Fire Ecology and Ecophysiology of *Pinus* Species

Sharon M. Hood, Andreas Bär, Giovanna Battipaglia, Stefan Mayr, Timothy Shearman, J. Morgan Varner, and Kamal J. K. Gandhi

Abstract Fire has played a driving role in the speciation and evolution of the genus *Pinus* (pines) and continues to exert dominant influences on *Pinus*-dominated forests around the world. This chapter is divided into two major sections: fire ecology and fire ecophysiology. In the fire ecology section, we review fire-adapted traits of *Pinus* that allow persistence and recovery after fire, including how traits cluster to form fire syndromes. Fire regimes are described as an emergent property of fire syndromes and climate. In the fire ecophysiology section, we review the effects of fire on *Pinus* carbon relations, water relations, defense, growth, and mortality.

Keywords Fire regimes · Nonstructural carbohydrates · Plant defense · Post-fire tree mortality · Syndromes · Traits · Tree hydraulics

S. M. Hood (✉)
USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT, USA
e-mail: sharon.hood@usda.gov

A. Bär · S. Mayr
Department of Botany, University of Innsbruck, Innsbruck, Austria

G. Battipaglia
Department of Environmental Biological and Pharmaceutical Sciences and Technologies, University of Campania Luigi Vanvitelli, Caserta, Italy

T. Shearman
College of Forestry, Wildlife and Environment, Auburn University, Auburn, AL, USA

J. M. Varner
Tall Timbers, Tallahassee, FL, USA

K. J. K. Gandhi
D.B. Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA, USA

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1 Fire Ecology

Fire ecology is the study of fire as an ecosystem process, including its relationships to living organisms and the physical environment (Kobziar et al. 2024). In this section, we describe traits in pines that allow persistence—via survival or via regeneration—in fire-prone environments and evolutionary pressures that shaped these traits. We then describe fire syndromes, life history strategies based on several correlated traits and their associated fire regimes. Numerous papers and reviews exist on this topic, and we refer readers to these for more details, especially for non-*Pinus* species (Keeley and Zedler 1998; Keeley et al. 2011; He et al. 2012; Keeley 2012; Archibald et al. 2018; Stevens et al. 2020; Keeley and Pausas 2022).

1.1 Fire-Adapted Traits

Fire and the genus *Pinus* have a long-intertwined history. Fires, because they can be lethal across life history stages from seed to adult, have served as a strong selective force on the speciation and phenotypic traits of *Pinus* (Keeley and Zedler 1998; Schwilk and Ackerly 2001; Jin et al. 2021) and continue to play an essential role in many pine-dominated forests. He et al. (2012) hypothesized that fire in the Cretaceous period may have been a primary selecting force that initiated the divergence of the two pine lineages—subgenus *Pinus* (the diploxylon or hard pines) and subgenus *Strobus* (the haploxylon or soft pines), with fire playing a driving role in pine diversification beginning in the Oligocene (Jin et al. 2021). Fire-adapted species are more prevalent in the *Pinus* subgenus than the *Strobus* lineage (Badik et al. 2018; Jin et al. 2021). These studies align with Bond and Scott (2010) that changing fire regimes in the Cretaceous promoted the spread of angiosperms. The diversity of fires, from frequent surface fires to rare crown fires, also resulted in a diversity of fire-adapted traits across the *Pinus* genus.

Pinus species have a variety of traits that correspond to their past or extant fire regimes (Fig. 1). Because fire generates heat of lethal temperatures to plant tissues, pines and other woody species have developed traits to avoid or endure heat across their life histories. Protective traits, such as rapid development of thick bark, "grass stage" seedling physiognomy, self-pruning of lower branches, and the "basal crook" of seedlings are all beneficial for protecting vital meristematic tissues from heat damage in frequent fire regimes (Keeley and Zedler 1998; Pausas 2015a; Jin et al. 2021). Other traits provide an advantage in recolonizing the post-fire environment, such as cone serotiny and basal or epicormic resprouting (Pausas and Keeley 2014). Still other traits, such as highly flammable litter, help ensure the continuity of fuels that allow surface fires to spread throughout the landscape and result in selective mortality of competitors (Keeley and Pausas 2022; Varner et al. 2022). The fire ecology and fire resistance has been reviewed for *Pinus* in Mexico (Rodríguez-Trejo and Fulé 2003) and Europe (Fernandes et al. 2008). However, there are still many

Fig. 1 Examples of fire-adapted traits in *Pinus*. (**a**) Bud survival from fire in *P. plaustris*; (**b**) epicormic resprouting after fire in *P. canariensis*; (**c**) basal resprouting after fire in *P. echinata*; (**d**) *P. ponderosa* self-pruning with frequent fire; (**e**) *P. contorta* regeneration after fire from serotinous cones; (**f**) black arrow pointing to thick bark in *P. brutia*

knowledge gaps about fire resistance traits for numerous pine species, and most of what is known is disproportionately from the United States and Europe. Identifying morphological traits that arose due to the selective pressure of fire regimes is difficult and not without criticism. Many traits that are considered "fire-adapted" can also be argued to be exaptations that arose from other selective pressures (Snyder 1984). In this section, we review fire-adapted traits of *Pinus* and how combinations of these traits form fire-adaptive syndromes.

1.1.1 Bark Thickness

A primary defense against heat from wildland fires is bark, providing protection of underlying phloem, vascular cambium and buds. There have been many studies on the protective nature of bark on trees in relation to fire (Hare 1965; Vines 1968; Hengst and Dawson 1994; Stephens and Libby 2006). Bark thickness, moisture content, bark density, thermal conductivity, and surface structure influence heat insulation capacity, but bark thickness has by far the most influence on thermal protection (Dickinson and Johnson 2004; Bär and Mayr 2020). Bark protection scales exponentially with bark thickness (Hare 1965). Thus, many post-fire tree mortality models include some measure of bark thickness (or tree size) as a variable when predicting mortality (Woolley et al. 2012). Although bark serves multiple functions in addition to fire protection (Rosell 2016), the development of thick bark is presumed to have evolved due to the selective force of historical fire regimes

(Pausas 2015b). Pine species occurring in frequently burned savannas and woodlands tend to develop thicker bark than those found in closed canopy forests that experience less frequent fire (Pellegrini et al. 2017).

Since bark generally increases in thickness with tree diameter, large trees of many species can have thick, fire protective bark regardless of whether they are considered "pyrophytic" (i.e., fire tolerant). For this reason, many studies have emphasized the need to examine the rate at which bark thickness accumulates in younger trees with relation to the fire regime (Jackson et al. 1999; Shearman et al. 2018). For instance, Jackson et al. (1999) found that bark development can change over an individual tree's lifetime with some species investing in thick bark at an early age, and reducing the investment later in life. Additionally, bark development differs along tree height, with rapid accumulation at the base where surface heating would be most intense (Shearman et al. 2018; Rodman et al. 2021). Fire's selective pressure is greatest on smaller trees that need to develop thick bark during the fire-free period to survive the next fire and ultimately to recruit into the canopy. As a juvenile, when bark is thin across most species, bark thickness may indeed be paramount. For species that develop thick bark with age, the relative importance of bark becomes less critical for surviving surface fires. For juvenile seedlings and saplings, accruing sufficient bark to resist cambial injury in the "fire trap" stage is critical (Hammond et al. 2015; Rodman et al. 2021). In *P. pinea*, Battipaglia et al. (2016) observed that bark plates twisted and flaked off during combustion, which reduced surface stem temperatures.

Bark in pines, as in other genera, varies among species and closely correlates with fire regime (Keeley and Zedler 1998; Schwilk and Ackerly 2001; Stevens et al. 2020). He et al. (2012) suggest that thick bark originated in the *Pinus* genus ca. 126 Ma. The two subgenera, competing with angiosperms, spread to inhabit different environmental conditions: the *Strobus* subgenus generally inhabit stressful alpine and desert conditions, while the *Pinus* subgenus adapted to frequent fire environments (Keeley and Zedler 1998; Keeley 2012). Building on this hypothesis, Varner et al. (2022) linked bark thickness development in pines of North America to their flammability and their hypothesized fire return interval. They found that species in subgenus *Pinus* that develop thick bark early also have litter that is highly flammable, consistent with the hypothesis that these pines have a strong evolutionary history with fire.

1.1.2 Self-Pruning

Another fire-adapted trait is the ability of a species to shed lower branches, so termed self-pruning, natural pruning, or branch shedding. Self-pruning is affected by multiple species-specific physiology and environmental conditions, including shade tolerance, neighborhood competition/light intensity, insects, soil, and weather (Millington and Chaney 1973). Pines seasonally abscise short shoots, or the needle fascicles, at the point of attachment to the long shoot (i.e., branch), but self-pruning of branches in pines does not involve abscission (i.e., programmed

cell death resulting in shedding of tissue). Rather, branch death is a slow process that occurs when the leaves on branches have low photosynthetic rates that do not meet maintenance demands and become susceptible to insects and disease (Millington and Chaney 1973; Sprugel et al. 1991). As pines are highly resinous, they are able to effectively seal dead branches from the rest of the tree, preventing disease spread. The degree of natural pruning of dead branches varies greatly by species and seems to be genetically and environmentally determined (Millington and Chaney 1973; Pallardy 2010). Self-pruning has been reported as a binary trait (He et al. 2012) and relativized scales (Keeley and Zedler 1998; Moris et al. 2022). These subjective measurements lead to uncertainty in the literature. For example, Keeley and Zedler (1998) rank *P. balfouriana* as a 2 (i.e., poor pruning ability), while He et al. (2012) suggests that it does shed branches (on a binary scale). There is clearly much more to learn about how pines shed branches and how these differ among species.

