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Management for forest adaptation to climate change requires an evolutionary lens: Lessons from bark beetles in western North American conifer forests

Running footer: Evolution, Bark Beetles, and Forest Adaptation

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Abstract

Forest adaptation to climate change is becoming a management priority, yet *in situ* genetic adaptation via natural selection is rarely incorporated into planning. Instead, strategies emphasize resistance and resilience—short-term properties that do not ensure long-term forest persistence and function. Conifer forests harbor high genetic diversity shaped by long evolutionary histories with climatic variability and disturbance, fostering local adaptation, phenotypic flexibility, and complex biotic interactions. These attributes are central to the persistence of long-lived, sessile species. Here, I review western conifer forests through an eco-evolutionary lens, focusing on genetic resilience and interactions with co-evolved disturbance agents, particularly tree-killing

bark beetles. I evaluate how prevailing management approaches may constrain natural selection and adaptive capacity and argue that passive or semi-passive strategies that allow selection to operate may better support long-term adaptation. Advancing such eco-evolutionary forestry will require a shift away from practices that prioritize short-term outcomes that neglect evolutionary processes and genetic consequences.

Key Points

- Forest adaptation requires integrating evolution; natural selection and genetic diversity are central to long-term persistence under climate change.
- Bark beetles act as ecosystem engineers and selective agents, driving forest structure, biodiversity, and rapid evolutionary change.
- Common management practices often override selection, reducing genetic diversity and potentially hindering long-term forest adaptation.

Keywords: ecological acclimation, forest resilience, genetic resilience, natural selection, natural selection override

Introduction

Western forests are experiencing rapid climate change. This, along with human activities, is driving major alterations in forest structure, function, and disturbance regimes over both short-

and long-time scales (Mote et al. 2013). Facilitating the maintenance of forest continuity and function will require rethinking management under increasingly novel and dynamic environmental conditions.

Forest management plans commonly emphasize increasing resistance, resilience, and adaptive capacity to climate change and climate-driven disturbances including insect outbreaks. Closer examination often reveals a reliance on traditional silvicultural goals and approaches developed initially to maximize timber production and that assume fast growth equates to forest health and recovery. There is also often little consideration of ecological function or the facilitation of adaptation to novel conditions (Ibáñez et al. 2019; Strickland et al. 2024) and conventional approaches still often set a goal of assisting forest recovery to a pre-disturbance reference state (Strickland et al. 2024). In contrast, some emerging strategies advocate highly interventionist approaches, including forest conversion (Lefèvre et al. 2014; Yao et al. 2025), selective breeding (often focused on one or a few traits) (Cortés et al. 2020; Laverdière et al. 2022), genetic engineering (again targeting single traits) (Committee on the Potential for Biotechnology to Address Forest Health et al. 2019; Polle et al. 2019; Li et al. 2025), or assisted migration to track shifting climatic envelopes (McLane and Aitken 2012; Palik et al. 2022). Traditional and innovative approaches alike are frequently narrow in scope, focusing on trees rather than the broader forest ecosystem, and overlook interaction networks, ecosystem processes, effects on biodiversity, and environmental feedbacks. While a growing number of papers in the scientific literature address these issues (e.g., Muller et al. 2022; Hurtado et al. 2025; Lindenmayer et al. 2025), they seldom are translated into management. One approach that has received

comparatively little attention in forest management and policy is *in situ* adaptation through natural selection.

In this review, I argue that forest management has failed to adequately recognize and leverage natural selection as a central mechanism for supporting *in situ* forest adaptation, and that continued neglect of this process risks severe ecological consequences. I first use a hypothetical forest responding to a changing climate to define terminology used in this synthesis. Because understanding evolution is paramount to understanding adaptation, I then discuss the co-evolutionary histories of conifer forests and their main biotic disturbance agents, tree-killing bark beetles (TKBB) (Curculionidae: Scolytinae) (recognizing that other pests and pathogens also exert evolutionary pressures with important effects) From the perspective of conifer forests as complex evolving systems, I then evaluate commonly prescribed forest resilience, resistance, and adaptation strategies in the context of their effects on forest adaptation, illustrating key concepts using TKBB. Finally, I argue that passive or semi-passive management should be considered a primary strategy in many forests as a means of promoting natural selection and long-term adaptive capacity. When intervention is deemed necessary it should be done in ways that best support the adaptive process. Although the examples here are drawn largely from conifer forests of the western United States, the principles discussed are broadly applicable to conifer forests worldwide.

Establishing terminology and a conceptual framework

81 A clear understanding and precise use of terminology are essential for developing effective forest
82 management strategies. Unfortunately, core terms are often applied inconsistently or without
83 explicit definition leading to misunderstanding and misapplication. For clarity, I present here a
84 conceptual illustration of potential responses of a forest to climate change through time and use it
85 to define the core concepts of persistence, resilience, adaptation, and ecological acclimation as
86 they are used in this synthesis.

