can J For Res 21(5):626–634
Tabacaru CA, Park J, Erbilgin N (2016) Prescribed fire does not promote outbreaks of a primary bark beetle at low-density populations. J Appl Ecol 53(1):222–232
Talluto MV, Benkman CW (2013) Landscape-scale eco-evolutionary dynamics: selection by seed predators and fire determine a major reproductive strategy. Ecol 94(6):1307–1316

Talucci AC, Lertzman KP, Krawchuk MA (2019) Drivers of lodgepole pine recruitment across a gradient of bark beetle outbreak and wildfire in British Columbia. For Ecol Manag 451:117500
Tapias R, Climent J, Pardos JA et al (2004) Life histories of Mediterranean pines. Plant Ecol 171:53–68
Tauer CG, Stewart JF, Will RE et al (2012) Hybridization leads to loss of genetic integrity in shortleaf pine: unexpected consequences of pine management and fire suppression. J For 110(4):216–224
Taylor KT, Maxwell BD, McWethy DB et al (2017) *Pinus contorta* invasions increase wildfire fuel loads and may create a positive feedback with fire. Ecology 98(3):678–687
Teste FP, Lieffers VJ, Landhäusser SM (2011) Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak. Ecol Appl 21(1):150–162
Thistle HW, Peterson H, Allwine G et al (2004) Surrogate pheromone plumes in three forest trunk spaces: composite statistics and case studies. For Sci 50(5):610–625
Thistle HW, Strom B, Strand T (2011) Atmospheric dispersion from a point source in four southern pine thinning scenarios: basic relationships and case studies. Trans ASABE 54(4):1219–1236
Turner MG, Romme WH, Gardner RH (1999) Prefire heterogeneity, fire severity, and early post-fire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. Int J Wildland Fire 9(1):21–36
Turner MG, Braziunas KH, Hansen WD et al (2019) Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. Proc Natl Acad Sci 116(23):11319–11,328
Valor T, Hood SM, Piqué M et al (2021) Resin ducts and bark thickness influence pine resistance to bark beetles after prescribed fire. For Ecol Manag 494:119322
Van Lear DH, Waldrop TA (1991) Prescribed burning for regeneration. In: Forest regeneration manual. Springer, pp 235–250
Varner JM, Hiers JK, Ottmar RD et al (2007) Overstory tree mortality resulting from reintroducing fire to long-unburned longleaf pine forests: the importance of duff moisture. Can J For Res 37(8):1349–1358
Vázquez-González C, Zas R, Erbilgin N et al (2020) Resin ducts as resistance traits in conifers: linking dendrochronology and resin-based defenses. Tree Physiol 40(10):1313–1326
Verrall AF (1938) The probable mechanism of the protective action of resin in fire wounds on red pine. J For 36(12):1231–1233
Vilà-Vilardell L, De Cáceres M, Piqué M et al (2023) Prescribed fire after thinning increased resistance of sub-Mediterranean pine forests to drought events and wildfires. For Ecol Manag 527:120602
Wallin KF, Kolb TE, Skov KR et al (2003) Effects of crown scorch on ponderosa pine resistance to bark beetles in northern Arizona. Environ Entomol 32(3):652–661
Wang GG (2002) Fire severity in relation to canopy composition within burned boreal mixedwood stands. For Ecol Manag 163(1–3):85–92
Westlind DJ, Kerns BK (2021) Repeated fall prescribed fire in previously thinned *Pinus ponderosa* increases growth and resistance to other disturbances. For Ecol Manag 480:118645
Whitehouse NJ (2000) Forest fires and insects: palaeoentomological research from a subfossil burnt forest. Palaeogeogr Palaeoclimatol Palaeoecol 164(1–4):231–246
Wikars LO (1997) Effects of forest fire and the ecology of fire-adapted insects, vol 272. Acta University Uppsala Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology, p 35
Williams AP, Abatzoglou JT, Gershunov A et al (2019) Observed impacts of anthropogenic climate change on wildfire in California. Earth's Future 7(8):892–910
Wrangham RW, Carmody RN (2010) Human adaptation to the control of fire. Evol Anthropol 19(5):187–199
Wrangham RW, Jones JH, Laden G et al (1999) The raw and the stolen: cooking and the ecology of human origins. Curr Anthropol 40(5):567–594
Wu H, Hu ZH (1997) Comparative anatomy of resin ducts of the Pinaceae. Trees 11:135–143

Wunder S, Calkin DE, Charlton V et al (2021) Resilient landscapes to prevent catastrophic forest fires: Socioeconomic insights towards a new paradigm. For Policy Econ 128:102458

Wylie FR, Peters B, DeBaar M et al (1999) Managing attack by bark and ambrosia beetles (Coleoptera: Scolytidae) in fire-damaged *Pinus* plantations and salvaged logs in Queensland, Australia. Aust For 62(2):148–153

Yan Z, Sun J, Don O et al (2005) The red turpentine beetle, *Dendroctonus valens* LeConte (Scolytidae): an exotic invasive pest of pine in China. Biodivers Conserv 14:1735–1760

Zalba SM, Cuevas YA, Boó RM (2008) Invasion of *Pinus halepensis* Mill. following a wildfire in an Argentine grassland nature reserve. J Environ Manag 88(3):539–546

Zhan Z, Yu L, Ren L (2022) Infestation patterns of incipient red turpentine beetle populations in fire-affected, logged and undisturbed forest stands of northern China. For Ecol Manage 521:120424

Zhang QH, Byers JA, Zhang XD (1993) Influence of bark thickness, trunk diameter and height on reproduction of the longhorned beetle, *Monochamus sutor* (Col., Cerambycidae) in burned larch and pine. J Appl Entomol 115(1–5):145–154