Self-pruning is relevant to fire ecology because mortality of mature *Pinus* tends to be driven primarily by injuries to the crown, thus increasing the distance from radiative and convective heat by pruning is advantageous (Varner et al. 2021). Beyond protection from heating from surface fires, this trait reduces ladder fuels that could otherwise allow fire to spread into the crown. Schwilk (2003) experimentally manipulated the crown of a non-pine (*Adenostoma fasciculatum*) to test whether crown architecture (pruning vs. non-pruning) affected fire behavior and found that non-pruned individuals had higher temperatures and heat release than the pruned treatments. In pines, Schwilk and Ackerly (2001) found positive correlation between pine species that have the self-pruning trait, thick bark, and tall height, suggesting that species with these traits are typically found in frequent surface fire regimes. In contrast, the retention of dead branches (i.e., no self-pruning) are hypothesized to increase crown flammability and to be correlated with cone serotiny (Keeley and Zedler 1998; Schwilk and Ackerly 2001).

1.1.3 Height and Height Growth

Being tall is advantageous in evading radiative and convective heating, and the rate at which species ascend to fire-safe heights matters. Pines vary widely in maximum heights, varying from shrub stature (<5 m tall) species to emergent canopy trees like *P. lambertiana* that can exceed 75 m. The rate of height growth enables seedlings and saplings to abbreviate the period of fire-sensitivity, as virtually all seedlings and saplings are susceptible to surface fire (but see Sect. 1.1.6). Several pines undergo rapid height growth during the "fire trap" (sensu Hoffmann et al. 2012) period where the crown is vulnerable to even low-intensity surface fires. Stevens et al. (2020) found that tall conifers (*P. jeffreyi*, *P. ponderosa*, and *P. lambertiana* included) had other fire-adapted traits that collectively enabled them to resist fire injury better than short-statured conifers.

1.1.4 Crown Traits

Crown injury, especially damage to foliage and buds, is the primary cause of mortality across pines (Hood et al. 2018; Cansler et al. 2020a). Self-pruning enables pines to evade surface heat, but the geometry and allometry of crowns matters. Savanna and woodland pines reflect these contrasting selective pressures via a typical physiognomy of flat-topped crowns that are pruned from below, but also spread widely. Pine crowns are differentially porous, with lacunarity varying widely across species. This lacunarity results in ventilation that allows heat to escape, and thus bypass sensitive tissues in the crown (Rowell et al. 2022). Other crown traits that can influence tree survival from fire include bud size, needle length and mass, and bud growth patterns (Fernandes et al. 2008). Large buds have higher heat tolerance and long, thick needles can shield buds from heat and mitigate meristem death (Varner et al. 2021). Pines can also have fixed or preformed buds that undergo one growth flush per year or exhibit continuous or multiple growth flushes per year (Businský 2016). Species with multiple growth flushes can recover more quickly from needle scorching if meristems are not killed compared to species that only have one growth flush per year (Wade and Johansen 1986). While some research reporting crown traits exists (Fernandes et al. 2008; Paula et al. 2009; Bär et al. 2021), measurements are lacking for many species, limiting understanding of how trait variation results in differential heating.

1.1.5 Cone Serotiny

A common trait in pines is the retention of a seed bank within crowns via cones that remain closed until they are exposed to heating. This trait, known as serotiny, is suggestive of a high intensity, high severity fire regime that enables the species to quickly reseed in the post-fire environment while mineral soil is exposed and competition is reduced (Lamont et al. 1991; Keeley et al. 2011; Pausas and Keeley 2014). Serotinous cones remain closed due to a resin seal that holds the scales together (Johnson and Gutsell 1993). When the cone is subjected to sufficient heat for enough time, the resin seal weakens and breaks, resulting in the scales reflexing away from the central axis of the cone and releasing the seeds. Serotinous cones differ anatomically from non-serotinous cones. Aside from the resin seal, serotinous cones are better insulators, with higher sclereid cell diameter and sclereid wall thickness (Moya et al. 2008). He et al. (2012) estimates that serotiny emerged in the *Pinus* subgenus approximately 89 Ma.

Cone serotiny is often reported across species as a binary trait but this is too simplistic, as there is notable polymorphism, with some individuals producing both serotinous and non-serotinous cones and differences in serotiny levels among populations (Muir and Lotan 1985b; Tinker et al. 1994; Climent et al. 2004; Radeloff et al. 2004; Greene et al. 2024). The degree of serotiny can vary based on age, landscape position, and fire frequency (McMaster and Zedler 1981; Tapias et al. 2001). For example, studies on *P. halepensis* showed that younger trees had cone opening

temperatures about 5 °C higher than older individuals and that opening temperatures between species varied from 45 to 60 °C (Gauthier et al. 1996; Tapias et al. 2001). Some pine species that display serotiny have dwarf growth forms that tend to have a higher degree of serotiny and occur in more frequently burned environments. Dwarf pitch pines (*P. rigida*) in the New Jersey Pine Plains, USA (which were subject to more frequent fires) have a higher percentage of serotinous cones than their taller counterparts in areas of less frequent fires (Ledig and Fryer 1972). Similarly, the shrub variety of *P. yunnanensis* in the Yunnan Province of China has a higher percentage of serotinous cones and experiences more frequent fires than the tree variety (Pausas et al. 2021).

Serotiny is a complex polymorphic trait and considerable research is needed to understand evolutionary pressures and environmental factors influencing its prevalence. While fire and herbivory are selective pressures favoring serotiny (Smith 1970; He et al. 2012), wind-dispersed pine species have ample opportunity for gene flow between serotinous and non-serotinous individuals that reduce selection pressure (Muir and Lotan 1985b). Serotiny also develops with age, potentially further reducing selection pressure. Numerous studies in pines have found the degree of serotiny in a population is most related to the fire regime, with areas of large, high-severity fire having higher proportions of serotiny and areas with complex, finer grain fires of mixed-severity having higher proportions of non-serotinous trees (Muir and Lotan 1985a; Gauthier et al. 1996; Radeloff et al. 2004). Serotiny is likely a bet-hedging strategy by which a species can reproduce under unpredictable disturbance regimes (Muir and Lotan 1985b). In a large study comparing cone and seed traits in serotinous versus non-serotinous conifer species, Greene et al. (2024) found little differences between the two cone types and demonstrated that seeds from non-serotinous cones can survive fire and contribute to post-fire regeneration. Collectively, this research highlights that while cone serotiny can certainly increase regeneration after fire, serotinous species are not entirely dependent on this trait to be resilient to fire.

Given the pressure of fire on the vulnerable reproductive period, there are likely other fire-cued or fire-adapted reproductive-related traits in pines. Strobili, pollen cones, and pollen all have vulnerable periods within pine crowns. Seeds of many pines lack thick protection once they disperse from cones and thus are vulnerable before germination and as juvenile seedlings. There has been scant work on investigating how these critical stages of pine life history may be cued to fire timing to avoid or evade heat via crown architecture or phenology more broadly.

1.1.6 Resprouting and Grass Stage

The ability to resprout after fire is rare in the *Pinus* genus, occurring in approximately 15 of all extant pines. For pines with this trait, resprouting can occur from basal or underground buds or higher up along the bole. Some species such as *P. echinata*, *P. rigida*, and presumably others develop a unique “basal crook” at the root collar where the stem grows horizontally at or below the mineral soil before turning

vertical (Little and Somes 1956). This morphological trait allows buds that develop in the crook to be protected from the heat of fire and sprout after fire. Evidence of the selective ability of fire on the basal crook trait have been demonstrated in studies of *P. echinata*, the less fire adapted *P. taeda* that lacks the basal crook and rarely resprouts after fire, and a hybrid between the two species that has a less pronounced crook and intermediate resprouting capability (Stewart et al. 2015; Bradley et al. 2016). *P. echinata* was able to persist in frequently burned sites, whereas *P. taeda* and the majority of hybrid individuals were eliminated (Stewart et al. 2015). Crown and epicormic resprouting are also notable, enabling scorched and consumed crowns to refoliate via stem sprouts on the bole or in the crown. Examples of epicormic resprouting include *P. serotina*, *P. echinata*, and *P. canariensis*. Resprouting, as with other traits, is often viewed and analyzed as a binary trait, ignoring the wide variation in resprouting and its vigor within species and across the *Pinus* genus (Lilly et al. 2012; Pausas and Keeley 2014).