87 The time scale extends from months to millennia but is intentionally left imprecise. This reflects
88 the nonlinearity of forest dynamics and their dependence on the rate, magnitude, and variability
89 of climate change; the forest's initial and evolving sensitivities; standing genetic variation; and
90 feedbacks within the also changing biotic community. The most important consideration here is
91 that forests evolve. This is often ignored in management and research, including predictive
92 models that focus primarily on current patterns of tree distributions that often treat tree species as
93 genetically homogeneous entities when forecasting forest responses to climate change
94 (Savolainen et al. 2007; Alberto et al. 2013; Kremer et al. 2025). This view is in strong contrast
95 with evidence that conifers are genetically diverse (Prunier et al. 2016) and capable of evolution
96 in short time scales (Petit and Hampe 2006; Kremer et al. 2025). Conifers are highly fecund and
97 have substantial generational overlap allowing for selection to influence many cohorts of
98 offspring over the lifetime of a single tree (Alberto et al. 2013). Conifers also show substantial
99 local adaptation even in the presence of considerable gene flow (Kremer et al. 2025). Most have
100 greater fundamental niche spaces than are currently occupied and accounted for in predictive
101 models (Iglesias et al. 2015; Kremer et al. 2025). Treating trees as non-evolving, uniform in their
102 responses to the environment, and operating independent of their biotic community, can lead to

considerable under- or over-estimation of changes in forest stability in the short- and long-term (Gilman et al. 2010).

In this framework (Figure 1), all processes operate continuously although their relative strength and tempo vary over time. Some act rapidly, while others unfold over decades or centuries. Together, they generate shifting and often non-linear selection pressures that feed back to influence tree performance, survival, and reproductive success. As a result, forests function as dynamic evolutionary systems in which trees experience climate change in an evolving landscape of interacting selective forces (Lefèvre et al. 2014). Further, as trees are long-lived, sessile organisms, they must respond to multiple, interacting stressors across several life stages, with selection operating across the genome both within and among generations (Lefèvre et al. 2014; Kremer et al. 2025). In multi-aged forests, various age cohorts experience different selective pressures, creating complex genetic mosaics that can facilitate adaptation to multiple stressors while maintaining high standing genetic variation via gene flow among cohorts and adjacent populations (Lefèvre et al. 2014; Kremer et al. 2025).

Figure 1 depicts a forest initially dominated by a single tree species with two to three co-dominant species, a situation common to many western forests. The relative abundance of each species over time is influenced by successional stage, historical and recent competition, site suitability, standing genetic variation, local adaptation, and interactions with the biotic community. At time zero, climate is relatively stable, and the forest, when perturbed, may exhibit resistance (Figure 1Aa), resilience (Figure 1Ab), or both, reflective of its evolutionary history and recent historic range of variability. Resistance is defined here as minimal-to-no change

following disturbance, where individuals tolerate stressors and the forest maintains structure and function with little alteration. Resistance reflects adaptation to past environmental conditions and retention of ecological legacies (Falk et al. 2022).

When a forest is exposed to stressors (such as drought) or disturbance (such as an insect outbreak) that results in widespread mortality, its capacity for recovery defines its resilience (Figure 1Ab) which depends on a continuing suitable environment for germination, establishment, and growth. A suitable environment includes abiotic factors and the structure and functioning of the biotic community and its interaction web. Disturbance opens space while also creating a transient decline in productivity that is followed by recovery either to the original state (*sensu* engineering resilience) or one of several states that provide similar structures and function (*sensu* ecological resilience) (Gunderson 2000, Gunderson and Holling 2002). The rate and degree of recovery (Figure 1Ab1, Ab2) depend on the condition and composition of the forest at the time of disturbance, its sensitivity to disturbance, and the type, severity, and extent and duration of the event among other factors. Resilience is more likely under a relatively stable climate than one undergoing considerable change and more likely under pulse rather than press perturbations.

With resilience in the narrowest sense, recovery will proceed predictably back to the pre-disturbance state. However, even in a stable climate many forests can reorganize to any one of several states after disturbance (Lecina-Diaz et al. 2026). With climate change, some of these alternate forest states may become more common, resulting in a shift in overall forest composition and function over time. However, even for resilience definitions that allow different

145 successional trajectories, a recognition of the importance of adaptive capacity is typically
146 lacking. Kremer et al. (2025) addressed this by extending resilience to include the capacity of
147 forest trees to withstand or recover from adverse conditions by maintaining adaptive potential at
148 the genetic level. This explicit recognition of the importance of genetics fundamentally shifts
149 how resilience is conceptualized and managed under climate change. Currently, many traditional
150 resilience-focused treatments implicitly assume environmental stationarity, ignoring the need for
151 evolution, and risk pushing forests to unsustainable states and collapse. In contrast, recognition
152 of genetic resilience facilitates approaches supporting adaptation and genetic rescue (Kremer et
153 al. 2025).

154 With only small changes in climate, when resistance and resilience (Figure 1 A) remain possible,
155 physiological acclimation and phenotypic plasticity play particularly important roles.
156 Physiological acclimation involves sometimes reversible adjustments within an individual over
157 days to months that improve performance under stress without genetic change (Kellomäki 2022).
158 Phenotypic plasticity refers to the capacity of an individual to express different phenotypes in
159 response to environmental variation (Agrawal 2001; de La Mata et al. 2022). Together, these
160 processes enhance fitness in variable environments and support short-term resistance and
161 resilience. Importantly, variability in both properties allows flexibility in responses of individual
162 trees to climatic shifts (Lande 1980). However, while plasticity may aid survival in variable
163 environments and may buy time for selection to act on later cohorts, it can also hinder adaptation
164 by supporting established trees (and their contributions to the gene pool) well past their climatic
165 optimum.