An even rarer trait is the "grass stage" juvenile form, occurring in only nine (<8%) pine species (e.g., *P. devoniana*, *P. merkusii*, and *P. palustris*) (Mirov 1967; Earle 2023). The grass stage is a juvenile form where no vertical growth occurs, instead the seedling invests growth in roots and radial growth. Beyond a threshold that may transpire in a year or over decades, the grass stage seedling rapidly ascends from its grass stage. This rapid juvenile height growth enables the seedling to exceed the height of injury from surface fires in a short period, perhaps taking advantage of stored carbohydrates to ascend beyond a fire-sensitive height. Recent investigations have better evaluated the grass stage (Pile et al. 2017; Knapp et al. 2018), but much is left to understand from this curious trait in *Pinus*. While the grass stage is rare in pines, this strategy of investing heavily in roots during juvenile development is relatively common in angiosperms as a strategy to allow rapid height growth after disturbance. For example, many species in tropical and subtropical savannas also have this life history strategy of early heavy belowground investment followed by a developmental shift to rapid height growth that can allow escape from grass fires (Schutz et al. 2009; Werner and Prior 2013).

1.1.7 Litter Flammability

Surface fire regimes in woodlands and forests are primarily driven by senesced foliage as surface litter. The flammability of litter has been documented for many tree species, pines a notable fraction of these (Fonda 2001; Varner et al. 2022). Mutch (1970) hypothesized that litter flammability is a selected trait in fire-dependent ecosystems, with species that occur in these systems having more flammable litter than species that have not experienced a long history with fire. Thus, pyrogenic species not only have adapted traits to protect them from fire, but also have adapted increased flammability to exclude species without defensive traits (Mutch 1970; Williamson and Black 1981; Bond and Midgley 1995; Gagnon et al. 2010). The Mutch (1970) hypothesis introduced somewhat of a paradox—fire is damaging to all plants to some degree, so the idea that a trait that increases injury to an individual is

beneficial in fire-prone environments seems counterintuitive to natural selection at the individual level (Snyder 1984). Snyder (1984) criticized this hypothesis stating that flammability could have evolved due to completely unrelated selective forces (i.e., exaptation; e.g., an increase in phenolic compounds that are highly flammable could be the result of selective pressure from herbivory).

Numerous hypotheses have since been proposed to explain how the flammability trait could evolve in a species. Bond and Midgley (1995) showed through simulation that it is possible for increased flammability to be a fitness benefit if the flammable species also has some of the other traits listed above and the nearby non-flammable species does not have any fire defensive or post-fire regenerative traits. Gagnon et al. (2010) hypothesized that increased flammability could actually benefit the individual plants because highly flammable litter would have less soil heating due to low flame residence times, and therefore, belowground roots and meristems would be protected. These hypotheses all assume that species already possess some traits that confer advantage to survive fire or to colonize the post-fire environment. However, Kerr et al. (1999) modeled a scenario that suggested the opposite: anatomical and reproductive traits that improve fitness in fire-prone environments may have evolved as a result of the evolution of flammability. Schwilk and Kerr (2002) proposed that increased flammability as a trait could spread through a population without any direct fitness benefit by creating localized gaps that are likely to be colonized by propagules possessing the high flammability trait, assuming mating and seed dispersal are local processes. Alternatively, Midgley (2013) argued that flammability is an emergent property conferring no advantage to individual plants, and therefore, is not a selected trait. Instead, anti-flammability is the trait that could be selected for and evolved with time. Regardless of whether adaptation or exaptation, flammability and the associated morphological and physiological traits are clearly linked in ecosystems that are maintained by recurring fire which occur in all pine-dominated ecosystems.

Pines vary tremendously in their flammability. In a synthesis of North American pine litter flammability, Varner et al. (2022) found species with rapid, high intensity flaming combustion (e.g., *P. palustris*, *P. ponderosa*, and *P. serotina*) and others with poor flammability (*P. contorta* varieties, *P. clausa* varieties, and many high-elevation pines). Flammability in those species was related to their phylogeny, with subgenus *Pinus* exceeding subgenus *Strobus*, and to needle length, with longer-needled pines having greater flammability than short-needled pines. Past work has also illustrated the chemical nature of flammability, as terpene composition and content is correlated with ignition and intensity (Ormeño et al. 2009). Work remains to be conducted on flammability of pines beyond the U.S. and Mediterranean regions, where there exists substantial diversity of pine species and fire regimes.

1.2 Fire Syndromes and Regimes

1.2.1 Syndromes

Several fire syndromes have been described for pine species with common combinations of traits (Agee 1998; Keeley and Zedler 1998; Schwilk and Ackerly 2001; Jin et al. 2021; Keeley and Pausas 2022). Fire tolerators or resisters typically survive low-intensity fires due to thick bark and self-pruning. Fire embracers and endurers are easily killed by fire but have traits that allow regeneration and recovery, such as cone serotiny and ability to resprout. Fire evaders have few traits to survive or regenerate after fire and can persist through unburned areas or fire refugia. Fire avoiders also have few traits to survive fire, but occupy environments that rarely burn (cold, wet, or desert). These categorical approaches suffer from confounding issues but are convenient to describe the diverse suites of traits that enable survival and fuel local fire regimes.

To illustrate how fire-adapted traits are associated with the entire *Pinus* genus, we constructed a classification of all 118 extant pines including subspecies *P. contorta* ssp. *contorta*, *bolanderi*, and *murrayana*, as well as varieties *P. elliottii* vars. *elliottii* and *densa* (Fig. 2). We used nonmetric multidimensional ordination (NMDS) on trait metrics with a Gower distance metric. The ordination includes

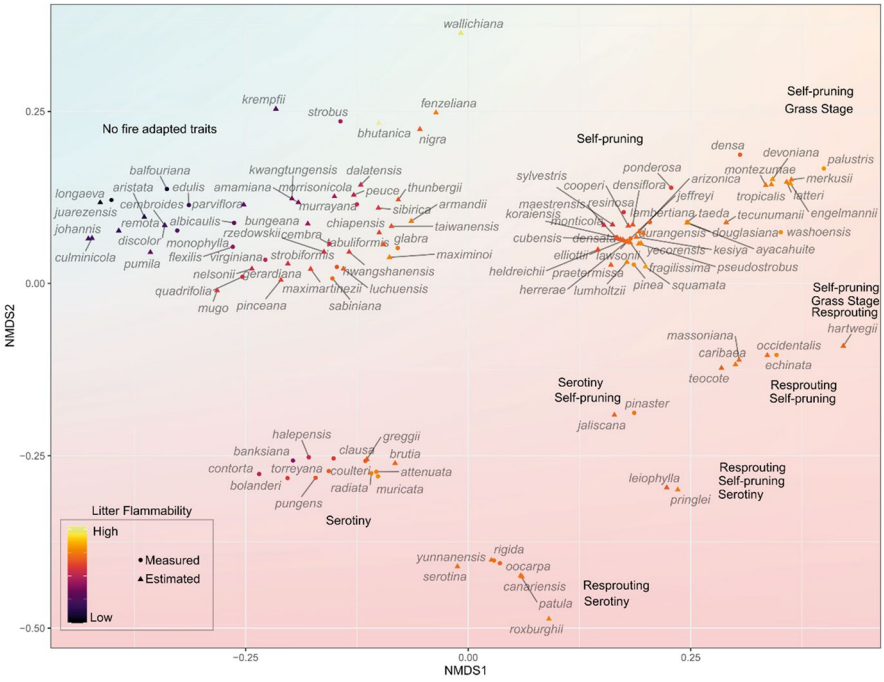

Fig. 2 Nonmetric Multidimensional Ordination (NMDS) showing relationship of *Pinus* species and fire-adapted traits

measured litter flammability for species as well as estimated flammability based on the relationship to leaf length found in Varner et al. (2022). Other traits include tree height and binary measures of serotiny, resprouting, grass stage, and pruning. Binary measurements from He et al. (2012) were used with some corrections and the additional species were estimated from various resources (Fire Effects Information System (FEIS); Perry 1991; Keeley and Zedler 1998; Saladin 2013). The binary measurements have a high influence on the ordination of species, which cluster into regions that relate to their hypothesized syndrome. The NMDS1 axis is correlated with response to fire, with fire avoiders clustered together with species that lack any of the fire-adapted traits, while fire resisters cluster in regions with species that have self-pruning and grass stage physiognomy. The NMDS2 axis separates species with serotiny versus self-pruning. The ordination also highlights species that have seemingly conflicting traits to any one syndrome. For example, serotiny and self-pruning are suggested to be negatively correlated (Schwilk and Ackerly 2001), yet the ordination suggests that some pines possess both of these traits. One possibility is that these species are using a "bet hedging" strategy for multiple fire regimes. Regardless, it is an indicator of how more studies on fire-adapted traits are needed.

1.2.2 Fire Regimes

Fire disturbance regimes are useful emergent properties that help describe general domains of fire dynamics over space and time (Agee 1993, 1998). Understanding historical fire regimes is essential to understanding how ecosystems evolved with wildland fire and for anticipating how they will respond to management, alterations to disturbance regimes, and climate change (Keeley and Pausas 2022). While individual plant traits influence relative resistance and responses to fire, in fire-affected systems, it is the distribution of fires *over time* (i.e., the fire regime) interacting with climate and topography, that determines the structure and composition of ecosystems (Moritz et al. 2005; Keeley et al. 2011). Fire regimes can include many characteristics, such as fire frequency, intensity (i.e., energy release), severity (i.e., fire effects such as tree mortality or soil heating), seasonality, type (i.e., ground, surface, or crown fire), extent (i.e., average size), geometry, or synergies with other disturbances (Agee 1993; Turner 2010). In practice, fire regimes are often reduced to simplified classifications of fire frequency and severity (Guyette et al. 2012; Blankenship et al. 2021) or fire type (Keeley and Pausas 2022). These groupings describe the dominant, or most likely fire attributes, but fires of any severity, frequency, and type can occur over smaller areas.

As fire exerts a large influence in many pine-dominated ecosystems, understanding the dominant fire regime is essential to understanding the system's ecology and departures from historical regimes (Falk et al. 2011; Greenberg and Collins 2021). Pines with broad distributions may have different species associations and, therefore, can be associated with different fire regimes. A fire regime is an emergent ecosystem property where a given climate and distribution of fire behavior favors

convergence of a fire-adaptation syndrome and associated species traits and forest characteristics (Table 1). Pine ecosystems with frequent, low-severity fire regimes are comprised of *tolerator* or *resistor* species with traits that allow survival of low-intensity surface fires, such as developing thick bark at an early age, self-pruning branches, and large or protected buds. Forests typically are open and have a low density of multiple age cohorts, but with little overlapping vertical strata. Infrequent, high-severity fire regimes are dominated by *embracer* species that are easily killed by fire and forest characteristics that typically support high-intensity crown fire behavior such as dense forests with continuous forest canopies. Although *embracers* and *endurers* are easily killed or top-killed by fire, they have traits to allow rapid recolonization of the site after fire, such as serotinous cones, light-wind born seed, or the ability to resprout. Mixed-severity fire regimes, as the name implies, have high spatial variability of fire intensities, allowing for *evaders* to survive by escaping the fire (i.e., *fire refugia*); *tolerators* and *embracers* can also occur. In areas where fire is rare, such as low productivity arid or cold environments, *avoiders* are not adapted to fires of any kind.

Fire regimes are governed by both top-down climatic factors and bottom-up factors of topography, human population density, and fine-scale forest mosaics (Falk et al. 2011; Guyette et al. 2012). Climate and its effect on fire vary greatly by geographic location, with synoptic circulation patterns, such as the El Niño-Southern

Table 1 Relationships between fire regimes and fire-adaptation syndromes, with associated fire-adapted traits and forest characteristics

Fire regime	Fire-adaptation syndrome	Associated fire-adapted species Traits	Associated forest characteristics	Example *Pinus* species
Frequent, low-severity	Tolerators[a], Resisters[b, c], Survivors[d]	Thick bark Self-pruning branches Open crown architecture Protected buds Grass stage	Low density Patchy, discontinuous vertical strata	*P. ponderosa* *P. palustris* *P. echinata* *P. jeffreyi* *P. pinaster* *P. nigra* *P. sylvestris*
Infrequent, high-severity	Embracers[a, d], Endurers[b, c]	Serotiny Thin bark at maturity	High density Connecting overstory crowns	*P. contorta* *P. clausa* *P. banksiana*
Mixed-severity	Evaders[b, c], Fire-refugia[d]		Complex topography to allow fire escape. Horizontal and vertical heterogeneity	*P. albicaulis* *P. uncinata*
Rare, little-to-no fire	Avoiders[a, c]	None	Low productivity with little understory	*P. edulis* *P. longeva* *P. mugo*

Footnotes are primary citations describing the fire-adaptation syndromes in more detail
[a]Keeley (2012)
[b]Agee (1998)
[c]Jin et al. (2021)
[d]Schwilk and Ackerly (2001)

Oscillation (ENSO) or the Pacific Decadal Oscillation (PDO), exerting large influences on regional fire activity (Swetnam and Betancourt 1998). In contrast to regional fire regime patterns, fire severity and frequency vary at finer scales as a function of forest vegetation, topography, and cultural fire use practices, and land use (Falk et al. 2011). As fire is sensitive to climate, anthropogenic climate change is now altering contemporary fire regimes (Jones et al. 2022). Changes in climate and fire regimes have ecological consequences for postfire resilience and recovery which may affect distributions of *Pinus* species and community associations.

2 Fire Ecophysiology

Plant ecophysiology is the study of a plant's physiological mechanisms interacting with its physical, chemical, and biological environment to determine survival, reproduction, and distribution (Lambers et al. 2008). In this section, we describe the effects of fire on the metabolic functions of carbon, hydraulics, and defenses that lead to growth and survival or tree death. This is an active area of research, with more unknowns than Sect. 1; therefore, we go into more detail in this section when research is available then the previous section. In the carbon and water relations sections we describe and summarize the evidence supporting the various hypothesized mechanisms of fire-caused tree death (Fig. 3).

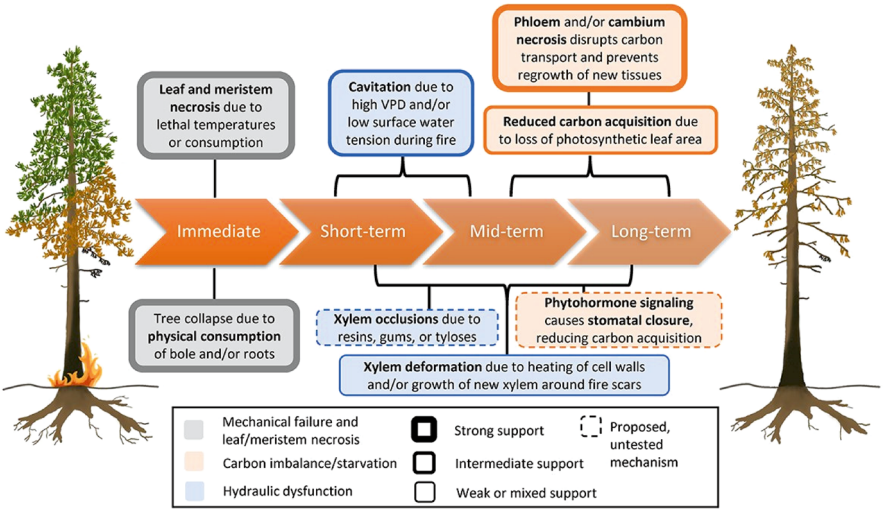

Fig. 3 Hypothesized mechanisms of fire-caused tree death illustrating the differential timing of the mechanisms and their level of support in the literature. VPD = vapor preesure deficit (Reprinted from Nolan et al. (2024), by permission of Oxford University Press)

2.1 Fire Effects on Carbon Relations

Fires can affect three important processes associated with carbon relations: acquisition, translocation, and storage. Pools of non-structural carbohydrates (NSCs; mainly sugars and starch) are essential for all plant metabolic processes (Hartmann and Trumbore 2016). They are involved with maintaining hydraulic function, phloem transport, plant defenses, cold tolerance, and buffering against stress (Dietze et al. 2014; Villar-Salvador et al. 2015; Martínez-Vilalta et al. 2016; Erbilgin et al. 2021).

First, post-fire carbon acquisition can be impaired due to heat-induced foliage loss, and there is intermediate supporting evidence that this can lead to tree mortality (Fig. 3) (Nolan et al. 2024). The amount of heat transferred to the crown and subsequent foliage death depends on fireline intensity, residence time, tree architecture, and crown component traits (Michaletz and Johnson 2007; Varner et al. 2021; see also Sect. 1.1.4). Necrotic foliage reduces the leaf area of affected trees limiting their overall photosynthetic capacity, but the unaffected foliage may increase photosynthetic efficiency to compensate (Wallin et al. 2003; Sayer et al. 2020). Especially when levels of leaf necrosis are high, the remaining foliage may not able to sustain whole tree carbohydrate demands, which consequently can limit foliage reestablishment, growth and carbon-based defense. Additionally, heat may have damaged photosystems of leaves that survived fire (Sparks et al. 2023). This can further curtail carbohydrate assimilation until the photosynthetic apparatus is repaired.

Second, the translocation of NSCs from source to sink organs can be limited or even blocked after fires. This fire-caused mortality mechanism is also strongly supported by experiments (Nolan et al. 2024). During combustion, heat can be conducted through the outer bark affecting the underlying phloem and cambium (Dickinson and Johnson 2001; Michaletz and Johnson 2007). If bark insulation is insufficient, heat transfer can cause cambium and phloem mortality which is widely assumed to happen at 60 °C (Hare 1961). As both tissues are located adjacent to each other and are composed of only a few cell rows, cambium and phloem necrosis likely occur in parallel. Although this can potentially occur around the whole circumference of a stem, partial necrosis is more common on the tree's leeward (downwind) side (Michaletz and Johnson 2007). This is due to the formation of leeward vortices during windy conditions which lead to increased bark surface temperatures in the lee of a tree stem. Dysfunctional phloem limits the carbon supply chain from leaves towards the stem base and/or roots (Hood et al. 2018; Bär et al. 2019). Cambium activity may regenerate phloem tissues unless the cambium was also killed by the heat. Blockages of carbohydrates impedes translocation and can trigger the depletion of NSC reserves below the killed cambium/phloem. Once those reserves are exhausted, tissues are considered to suffer from carbon starvation which ultimately may lead to dieback. Hoffmann et al. (2024) recently proposed another mechanism that could impact NSC acquisition through phytohormone signaling that causes stomatal closure. Further research is needed to determine if this could lead to reduced NSCs and eventual tree death in fire-injured trees.