When climate change, a press perturbation, progresses to where recovery to or near the original state is no longer possible, forest continuity involves community reorganization and adaptation of the species that remain in place (Figure 1B) (Alberto et al. 2013). Community reorganization involves shifts in dominance and composition, while adaptation is an expression of genetic resilience via natural selection acting on standing genetic variation (the presence of multiple alleles at individual loci upon which selection can act). With adaptation, individuals tolerant of new conditions survive and reproduce in proportionately higher numbers leading to shifts in the population to genetic compositions that promote continuity. Evolutionary history may also contribute as alleles valuable in the past may be beneficial under new climate conditions and some may take on new functions helping maintain adaptively flexible traits (Schaberg et al. 2008). Dispersal of climate tolerant genotypes via pollen or seed may accelerate adaptation but carries the risk of introducing maladaptive alleles (Ledig 1992). Over the longer term, selection on new mutations and epigenetic changes may also contribute to adaptation. If climate stabilizes for an extended period, an adapted population may again express resistance (Figure 1 Ba) and resilience (Figure 1 Bb), but relative to a new range of variability reflecting not only responses to climate *per se*, but to accompanying shifts in interactions within an altered biotic community. Because climate stability is always transient, it is useful to emphasize the many properties and processes at play in a forest under the umbrella of ecosystem acclimation (Stemkovski et al. 2025). Ecosystem acclimation refers to adjustments that occur via multiple co-occurring processes acting across many interacting ecosystem components that reduce disequilibrium with climate. The transient sensitive states of the forest that occur between periods of relative equilibrium are characterized by declines in productivity before recovery occurs as forests adapt

and reassemble under the new set of conditions (Stemkovski et al. 2025). Sensitive states (Figure 1, dips) are periods of strong natural selection resulting in rapid genotypic shifts over generations and transcriptional shifts within generations (Stemkovski et al. 2025). Some forests may reach new equilibria (Figure 1, dotted lines) with equal, higher, or lower productivity than occurred initially, others may operate perpetually in disequilibrium (as do some forests currently) (Figure 1 C), and some may cross thresholds leading to rapid (Figure 1 Da) or slow (Figure 1 Db) vegetation state changes to non-forest. Losses in genetic diversity and climate driven mega-disturbances (Figure 1 Dc) may cause thresholds to be crossed sooner. Shifts to non-forest types may occur anywhere on the timeline whenever ecosystem acclimation is no longer supported (Lecina-Diaz et al. 2026).

In the remaining sections, I use this terminology and framework to illustrate why an evolutionary lens is essential to develop forest management approaches for climate adaptation.

Big conifers and tiny ecosystem engineers: A deep dive into complex evolving systems

Every property and process illustrated in Figure 1 is shaped by genetics and evolution. Thus, the evolutionary history of a forest has much to tell us about how it will be affected by climate change and our management practices. Here, I consider the evolutionary histories of western conifers in relation to their most influential biotic disturbance agents, TKBB.

Conifer-Scolytinae associations are ancient and date to the Mesozoic (Sequeira et al. 2000).

Scolytinae categorized as bark beetles feed mostly in the phloem under the outer bark of woody plants. Some, including TKBB, also feed on fungi (Six and Biedermann 2023).

Conifer-colonizing bark beetle lifestyles range from saprophytic to parasitic and from scavenging on dying or weakened trees to preying on live and sometimes healthy trees. Tree-killing is a derived trait that has evolved only a few times (<20 species) out of various clades of non-tree-killing Scolytinae. The TKBB can be categorized as aggressive or aggressive secondary (Six 2020a). Aggressive TKBB exploit weak trees during non-outbreak periods but can attack and maintain expanding populations in healthy trees when their numbers are high. In contrast, aggressive secondaries colonize weak, dying, or recently dead trees and can develop outbreaks when disturbance or drought creates large numbers of compromised hosts. However, as weakened trees are depleted and beetles are forced into healthy trees, their populations quickly collapse.

In western North America, the TKBB are the aggressive mountain pine beetle (*Dendroctonus ponderosae*), and the aggressive secondaries, western pine beetle (*D. brevicomis*), Jeffrey pine beetle (*D. jeffreyi*), spruce beetle (*D. rufipennis*), Douglas-fir beetle (*D. pseudotsugae*), pine engraver (*Ips pini*), fir engraver (*Scolytus ventralis*), and western balsam bark beetle (*Dryocoetes confusus*). *Dendroctonus* is estimated to have originated in North America ~52 MYA (Ramírez-Reyes et al. 2023) and while *Ips* emerged around ~4-5 mya (Jordal and Cognato 2012) with speciation in both genera coinciding with diversification of their conifer hosts. Another notable period of diversification occurred post-Pleistocene glaciation as conifers re-established in the north following periods of isolation in southern refugia (18-25 KYA) (Bracewell et al. 2018; Havill et al. 2019).

Not surprisingly, the evolution of TKBB continues into recent times. Notably, mountain pine beetle, with its extensive geographic range, shows evidence of differentiation due to isolation and distance (Bracewell et al. 2013; Dowle et al. 2017). The beetle also exhibits post-zygotic male sterility that results in extremely low egg viability when individuals from distant populations are crossed (Dowle et al. 2017).

TKBB also exhibit evidence of evolution in response to climate. Many (but not all) TKBB must synchronize emergence for mass attacks on trees and development of stages capable of cold-hardening prior to the onset of winter (Bentz and Powell 2014). Beetles are ectotherms with warmer temperatures supporting faster growth (until an upper limit is reached). To avoid maladaptive phenologies resulting from brood growing too fast or too slow, mountain pine beetles living under different climatic regimes have evolved to grow at different rates. For example, southern mountain pine beetle brood develop more slowly than those in the colder north creating similar life cycle lengths even with greater thermal input (Bentz et al. 2014).