Third, trees may exploit NSCs which were stored before the fire to ensure carbon assimilation (Smith et al. 2017) and water uptake (Varner et al. 2009) after a fire. The importance of NSCs as an actively regulated storage pool required for plant growth and respiration maintenance is increasingly recognized, with strong evidence that plant death occurs if NSCs decline below a minimum threshold (Martínez-Vilalta et al. 2016; Barker Plotkin et al. 2021). Exact thresholds are unclear; however, and seem to vary across species, functional groups, and tissue types (Adams et al. 2017). NSCs are more tightly linked to hydraulic function and drought resistance in gymnosperms than angiosperms, with reductions in NSCs associated with lower resistance to xylem embolism (Adams et al. 2017). NSC stores may also be used post-fire to repair the photosynthetic apparatus, regrow buds/leaves or fine roots.

The effects of fire-induced impairments of carbon acquisition, translocation, and storage are often assessed indirectly by examining growth limitations (see below and Sect. 2.4) as a final consequence, and inferring conclusions on NSC dynamics. However, only a few studies have directly quantified the effects of fire on NSC pools in obligate seeders such as *Pinus* species; most research has focused on resprouting angiosperms (Piper and Paula 2020). In a study on *P. palustris*, NSC concentrations after long-duration smoldering duff fires declined in coarse roots but not in fine roots, probably because carbon reserves of coarse roots were re-allocated to rebuild damaged fine roots (Varner et al. 2009). Fall burning of *P. palustris* saplings caused reduced shoot starch concentrations for several months, as well as reduced radial growth, and the authors attributed these declines to crown scorch and high NSC demand to replenish foliage (Sayer et al. 2020). In laboratory-burned 2-year-old *P. ponderosa*, NSCs of stems and roots of burned trees were lower than unburned controls as soon as 1 week after exposure to lethal fire (Partelli-Feltrin et al. 2022). The authors hypothesized that fire-induced phloem death likely impeded the translocation of NSCs. Reed and Hood (2024) measured NSCs pre-fire and six timesteps after a spring prescribed fire (4 days through 16 months) in young *P. ponderosa* that experienced varying levels of crown scorch. No trees were immediately killed by the fire and all trees showed some degree of bud survival and new needle growth. NSC concentrations declined quickly in burned trees relative to unburned controls over the same post-fire period. The decline was strongest for trees that eventually died, with surviving trees recovering to unburned levels within 14 months post-fire. Two months post-fire, phloem NSCs in the main stem were strongly negatively related to crown scorch levels. Taken together, these studies support the importance of NSCs for tree survival and recovery post-fire and suggest that post-fire NSC depletion may occur due to reduced photosynthetic leaf area, phloem death, and use of remaining NSC pools for repair and regrowth processes.

The cumulative effects of fire on NSCs can also influence subsequent long-term tree growth. *P. palustris* trees with longer duration smoldering suffered growth declines as much as a decade following burning, with the effects most severe in drought years (Slack et al. 2016). Niccoli et al. (2023a) found a delay in cambial phenology of burned *P. pinaster* individuals with a lower number of mature xylem cells during the growing season compared to unburned stands. Generally, in

conifers, the formation of new xylem cells is fueled by the photosynthates of the current year rather than by the stored carbon (Hansen and Beck 1994). Hence, the post-fire decline in overall photosynthetic capacity for burned trees likely compromised the ability to support required carbohydrate acquisition (Valor et al. 2018), causing severe limitations in cambium productivity (Gričar et al. 2020) and regrowth of killed needles (Sayer et al. 2020; Reed and Hood 2024). In fact, in cases of severe defoliation, only a small part of the carbohydrate reserves is allocated to growth and foliage because the majority is used primarily to ensure cell respiration (Jacquet et al. 2014).

2.2 Fire Effects on Water Relations

Water relations are a major critical physiological component in plant life and rely on sufficient water uptake, water transport, and storage, as well as transpirational control, the latter obtained by the combination of hydrophobic shields (cuticula and tissues containing suberin) and stomatal adjustment. Water transport is based on a meta-stable state of water (Tyree and Zimmermann 2002), which is under tension (i.e., negative water potential) due to transport resistances (under transpirational conditions), limited soil humidity, and gravitational forces (which are relevant in trees), and thus at risk for xylem embolism and/or impairments of extra-vascular pathways.

During a forest fire, heat may affect all components (water uptake, transport and storage, and transpiration) and organs involved in tree water relations, though with varying heat transfer rates (Michaletz and Johnson 2007; Hood et al. 2018). The water uptake system (i.e., root system) is affected by heat conduction from fuels burning above and within the soil. The aboveground water transport system (i.e., stem and axes system) is exposed to heat by primarily via radiation and convection processes, although conduction can occur at the base of the stem through smoldering combustion. When fires move through forest stands, stem bases are often exposed to high temperatures, which may affect main sections of the xylem and thus respective water transport and storage capacities. Exposure of leaves to heat (by radiation and convection; Michaletz and Johnson 2007; Varner et al. 2021) can empty leaf water reservoirs and dramatically increase transpiration. Longer-term, fire-caused loss of foliage may also reduce transpiration.

Plant water relations are based on optimized physical and chemical properties of the water phase and of cellular structures in all organs and tissues (Bär et al. 2019). Heat can affect both the stability of water bodies (non-structurally, by reduction of the surface tension and/or of xylem water potential), as well as the structural integrity (e.g., by altering physical xylem structures in conduits). Symplastic structures may be repaired, while apoplastic components, like the xylem conduits, have to be replaced and thus the damage of meristematic tissues during fires is also hydraulically relevant. In the following, mechanisms underlying fire and post-fire damage of plant hydraulic systems and potential counter strategies are discussed.

Structural alterations of the xylem can occur when the heat arriving at stem surfaces is conducted towards the stem or root center (Michaletz and Johnson 2007). The amount of heat able to penetrate the xylem depends on the energy dose released during the fire and on the bark's thermal insulation capability—which is determined mainly by bark thickness, as well as density and moisture (Pausas 2015a; Bär and Mayr 2020). Without sufficient bark insulation, phloem, vascular cambium and xylem can reach critical temperatures (Michaletz et al. 2012). Xylem conduit walls are composed of viscoelastic polymers (lignin, cellulose, and hemicellulose) which start to soften above threshold temperatures ("glass transition point") transitioning from a solid to a viscous state. Xylem softening has been demonstrated to occur between 60 and 90 °C with variations among species, as exact transition temperatures are affected by molecular structures of the cell wall matrix and present moisture content (Hillis and Rozsa 1985; Olsson and Salmén 2004; Börcsök and Pásztory 2021). During this softening phase, alterations of the conduit cell walls (e.g., deformations and/or ruptures) can occur, which become permanent after the xylem cools. Such physical changes of conduit structures can potentially impair both the hydraulic efficiency (e.g., clogging of pits by ruptured wall particles) and the hydraulic vulnerability (e.g., modification of the pit architecture) of affected xylem.

Support for heat-induced structural alterations and reduced hydraulic efficiency is weak or mixed (Fig. 3), largely due to limitations in experiments that do not mimic the conditions that occur during fire (Nolan et al. 2024). Various heat experiments, as well as after a wildfire, have shown that reduced hydraulic efficiency can occur and that it may be due to xylem cell alterations (Michaletz et al. 2012; West et al. 2016; Bär et al. 2018). Alterations of secondary cell walls after exposure to 90 °C were also detected for *P. sylvestris* (Bär et al. 2018), however without any permanent effects on hydraulic efficiency. When small *P. ponderosa* were exposed to controlled surface fires (Partelli-Feltrin et al. 2020, 2022), the xylem did not reach temperatures provoking physical alterations of conduits and accordingly, no reduction in hydraulic conductivity was observed. Similarly, no hydraulic limitations were found in the main stem of mature *P. pinea* after a prescribed fire (Battipaglia et al. 2016). These results indicate that conifer tracheids possess a high mechanical resistance against heat-induced destabilization of the overall wall geometry. This can be attributed to their high ratio between wall thickness and lumen size, which was attributed to higher hydraulic safety (Hacke and Sperry 2001), but also may prevent major wall ruptures even under comparatively high heat transfer rates to the xylem. Thus, limitations of the hydraulic efficiency by heat-induced wall deformations and/or ruptures seem to be unlikely in pines, while other mechanisms may play a role. Hydraulic conductivity can also be reduced by traumatic resinosis as response to fire-induced wounding (Smith et al. 2016; Partelli-Feltrin et al. 2020). Post-fire resin soaking can extend from the heat-killed area radially towards the pith plugging pit connections and impairing the water flow through the xylem. Non-conductive xylem close to fire wounds in *P. ponderosa* has previously been associated with resin depositions using staining techniques (Partelli-Feltrin et al. 2020). However, the exact effect of resin blockages on hydraulic conductivity is unevaluated (Hoffmann et al. 2024; Nolan

et al. 2024), as the amount of resin released after injuries can vary widely within the genus *Pinus* (Hood and Sala 2015).

Heat-initiated alterations of conduit structures can also affect the xylem's hydraulic vulnerability post-fire. As vulnerability to drought-induced embolism is closely linked to pit architecture (Tyree and Zimmermann 2002), any physical irregularities of pit structures can facilitate embolism formation and therefore permanently shift vulnerability thresholds (Plavcová et al. 2013). It is assumed that thermal softening of lignin and hemicelluloses can result in pit modifications and enable movements of cellulose microfibrils, which both favor torus sealing failures (Michaletz et al. 2012; Bär et al. 2019). Heat-induced changes in hydraulic vulnerability were demonstrated for *P. sylvestris* (Bär et al. 2018) and *P. ponderosa* (Partelli-Feltrin et al. 2020). Shifts of 1.3 MPa (from −3.6 to −2.3 MPa) and 0.6 MPa (from −3.4 to −2.8 MPa) in the water potential inducing 50% loss of conductivity were detected in branches of *P. sylvestris* after heat treatments and after a wildfire, respectively (Fig. 4). Experimental heat exposure using water baths may not always reflect heat regimes during fires and changes in vulnerabilities thus vary. While Bär et al. (2018) assigned changes of thresholds to structural alterations which occurred during xylem heating, Partelli-Feltrin et al. (2020) demonstrated on *P. ponderosa* saplings that the development of traumatic xylem elements post-fire can also increase vulnerability. They

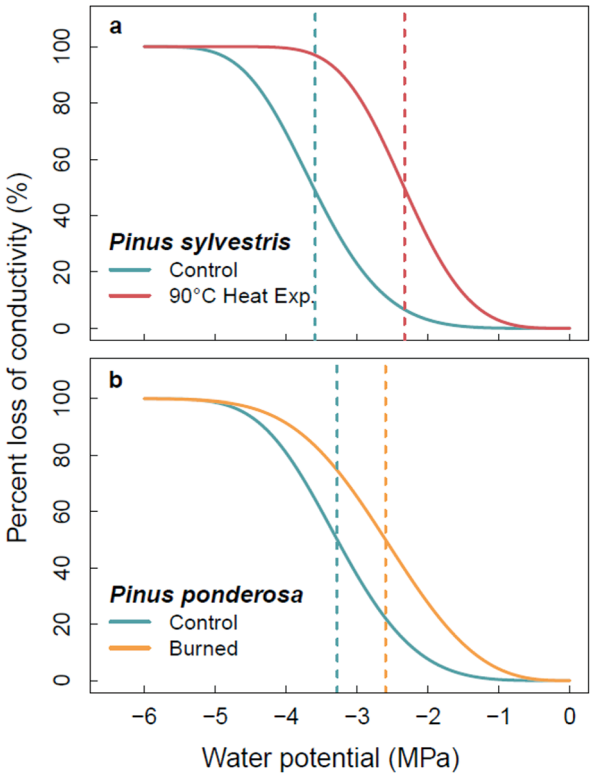

Fig. 4 Hydraulic vulnerability curves as a function of loss of hydraulic conductivity and water potential for (**a**) *P. sylvestris* control branches and exposed to a heated water bath and (**b**) burned and control *P. ponderosa* stems 21 months post-fire. (Adapted from Bär et al. (2018) and Partelli-Feltrin et al. (2020), respectively)

found newly formed tracheids in the vicinity of the fire scar to be disorganized and deformed, which facilitated drought-induced embolism formation.

Besides xylem structures, fire can also affect the water phase by enhancing the likelihood of embolism formation, and there is intermediate support for these hypotheses (Nolan et al. 2024). First, heat transferred to the xylem also raises the temperature of the sap which is associated with a reduction of its surface tension (Lodge et al. 2018). Sap surface tension impacts the vulnerability to embolism formation (Michaletz et al. 2012; West et al. 2016; Losso et al. 2017). Rapid threshold shifts can potentially lead to embolism formation, especially when tensions in the xylem are already enhanced due to pre-fire drought stress, or when atmospheric conditions during the fire add additional stress on the water columns (as described in the following).

It is assumed that the heat plume of hot air associated with fire can provoke extremely low water potentials in the xylem network (Kavanagh et al. 2010; Midgley et al. 2011; West et al. 2016; Hoffmann et al. 2021). Abrupt shifts of air temperature and humidity above flames lead to a high leaf-to-air vapor pressure deficit (VPD). This "heat plume hypothesis" assumes that stomatal response is slower than the heat plume passage, and therefore high VPDs can trigger extensive water loss and decrease xylem water potentials to critical levels and thus embolism formation. In vessel-bearing species, high water loss rates and extensive embolism formation have been documented after exposing branches to experimental fires and to simulated heat-plumes, respectively (West et al. 2016; Hoffmann et al. 2021). In contrast, no heat plume-related conductivity losses were detected in stems of *P. ponderosa* saplings burned under controlled conditions (Partelli-Feltrin et al. 2020, 2022). This suggests that the valve-like pit structures of conifers provide additional hydraulic protection during fires. The sudden rise of VPD creates a steep water potential gradient in the xylem which probably triggers pit closure (aspiration of the torus sealing the pit aperture; Tyree and Zimmermann 2002). Aspirated pits isolate tracheids and prevent air entry unless the water potential reaches critical levels. Then, this safety mechanism fails, whereas the subsequent propagation of embolism in conifer xylem depends on the time of exposure to pressure gradients (Mayr et al. 2006). Especially during fast moving fires with short residence times, it is likely that embolism therefore may not spread far into the xylem of proximal branch parts or the main stem. However, when residence times are longer, VPD-driven embolism can also affect hydraulic efficiency in stem xylem of conifers. This was demonstrated in experiments with *Sequoia sempervirens* where conductivity losses of 23% and higher were detected when branches were exposed to heat plumes of 70 °C for 6 min and longer (Salladay and Pittermann 2023). Further studies are required to better understand the underlying physical mechanisms and their interplay with the hydraulic architecture of trees. Conifers, with their needles, might substantially differ from broadleaved-angiosperms due to lower specific leaf area, higher cuticular protection, and xylem hydraulic segmentation.

Studies indicate that pines benefit from xylem structures resistant to fire and thus to hydraulic impairments (although the number of studies is limited). The high mechanical resistance and the sealing mechanism of tracheids may help prevent

extensive conductivity losses, especially during fast moving surface fires. Many pine species also profit from bark insulation and develop relatively thick bark with advancing age, which provides additional thermal protection of the xylem. However, if the amount of heat released during the fire is high enough to induce wounding of stem internal tissues, hydraulic functions can be long-term impaired, e.g., by physical alterations or the formation of traumatic xylem and resinosis. In addition, conductive sapwood may be directly consumed in recurrent fires. Affected xylem needs to be replaced in order to restore full hydraulic capacity. Replacement times can vary from few years up to decades depending on species and its number of active sapwood rings. Long-term limitations of hydraulic efficiency and vulnerability can have important impacts on post-fire tree physiology (Bär et al. 2019). On one hand, reduced conductivity curtails the water supply to more distal tree parts, which can cause low water potentials in the xylem and leaves, as well as affect leaf turgor. In consequence, stomatal regulation may result in reductions in assimilation and productivity. On the other, fire-caused increases of hydraulic vulnerability imply that affected trees have to cope with reduced hydraulic "safety margins." Trees will be less tolerant to embolism formation during future drought events, which particularly affects species operating at water potentials close to hydraulic failure (Choat et al. 2012).

2.3 Fire Effects on Defenses

Wildland fire can affect resin-based defenses in pines, including resin flow, chemistry, and ducts (i.e., canals), but the effects attenuate with time and are dependent on burn severity and level of fire-caused injuries (Hood 2020; Fettig et al. 2022). See chapter 4 by Gandhi and Hood (2026) for a more detailed discussion of pine defenses. Immediately after fire and in trees with high levels of injury, fire-induced susceptibility may increase colonization by bark and woodboring beetles (Coleoptera: Buprestidae, Cerambycidae, Curculionidae), leading to mortality in trees that may have otherwise survived fire's initial injury (e.g., McHugh et al. 2003; Lerch et al. 2016; Westlind and Kelsey 2019; Valor et al. 2021). In trees with high levels of crown scorch and basal cambium kill from fires, the injuries can limit phloem transport, photosynthetic potential, and reduce resources necessary for compartmentalizing basal wounds and mounting an energetically demanding defense response (Hood et al. 2018; Bär et al. 2019). However, trees with high burn injury levels are also poor hosts for bark beetle brood development due to low substrate quality (Lombardero and Ayres 2011; Powell et al. 2012), suggesting a unimodal response of beetles to fire-caused injury levels, with attacks most common in moderately-injured trees.

The pulse of bark beetle-caused mortality after fire in numerous pines species (e.g., *P. radiata*, *P. pinaster*, *P. ponderosa*, *P. contorta*) is typically short-lived, persisting only 1 or 2 years and not leading to outbreaks outside of the burned area (Schwilk et al. 2006; Lombardero and Ayres 2011; Davis et al. 2012; Powell et al. 2012; Tabacaru et al. 2016). More research is needed for other pine species and to

determine the duration of susceptibility and how the response is modulated by other factors (e.g., insect species, tree injury level, drought, host characteristics such as size, and bark beetle predation). For example, in contrast to the ephemeral short-term increase in susceptibility to bark beetles from burning that is often reported in pines, *P. lambertiana* mortality from *Dendroctonus ponderosae* was much higher after low-intensity prescribed burns compared to unburned areas (Maloney et al. 2008), with the increased susceptibility lasting over 15 years and exacerbated by extreme drought (Steel et al. 2021). *Ips sexdentatus* preferentially attacked *P. sylvestris* over *P. nigra* after prescribed burning, but for both species, trees with faster growth, higher resin duct area, and larger resin ducts were more likely to survive attacks (Valor et al. 2021).