Currently warming is supporting the movement of mountain pine beetles into areas that were previously too cold including into higher elevations and in the boreal forest (Carroll et al. 2003).

Local adaptation can be expected to fine tune their phenologies to conditions in these new, but still thermally challenging, locations (Thompson et al. 2020).

TKBB have evolved to specialize on one or a few closely related tree species (Kelley and Farrell 1998). Specialization is not surprising as beetles must be able to detoxify tree species-specific defenses and to alter host tree chemicals into beetle species-specific pheromones for attracting

mates and coordinating mass attack. Such specialization has locked most TKBB and their host trees together for millennia.

A compelling illustration of the effects of beetle–host tree specialization is provided by the ponderosa pine–mountain pine beetle–western pine beetle system. Ponderosa pine is a widespread lower montane species occurring throughout western North America, from Mexico to Canada. Across this range, it exhibits substantial variation in climatic tolerances, morphology, genetic structure, and secondary chemistry (Potter et al. 2013; Shinneman et al. 2016; Smith et al. 1969). This variation is driven by genetic differentiation sufficient to justify division into four species, although these taxa are currently classified as varieties: ponderosa pine (*P. ponderosa* var. *ponderosa*), Pacific ponderosa pine (*P. ponderosa* var. *benthamiana*), Rocky Mountain ponderosa pine (*P. ponderosa* var. *brachyptera*), and interior ponderosa pine (*P. ponderosa* var. *scopulorum*) (Shinneman et al. 2016).

The contemporary distribution of these varieties reflects postglacial northward migration from multiple refugia beginning approximately twelve thousand years ago. However, phylogenetic evidence indicates that divergence predates the last glacial maximum. Indeed, some varieties are more closely related to other species within *Pinus* subsection *ponderosae* than to each other, and current zones of sympatry likely represent secondary contact among non-sister taxa rather than sister taxa (Willyard et al. 2017). More recent local adaptation within each has produced populations with distinct climatic optima and functional traits. Thus, ponderosa pine represents a complex mosaic of cryptic species, with populations of each composed of highly divergent genotypes and phenotypes (Willyard et al. 2017).

Consistent with this, TKBB associated with *P. ponderosa sensu lato* exhibit marked differences in host use and population dynamics. The mountain pine beetle (*Dendroctonus ponderosae*) functions as an aggressive secondary colonizer in ponderosa, Pacific, and Rocky Mountain ponderosa pine, but behaves as a primary aggressive species in interior ponderosa pine (Graham et al. 2016). Moreover, eastern populations of mountain pine beetle associated with interior ponderosa pine are genetically distinct and exhibit partial to complete reproductive incompatibility with western populations, suggesting incipient or realized speciation (Dowle et al. 2017). In contrast, the western pine beetle (*Dendroctonus brevicomis*), a major TKBB specializing on ponderosa and Rocky Mountain ponderosa pine, does not colonize interior ponderosa pine, even within zones of geographic contact and introgression. Host ponderosa pines and their associated bark beetles are thought to have originated in Mexico and subsequently migrated northward post-glaciation. East and west populations of western pine beetles and their fungal symbionts appear to have co-migrated with their hosts, undergoing co-speciation in a striking example of cascading diversification across trophic levels. This process has resulted in reproductive incompatibilities among beetle lineages and partial incompatibilities with their mutualistic fungi (Bracewell and Six 2015; Bracewell et al. 2018).

Genetic variation is also evident within and among populations of each ponderosa pine variety. Abrupt shifts in growth responses to temperature and moisture across elevational and environmental gradients indicate strong local adaptation is common (Rehfeldt 1991; Rehfeldt et al. 2014; McCullough et al. 2017). Populations exposed to greater microhabitat heterogeneity exhibit increased phenotypic plasticity, and trees from xeric environments show greater plasticity than those from mesic sites (de la Mata 2022). Notably, phenotypic and genotypic divergence

can occur over relatively small spatial scales. For example, interior ponderosa pine populations in the Black Hills separated by ~190 km differ significantly in secondary chemistry, genetic structure, and genetic diversity (Six and Alverson 2025). Within these populations, tree groups exhibit divergent growth responses to climate, and individuals killed by mountain pine beetle tend to have slower growth rates and reduced climatic sensitivity over their lifespans relative to surviving neighbors. Additionally, growth–climate relationships differ between older and younger cohorts, suggesting cohort-specific selection associated with climatic conditions at seedling establishment.

These findings align with broader evidence that local adaptation in conifers is common despite high levels of gene flow and phenotypic plasticity (Savolainen et al. 2007; Crispo 2008; Tigano and Friesen 2016). Age- and stage-specific selection, along with differential selection acting on overlapping generations established under varying climatic regimes, may facilitate adaptation to changing conditions while maintaining genetic diversity within populations (Ellner and Hairston 1994). For example, evidence of local adaptation and phenotypic variation within and among populations of high elevation whitebark pine has been found in populations only 27 km apart. Growth rates within populations in response to climate differed between age groups and between mountain pine beetle-killed whitebark pine and those surviving an outbreak. However, responses were dissimilar across populations. At some sites, survivors grew faster than trees eventually killed by the beetle (Six et al. 2021), while the opposite was true at others (Alverson and Six 2026). In each population a suite of secondary chemical compounds was significantly correlated with survival during a mountain pine beetle outbreak, but these suites were not consistent among populations (Six et al. 2021).