Likely mechanisms for the oft-observed switch in surviving pines from increased susceptibility to increased resistance are increases in resin flow and resin ducts. These increases in defenses can contribute to declines in attack success and begin within a month to a year after fire. The exact timing of this switch depends on the specific bark beetle and host tree species involved, growing season length, and post-fire climate. There is widespread evidence of increased resin flow after fire in several pine species, including *P. resinosa* (Santoro et al. 2001; Lombardero et al. 2006), *P. ponderosa* (Wallin et al. 2004; Six and Skov 2009; Davis et al. 2011; Perrakis et al. 2011), *P. pungens*, *P. rigida*, *P. strobus*, *P. virginiana* (Knebel and Wentworth 2007), and *P. nigra* (Cannac et al. 2009). Wildfire resulted in higher resin yields in *P. merkusii* after tapping for resin production compared to unburned trees; the response was highest in trees with stem charring compared to trees where the fire did not affect the stem, as well as for trees with crown scorch (Della Prasetya et al. 2017). In contrast, prescribed fire did not affect resin production of tapped *P. pinaster* relative to unburned tapped trees (Rodríguez-García et al. 2018). The increases in resin flow after fire declined over time, such that 4 years post-fire resin flows were no different than unburned pines (Cannac et al. 2009; Perrakis et al. 2011). Increased resin flow after fire may also help with compartmentalizing fire-cause basal wounds and limiting wood decay (Verrall 1938).

Low-severity fire can induce resin ducts, which, as the sites of resin synthesis, storage, and delivery, are strongly positively correlated with tree resistance to bark beetles (reviewed in Vázquez-González et al. 2020). Because resin ducts remain functional for years (Hood and Sala 2015), the 1- or 2-year increase in resin ducts after fire is consistent with the long-term increase in resin flow found in previous studies. Initial increases in resin flow could occur by *de novo* resin synthesis in existing ducts and then continue to increase if fire induces increases in resin ducts, as axial resin duct density is positively related to resin flow (Blanche et al. 1992; Hood and Sala 2015). Fire increased resin duct defenses in surviving *P. ponderosa* 1–2 years after wildfire, and those defenses declined when frequent fire ceased (Hood et al. 2015). Studies of duct responses after prescribed fire report conflicting results. In *P. ponderosa*, fall prescribed burns showed no increases in duct responses, even when accounting for fire intensity (Sparks et al. 2017), while spring prescribed burns were associated with small increases in total duct area, but the magnitude was very small compared to the effects of mechanical thinning (Hood et al. 2016) and

not associated with crown scorch levels (Vilà-Vilardell et al. 2024). Prescribed burning reduced resin duct area and size in *P. palustris*, where smoldering time of duff was negatively related to resin duct size in the dry years post-fire (Slack et al. 2016). *P. lambertiana* resin ducts increased after fall prescribed burning (Bernal et al. 2023). In this study, defense response interacted with local competition in the burned treatments, with higher likelihood of mortality in trees with high competition and lower resin duct density and relative duct area. The competition × defense response was not observed in unburned treatments. Prescribed burning combined with tapping for resin production in *P. pinaster* only increased resin duct frequency and size near the tapped site, but the response did not lead to an increase in resin flow (Rodríguez-García et al. 2018).

Fire can also affect resin chemistry. *P. ponderosa* that had experienced a prescribed burn had different phloem resin chemical composition 10 years after burning, with lower levels of several specific monoterpenes known to benefit *D. ponderosae* attacks (Raffa 2014), including (−)- α- pinene, myrcene, and 3-carene (Hood et al. 2016). Wildfire reduced induced phloem resin concentrations in *P. contorta* and altered relative composition of resin monoterpenes (Powell and Raffa 2011). In contrast to Hood et al. (2016), burned trees had increased proportions of (−)- α- pinene compared to unburned trees 1 year post-fire, but both studies found increased limonene, a monoterpene highly toxic to bark beetles, in burned trees. Much more research is needed about the extent to which fire severity alters resin chemistry and how responses affect resistance to bark beetles.

While increased resin duct production after fire is likely a direct response to wounding by fire, changes in microclimate due to frequent, low-severity fire may also enhance resin duct production via changes in stand structure (Hood et al. 2016; Bernal et al. 2023). Low-severity fire can reduce tree density, which can reduce water stress in surviving trees, but also increase surface temperatures due to increased solar radiation. Resin duct area is positively correlated with both warmer and wetter conditions and with ring width (Rigling et al. 2003; Hood et al. 2015). Hence, increases in tree radial growth in response to higher water availability, combined with warmer temperatures may also further stimulate resin duct production beyond the effects of fire alone. Favorable environmental conditions from fire or thinning may increase duct production and resin flow in the long-term (Zausen et al. 2005), while low-severity fire can provide a pulsed increase in resin duct-related defenses. Top-down control of bark beetles by competitors and predators also increase after fire and can further decrease bark beetle attacks (Tabacaru and Erbilgin 2015). Therefore, frequent, low-severity fire can increase pine forests' resistance to bark beetles via these mechanisms—direct, physiological stimulation of defenses, indirect changes in stand structure, and bark beetle predation (Fig. 5). As resin duct traits are heritable (Westbrook et al. 2015; Fabián-Plesníková et al. 2021), low-severity fire could favor evolution of increased pine defenses via bark beetles using a window of susceptibility after fire to attack weakened trees until the fire-induced defenses increase to bolster resistance (Lombardero et al. 2006; Hood et al. 2015). This hypothesized relationship with fire and defense likely only applies to resister or tolerator pine species that can survive low-intensity fire.

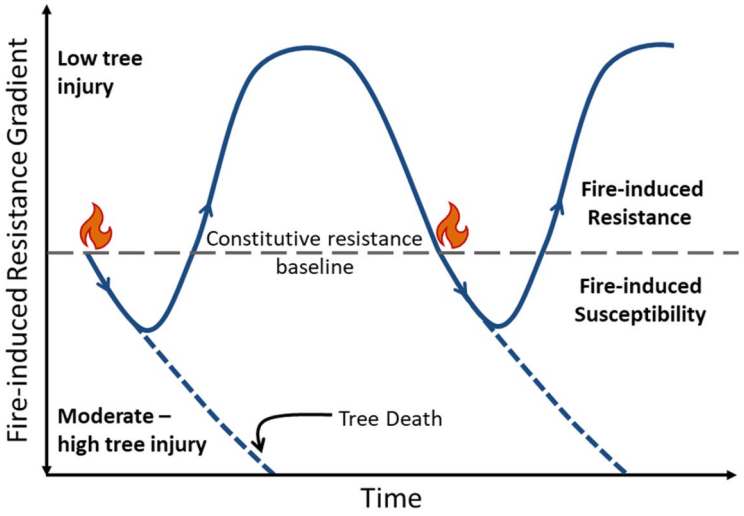

Fig. 5 Hypothesized conceptual model of fire-induced tree defenses and forest-level resistance from repeated fire in pines adapted to frequent, low-intensity fire regimes. Solid line—For trees with low levels of injury, fire causes a brief (days—1 growing season) reduction in resistance to bark beetle attacks before induced resin ducts form, followed by a period of increased resistance that may last for several years before returning to constitutive levels as induced resin ducts lose connectively due to annual tree growth. Repeated low-severity fires foster low-density forests that reinforce resistance to bark beetles. Dashed line—Fire increases susceptibility to attack and death for trees with moderate to high levels of injury. (Adapted from Hood et al. (2015))

2.4 Fire Effects on Tree Mortality and Growth

By killing trees, fire controls forest structure, tree density and species dominance, with cascading positive and negative impacts to biodiversity, carbon stores, hydrologic processes, and economic and social services (Bond and Keeley 2005). Tree sensitivity to fire varies by species, size, and phenology, as well as indirect interactions with insects, diseases, and climate (Hood et al. 2018). In fire-adapted ecosystems where trees have traits to survive or regenerate after fire (see Sect. 1), climate-driven alterations to fire regimes are an emerging threat, with increasing fire size, frequency, and severity potentially having long-term consequences via fire-induced tree mortality (Seidl et al. 2016). Climate-mediated increases in fire severity and frequency are projected to cause large decreases in carbon stocks through loss in forested area (Liang et al. 2017)—changes that can shift forests to nonforested states (Nolan et al. 2021). Understanding these direct, indirect, and long-term effects of fire on tree mortality and tree growth is essential to predicting fire effects from local to global scales.

2.4.1 Direct and Short-Term Indirect Fire Effects on Pine Mortality

Post-fire tree mortality can be caused either directly from fire-caused injury or from indirect effects, with tree death occurring immediately to several years after fire (Fig. 3). Direct tree death from fire is due to cambium necrosis via heat transfer to the crown, stem, and root tissue (Dickinson and Johnson 2001) or the physical consumption of the tree stem that causes collapse (Nolan et al. 2021). Tree death results from either complete necrosis to any of these tissues or if partial injuries to multiple tissues are severe. A general threshold for tissue death is 60 °C, although longer exposure at lower temperatures can also be lethal (Hare 1961; Pingree and Kobziar 2019). Delayed tree death in the years following fire can occur as a direct result of high levels of fire-caused tissue injuries or through secondary interactions of injuries with climate or bark beetles. We direct readers to existing reviews on fire effects on trees for more details (Dickinson and Johnson 2001; Michaletz and Johnson 2007; Hood et al. 2018; Bär et al. 2019; Kleynhans et al. 2021) and focus the following sections on pines.