The diversity seen among trees is also seen in the beetles that colonize them. For some TKBB, like the pine engraver, and western and eastern mountain pine beetles, we have a wealth of information on how genetic differentiation in the host and the beetle correlates with changes in host tree and beetle physiologies and beetle behavior, including shifts in tree chemistry that influence attractiveness to beetles and their production of pheromones (Miller et al. 1997; Pureswaran et al. 2016). For others, like Jeffrey pine beetle and Douglas-fir beetle and their host trees, neutral molecular markers have been useful to elucidate the relative roles of isolation and gene flow in shaping their genetic structures (Six et al. 1999; Ruiz et al. 2009), but we still have little understanding of how genetic differentiation in these species has influenced their behavior and adaptive capacity. However, one thing is clear; while we assign discrete common and scientific names to beetles and trees for practical purposes, the living entities represented by those neat labels are far from homogeneous.

Many organisms coexist and evolve through time, but only some co-evolve. Co-evolution requires reciprocal adaptations. With TKBB, specialization of TKBB on their host trees has resulted in co-evolution where trees have intensified and diversified their defenses in response to beetle assaults, while the beetles, in turn, have evolved behaviors and detoxification systems to avoid or overcome tree defenses (Ullah et al. 2021). In some cases, beetles have even co-opted tree secondary chemical compounds to produce the very pheromones they use to initiate mass attacks and attract mates (Blomquist et al. 2010). This ongoing ‘arms race’ results in natural selection operating at local scales that, along with selection pressures from other stressors, genetic drift, and mutation, has resulted in considerable heterogeneity in the pool of host trees available to any given population of beetles. To optimize survival and fitness, beetles must

choose a tree rapidly as prolonged searching depletes energy and increases mortality risk (Six et al. 2026). However, in a sea of trees with diverse chemical, nutritional, and anatomical phenotypes, locating a suitable tree of the right size and correct condition is challenging. This intraspecific diversity in trees presents a formidable form of diffuse resistance, reducing the number of beetles that succeed in colonizing hosts and making co-evolutionary adaptations more difficult.

Although the cues used by TKBB in host choice are not well understood, it is clear they are highly selective and exploit signals related to physiological processes of the tree linked to defense. For example, greater radial resin duct area correlates with the likelihood of survival during outbreaks of mountain pine beetle in whitebark and ponderosa pine (Kane and Kolb 2010; Ferrenberg et al. 2014; Hood and Sala 2015; Kichas et al. 2020). Studies have also found differences in constitutive and induced defenses (Bentz et al. 2015; Kichas et al. 2021; Bellostes et al. 2025), growth rates in response to climate (Kichas et al. 2021; Six et al. 2021, Alverson and Six 2026), and genetic profiles, among trees that were attacked, avoided, or unsuccessfully attacked (Six et al. 2018; Six et al. 2021; Korecký et al. 2023). Some TKBB differentiate between trees that are healthy or stressed by drought (Lusebrink et al. 2011; Boone et al. 2013; Netherer et al. 2015), high temperatures (Trowbridge et al. 2021), or fire scorch (Hood et al. 2015), factors that influence tree physiology and defense.

During outbreaks, TKBB can kill thousands or even millions of trees, and their selective behavior during these events ramps up the arms race and makes them significant drivers of natural selection. Trees that survive are either able to repel attacks—indicating stronger

defenses—or evade them altogether, which suggests repellency or masking. Both types of resistance can be found within the same population and highlight the important role genetic diversity plays in tree survival. Bentz et al. (2015) studied whitebark pines that were successfully and unsuccessfully attacked and found clear differences in their terpene profiles. Similarly, Six et al. (2021) compared trees killed by mountain pine beetles with nearby unattacked survivors and observed variations in genetic and chemical profiles, as well as growth rates. In a population where whitebark and lodgepole pines grew together, surviving unattacked individuals from each species formed two distinct clades suggesting multiple genotypes contribute to avoidance during outbreaks (Six et al. 2018).

During non-outbreak periods when beetle-caused tree mortality is very low, TKBB natural selection on trees is likely negligible. However, during outbreaks, when beetles selectively kill large numbers of trees altered by abiotic factors, they may become agents of rapid evolution. Kuparenin et al. (2010) used quantitative genetic individual-based simulations to investigate the relative roles of mortality, dispersal ability, and maturation age to investigate the speed of tree adaptation of a pine forest to climate change. These simulations predicted that after 100 years, adaptation would lag substantially behind the pace of climate change. However, this lag was considerably reduced when natural selection against maladapted individuals was included. Thus, forests affected by selective mortality agents such as TKBB that remove trees maladapted to a new climate may be the quickest to adapt (Kuparenin et al. 2010).

Climate, trees, and beetles

Insights into how TKBB selectivity may support adaption of conifer forests to climate change will come from a deeper understanding of how climate influences attractiveness and susceptibility (these may differ in their supporting mechanisms). Warm temperatures combined with drought are often correlated with TKBB outbreak development and can cause shifts in tree defenses and susceptibility (Gaylord et al. 2013; Netherer et al. 2015). However, the exact mechanisms at play are not well understood.

Terpenes and phenolics are carbon-based compounds that can act as defensive compounds in conifers. Their production carries a high energetic cost (Gershenzon 1994; Howe et al. 2020). As photosynthesis varies over time with temperature and moisture availability, so does carbon (C) uptake and trees must balance investments of C to defense with that needed for respiration, osmoregulation, and growth (Stamp 2003; Huang et al. 2020). Pinaceae hosts of TKBB are isohydrous, closing their stomata to maintain water potential during periods of drought halting C uptake.

An enduring hypothesis suggests that reduced photosynthesis during these periods constrains *de novo* defense production leading to increased susceptibility to TKBB (described in Malone et al. 2025). However, the timing of defensive responses may be more critical than their magnitude. Mass attacks (TKBB) on individual trees typically occur over a few days, and only rarely extend to weeks, requiring trees to mount rapid defenses to survive. The speed of response depends on whether defenses rely on locally available resources, mobilization of stored reserves, or *de novo* synthesis. In pinyon pine (*Pinus edulis*), induced defensive responses (initiated in response to attack and thus lagged) produced an order of magnitude more terpenes at attack sites than could

be accounted for by local reserves alone, indicating substantial mobilization of stored resources (Thompson et al. 2024). However, tree survival was more strongly associated with the *rapidity* of constitutive defenses (immediate responses by pre-existing resin). Trees that maximized constitutive resin flow within 24 hours survived even with low terpene concentrations, whereas trees that produced higher terpene levels over longer periods were more susceptible. These findings suggest that trees predisposed to pre-attack investment in constitutive resin, a trait likely to have a genetic basis, have a survival advantage and incur lower physiological costs (Thompson et al. 2024).

Temperature also influences defensive chemistry. In pinyon pine, drought alone elicited a transient increase in monoterpene concentrations. In contrast, the combined effects of heat and drought produced sustained increases in monoterpenes that persisted for multiple growing seasons (Trowbridge et al. 2021).

Water and carbon dynamics must also be considered jointly. Phloem transport of carbon is driven by hydrostatic pressure generated through the xylem water supply, and adequate turgor pressure in resin duct epithelial cells is essential for effective resin exudation at sites of beetle entry. Consequently, impaired water relations that reduce turgor pressure may lead to diminished resin flow and weakened defense capacity (Malone et al. 2025).

Most research on the effects of drought on tree defenses and susceptibility to TKBB has been done in moisture-limited forests. Information on how drought influences trees that grow under, and are likely adapted to, energy limitation is mostly lacking. In these forests precipitation typically exceeds demand and growth is constrained by short cool growing seasons. However,

with climate change, water limitation may increasingly affect these forests. For example, Dudney et al. (2023) found subalpine whitebark pine in California's Sierra Nevada now alternate between energy and water limitation depending on degree of heat and drought. Additionally, in recent years, drought has been linked to widespread mortality of high elevation whitebark pine from mountain pine beetle (Buotte et al. 2016).

How drought influences susceptibility in energy-limited pines is just beginning to be studied.

Kichas et al. (2023) found whitebark pine increased growth and resin duct area in response to warmer temperatures and that Palmer drought severity index values (PDSI - a measure of cumulative soil dryness in comparison with the mean) were often positively correlated with increased rather than decreased growth as is typically seen in moisture-limited systems. A climate-dendrochronological study conducted in whitebark pine at three cool, arid sites and two warmer, mesic sites found growth increased as conditions warmed (Alverson and Six 2026) and, while each population experienced several droughts, only severe hot droughts reduced growth. More typically, reductions in precipitation accompanied by elevated temperatures resulted in increased growth suggesting thermal inputs outweighed moisture constraints. Interestingly, during the most recent drought, outbreaks of mountain pine beetle only occurred at the cooler arid sites where tree growth was positively correlated with more negative PDSI values. No outbreaks occurred at the hottest sites, including the only site where trees exhibited decreased growth with increased drought severity (Alverson and Six 2026). These results contrast with observations in low elevation water-limited systems where drought severity is often correlated with slower tree growth and greater mortality due to TKBB (Knapp et al. 2013; Creeden et al.

2014; de La Mata et al. 2022). These disparities may reflect fundamental differences in tree physiological processes in high- and low- elevation systems.

Conifers exhibit drought resistance (ability to withstand drought exposure) or drought resilience (ability to recover after drought). Drought resistance involves stomatal control, patterns of root and shoot growth that affect a tree's ability to reduce drought damage, xylem morphology, the production of protective molecules, carbohydrate metabolism, and defense responses (Moran et al. 2017). Drought resilience involves the ability to recover photosynthesis and other processes, including the ability to refill xylem after cavitation and to repair structural damage. Neither of these traits have simple underpinnings. Resistance and tolerance are controlled by many genes that vary considerably among taxa (Moran et al. 2017). Interestingly, some long-diverged conifers (*Picea* and *Pinus*) express convergent local evolution for resilience to temperature and drought based on a large, shared suite of genes. However, each genus also exhibits heterogeneous non-convergent responses at many other genes likely due to local adaptation to other factors (Yeaman et al. 2014) highlighting the need to consider that long-lived trees need to adapt to many different conditions and stressors across complex environments.