Post-fire tree mortality has been extensively studied in many pine species due to their wide distribution range and high commercial and ecological value, with a large body of research related to predicting mortality from fire. The Fire and Tree Mortality (FTM) database of fire-caused tree injury and mortality data in the USA, contains records for 98,100 pines from 24 species, representing 58% of the total database (Cansler et al. 2020b). Post-fire tree mortality models are overwhelming based on empirical data using logistic regression (i.e., binary outcome of the tree surviving or dying from fire). Common important predictive variables include species, some measure of crown injury, and some measure of resistance such as tree diameter or bark thickness (Woolley et al. 2012; Cansler et al. 2020a). Mortality models have been developed for numerous pine species in the US (e.g., Woolley et al. 2012; Hood and Lutes 2017) and Europe (e.g., Fernandes et al. 2008; Catry et al. 2010), and to a lesser degree in Asia (Kwon et al. 2021) and other tropical areas (Rodríguez-Trejo et al. 2007; Pantoja-Campa et al. 2018; Hernández-Correa et al. 2019; Gómez-Mendoza and Rodríguez-Trejo 2021).

2.4.2 Long-Term Fire Effects on Tree Growth and Survival

Growth of trees that survive fire can remain unchanged, increase, or decrease depending on fire-caused injuries, changes to local competition, biophysical and environmental characteristics, and susceptibility to insect attack (Fig. 6). Growth declines due to fire-caused injuries to the crown can reduce photosynthesis while injury to the main stem cambium can limit translocation of photosynthates (Michaletz and Johnson 2007). Several studies have reported a decrease of tree radial growth after fire in different pine species due to injuries (Peterson et al. 1991; De Micco et al. 2013; Battipaglia et al. 2014a; Valor et al. 2015; Seifert et al. 2017; Swann et al. 2022; Wenderott et al. 2022) and with increasing fire intensity (Sparks et al. 2017; Johnston et al. 2019; Swann et al. 2022). Low-intensity fire may not

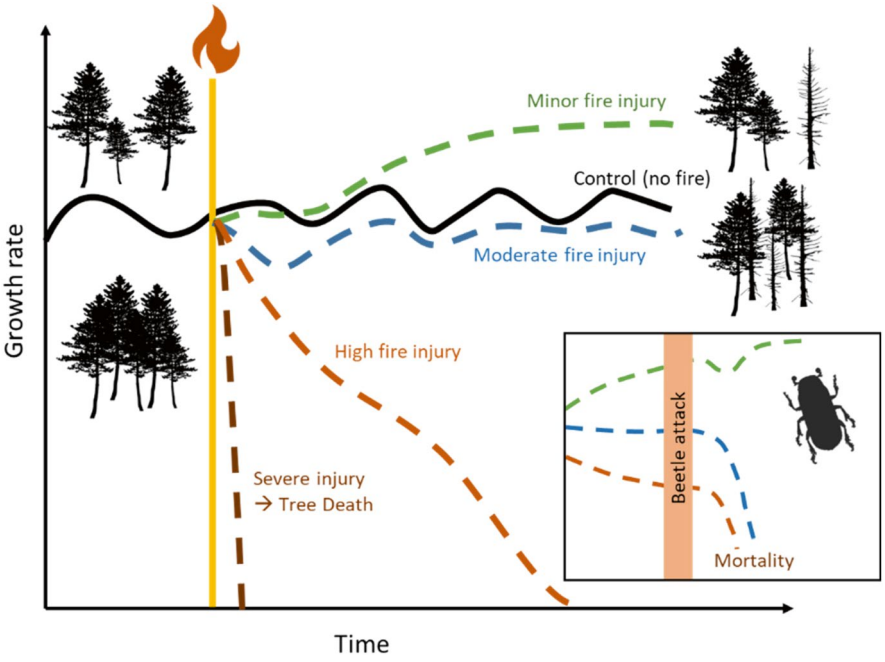

Fig. 6 Hypothetical tree growth responses to fire depending on tree injury, local competition, and bark beetle attack

affect growth if little-to-no tree injury or reduction in forest density occurs (Rozas et al. 2011; Espinosa et al. 2021; Zald et al. 2022). On the other hand, fire-caused reductions in competition can improve post-fire growth of surviving trees if tree injury is low. For example, crown scorch >30% reduced growth in *P. halepensis* relative to unburned trees, while growth increased in pines that had competitive release due to burning coupled with low crown scorch (Valor et al. 2018). Fire reduced local competition and led to an increase in *P. halepensis* growth, but only on the wetter sites, suggesting responses are dependent on environmental factors and water availability (Alfaro-Sánchez et al. 2016). In contrast, high-intensity fire increased growth after an initial reduction in *P. canariensis* on drought-prone sites (Rozas et al. 2011) and via increasing intrinsic water use efficiency (Renninger et al. 2013; Battipaglia et al. 2014b).

With frequent and low-intensity fire, positive long-term growth responses have been reported due to reduced competition with other individuals for soil resources and water was observed (Agee 1993; Stone et al. 1999; Keeling and Sala 2012). Beghin et al. (2011) demonstrated that *P. sylvestris* increased photosynthetic activity during the 5 years following a fire, likely due to trees having less competition for water and nutrients. Prescribed burning enhanced growth of mature *P. halepensis* probably through enhanced short-term water and nutrient availability (Valor et al. 2015), but young pines experienced more intense competition and reduced stomatal

conductance, thus showing little improvement in productivity (Battipaglia et al. 2014b). In contrast, successive wildfires in French *P. halepensis* forests caused a decreased growth and stomatal conductance (Battipaglia et al. 2014a), probably due to more severe injuries to carbon sinks (De Micco et al. 2014).

Fires can affect chemical-physical and biological components of the soil, which in turn may affect tree growth. Depending on fire intensity and type of fire (i.e., crown, surface, and ground), fire effects on soil organic matter can vary from slight distillation (volatilization of minor constituents), charring, or complete oxidation (Certini 2005). Consequently, the total nutrient content of soil may decrease (Prieto-Fernández et al. 1993). When those processes occur, a consistent decrease in tree-ring growth can occur, as well as an increasing numbers of missing rings, as has been reported in *P. sylvestris* (Beghin et al. 2011) and *P. halepensis* (Battipaglia et al. 2014b) and intra-annual density fluctuations in *P. pinaster* (Niccoli et al. 2019, 2023b) and *P. pinea* (Battipaglia et al. 2016).

Fires may also affect tree survival to subsequent drought and bark beetle outbreaks, although results are scant and mixed with both increased susceptibility (Steel et al. 2021) and increased resistance (McNichol et al. 2019) to bark beetles under reported drought. Partelli-Feltrin et al. (2020) found experimental burning increased vulnerability to water stress that developed over the 21 months after the fire in *P. ponderosa*, suggesting deformation of xylem conduits formed after the fire can reduce hydraulic function and increase vulnerability to drought stress. More research is needed how fire-caused injury interacts with climate to influence long-term tree survival.

3 Conclusion

This chapter synthesizes knowledge of fire ecology and ecophysiology of *Pinus* species and pine-dominated forests, which is essential to the conservation of species and responsible forest management. In doing so, several knowledge gaps emerged. To provide a comprehensive evolutionary and ecological understanding of how fire affects pines at the individual, stand, and landscape-levels, especially under anthropogenic climate change, more research is needed on the following topics:

- Our understanding of fire-adapted traits is hampered by several factors that stymie synthesis and our ability to quantify advantages conferred to pines and other species. Better quantification of traits beyond binary presence or absence or simple rankings is needed. For some traits (e.g., bark thickness accumulation, litter flammability), robust datasets exist that allow for synthesis and analyses; other traits like crown morphology, self-pruning, and serotiny are relegated to binary possibilities that contrast with reality (and often with the literature), but also lack measurement.
- Literature bias in favor of American, Canadian, and European species largely overlooks the diversity of pines outside of these regions. The high diversity of

pines in Mexico and the aggregations of pines in east Asia lack measurement or reporting in English-language articles such that they may be omitted from syntheses of our global understanding of fire and pines.
- How does fire determine the extant relationships between pines and herbivorous insects, and how would they alter under varying forest management and climate change? Fire and native insects are often both major disturbances in pine forests, with the potential for one to subsequently affect the other. Additional research is needed on how forest management and fire can increase resistance to insects, especially in light of climate change that can alter physiology of both trees and insects.
- More research is needed on the ecophysiological effects of fire on pines and other species. This research is essential to develop process-based models of fire-caused tree mortality under novel climate conditions.

Fire has played a driving role in the speciation and evolution of the genus *Pinus* and continues to be a major influence in many *Pinus* forests around the world (He et al. 2012; Jin et al. 2021). Altered fire regimes due to past management and fire suppression have increased susceptibility of many pine forests to fire through increased fuel loading and forest density. These changes, coupled with hotter and drier climate, can lead to higher intensity fires that make even fire-resistant pine species vulnerable. However, many pine species are well-adapted to warm climates and can survive frequent, low-intensity fire. Applying knowledge of historical fire regimes, trait syndromes, and the effects of fire on tree ecophysiology can guide management to create fire-resilient pine forests.

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