Adding to this complexity, conifers show considerable local adaptation and within-population variation in responses to heat and/or drought. Variability within species should not be surprising. Most species have occupied areas with vastly different climates over lengthy periods of time and adaptation to prevailing conditions would have been common. This adaptation extends into current times. Common garden studies growing trees from seed collected over their ranges have shown time and again that local adaptation is frequent across elevational and moisture gradients

and at small geographic scales (Rehfeldt 1989; Cobb et al. 1994; Kolb et al. 2016). Additionally, many trees are currently constrained to a realized niche that may be much smaller than their fundamental niche because of competition, pathogen pressure, human activities, and many other factors. This suggests trees carry many alleles useful under climatic conditions other than those that occur in their current range (Iglesias et al. 2015).

The microbial partners

Conifers and TKBB do not operate alone but with diverse microbiomes. These microbiomes consist primarily of fungi and bacteria that can be beneficial, neutral, or antagonistic. Some are incidental and transient while others are omnipresent. Here, I discuss those we know best and are most likely to influence beetle and tree fitness and adaptive capacities under climate change.

TKBB microbiomes

The filamentous fungi are the best studied of the TKBB microbiome. The beetles acquire an array of fungi on their exoskeleton as they leave their natal host and introduce them into the new tree where their brood will develop. Many of these fungi are common species ubiquitous in the dead wood environment and include saprotrophs, mycoparasites, and entomopathogens (Kandasamy et al. 2019; Mann and Davis 2021). Others comprise a mix of beetle-associated commensals (saprotrophs and necrotrophs, often Ascomycota in the Ophiostomatales) that

opportunistically exploit several bark beetle species as vectors and whose incidence varies by geographic location, temperature, and host tree species (Six et al. 2026 and references therein).

The fungi of most interest here are the mutualists. All western TKBB have 1-3 specific mutualist fungi that are transported in specialized structures of the adult exoskeleton called mycangia that ensure vertical transmission from generation to generation (Six 2012). Most fungal mutualists of TKBB are Ophiostomatales. Some are saprotrophs while others are necrotrophs that can grow into and kill living tissue and metabolize tree terpenes and phenolics, although the specific compounds they degrade vary by species and even by isolate (DiGuistini et al. 2011; Hammerbacher et al. 2013; Zhao et al. 2019). Of our western TKBB, only western pine beetle has Basidiomycota mutualists that can degrade cellulose and lignin (Six 2020b).

Benefits to the fungi start with transport to an appropriate host tree species via the beetle mycangium. Gallery construction by adult beetles for egg laying also supports dissemination of the fungi within the tree while increasing oxygen and reducing moisture supporting growth of the fungi and early instars alike (Adams and Six 2007; Bleiker and Six 2007). Once larvae mature, the chambers they excavate for pupation create space within the phloem for the formation of fungal fruiting structures in proximity to new adult beetles. This proximity ensures spore acquisition in the beetle mycangia and transport of the fungi to a new tree and next generation of beetles (Six and Paine 1998; Bleiker and Six 2007; Addison et al. 2013).

Importantly, the fungi redistribute nutrients within the tree. The fungi begin growth in phloem but then move into the ray parenchyma of the sapwood where they forage for sugars, simple carbohydrates, and amino acids. This supports the acquisition and then translocation of nitrogen

(N), phosphorus (P), and non-structural C to the phloem to maintain older mycelium and later for production of reproductive structures and spores in pupal chambers. The translocation of elements from sapwood to phloem by the fungi to support their own needs creates the by-product effect of providing these same nutrients to larvae feeding on phloem containing fungal hyphae. While many fungi translocate nutrients to support various functions occurring in different parts of their mycelium (Lindahl et al. 2001; Schmieder et al. 2019; Bullington et al. 2026), the mutualistic fungi excel at nutrient delivery (Six and Elser 2020) and invest more heavily in the production of spores. Newly eclosed adults feed on spores, an activity that supports both beetle reproduction (e.g., mountain pine beetle does not produce eggs without spore feeding (Six and Paine 1998) and packing of mycangia for fungal dispersal (Addison et al. 2013). Without their mutualistic fungi, beetles produce few to no young and larval development, when it does occur, can be prolonged resulting in small offspring with low fitness (Barras 1973; Six and Paine 1998; Kopper et al. 2004). Mutualist fungi that metabolize tree-produced terpenes and phenolics use them as carbon sources (Hammerbacher et al. 2013; Wadke et al. 2016 Apr 22; Zhao et al. 2019). This process, when it targets compounds that act as tree defenses, can be beneficial to both fungi (as food/energy) and beetles (via detoxification).

In each mutualism, the nutrient demands of the beetle have been molded by host tree quality, fungal capabilities and efficiencies, and beetle life history. For example, the mountain pine beetle packs into living trees in high densities during mass attacks. High larval densities could lead to strong intra-specific competition if larvae had to rely on phloem alone to meet nutritional requirements. Instead, each larva constructs a relatively short feeding gallery and its mycangial fungi subsidize its diet with 33-40% more N than found in phloem alone (Six et al. 2025). In

contrast, the pine engraver has high requirements for both N and P. Its fungus provides high amounts of P but only moderate amounts of N which the beetle appears to acquire via high consumption of phloem (Six and Elser 2020).

The western pine beetle is radically different in that it develops mostly in dead and extremely nutrient poor outer bark and has obligate Basidiomycota and Ascomycota mutualists (Six and Elser 2019; Araújo et al. 2021). Its fungi move virtually all P and most N from the large volume of sapwood to the larvae feeding on fungal layers in chambers in the outer bark (Six and Elser 2019). The basidiomycete also degrades cellulose and lignin and may contribute C to developing larvae (Six 2020b). Despite the high efficiency of its mutualists, P remains relatively low in the beetle's diet. To contend with this, the beetle appears to have evolved a very low P requirement (Six and Elser 2019).

Mutualisms of fungi and tree-killing bark beetles (TKBB) depend on substantial phenological overlap to persist and function over time (Addison et al. 2015). Temperature is the primary factor governing alignment between beetles and their fungal symbionts at critical life stages. Fungal partners appear to be especially constrained by thermal conditions. In systems with a single mutualist (e.g., spruce beetle, *Dendroctonus rufipennis*), the thermal tolerance of the fungus likely circumscribes the ecological amplitude of the host beetle. In contrast, associations involving multiple fungi may broaden this amplitude. For example, the mountain pine beetle associates with three fungal species whose thermal niches overlap but differ in optima and range: two are adapted to cooler conditions, whereas a third tolerates higher temperatures (Six and Bentz 2007).

Variation in thermal tolerances among fungal symbionts also influences their within-tree dynamics, including growth rates, resource capture, and the proportion of beetle brood (and eventual vectors) contacted. It further determines which fungi sporulate in pupal chambers and are subsequently acquired in mycangia for transmission to the next generation (Addison et al. 2013). This is important because fungal partners differ in the benefits they confer. In the mountain pine beetle system, fungi adapted to cooler temperatures support greater brood production and larger offspring than the warm-adapted species (Bleiker and Six 2007). Consequently, temperature-driven shifts in fungal prevalence can alter beetle fitness across seasonal, annual, and geographic scales.

The strong influence of temperature highlights a central vulnerability of these mutualisms: dependence entails risk. Elevated temperatures can slow fungal growth, reducing nutrient provisioning to larvae. Heat can also disrupt sporulation, limiting or preventing spore production during the critical period of maturation feeding and mycangial loading by emerging adults (Addison et al. 2015). Failure to feed on spores may reduce or eliminate beetle reproduction (Six and Paine 1998), while failure to transmit fungi to the next tree risks starvation of subsequent brood (Six et al. 2025). Thus, in areas that warm considerably, some mutualisms may begin to decouple with negative effects on population growth and persistence.

Yeasts (predominantly single-celled fungi) and bacteria make up the bulk of the remainder of the TKBB microbiome. Studies have identified a loose core yeast microbiome (Rivera et al. 2009; Vazquez-Ortiz et al. 2025) and a core bacteriome for *Dendroctonus* (Morales-Jiménez et al. 2012; Boone et al. 2013; Morales-Jiménez et al. 2013; Mason et al. 2016; Briones-Roblero et al.

2017; Hernández-García et al. 2018; Durand et al. 2019) and *Ips* (Chakraborty et al. 2020).

Further study is needed to determine their influence on host beetles.

Conifer microbiomes

Every above and below ground organ of a tree is populated by microbes at the time of beetle entry. These microbes often occur as a mosaic of pathogens, saprophytes, and endophytes of unknown trophic type. Unfortunately, most studies on microbiomes of conifers have focused on foliar and root tissues and not on the phloem and sapwood where TKBB and their fungi live and forage (Rodriguez et al. 2011). However, knowledge of tree microbiomes in general may help inform us on their effects on TKBB and their host trees. For example, plant mycobiomes (the fungal component) can protect against invading fungi and insects and alter herbivore performance (Sumarah et al. 2008; Bizjak et al. 2023). In above-ground tissues, fungal endophytes can induce host defenses (Mejía et al., 2014) and inhibit pathogenic fungi (Bullington et al. 2024). Below ground, ectomycorrhizal fungi can enhance nutrient uptake and enhance defense against pathogens and insects by inducing terpene production (Bullington et al., 2024). Drought and high temperatures can trigger latent pathogen growth (Blumenstein et al. 2021) and reduce root colonization and diversity of ectomycorrhizal fungi (Gehring et al. 2020) altering tree nutrient uptake, storage, and defensive capacity. Some endophytes fix N (Moyes et al. 2016; Puri et al. 2018; Bizjak et al. 2023) which may increase its availability to TKBB and their fungi. Variations in these microbiomes among trees and populations may influence tree

adaptation by alleviating or exacerbating responses to changing environmental conditions and disturbance.

Only two studies have examined conifer mycobiomes before and after colonization by bark beetles and their fungal symbionts. Both Skelton et al. (2019) and Bullington et al. (2026) reported diverse endophytic fungal communities in pines prior to beetle attack, and an increase in fungal diversity following colonization. In both cases, resident endophytes were largely displaced by beetle-associated fungi while some persisted as saprotrophs in beetle-excluded logs. Bullington et al. (2026) found fungal turnover was high in both colonized and uncolonized logs, but community composition diverged markedly between treatments, with beetle-colonized logs exhibiting significantly greater sapwood density loss. Bark beetle colonization also altered nutrient distributions within host tissues, enriching C, N, and P in the phloem while reducing N in the sapwood. Together, these findings indicate that beetle–fungal introductions not only restructure resident microbial communities, but also redirect community assembly trajectories, with cascading consequences for wood decay dynamics and carbon cycling.

Bark beetles as forest ecosystem engineers

TKBB are ecosystem engineers (Przepióra and Ciach 2025), organisms that modify physical environments in ways that influence ecosystem structure and species persistence (Jones et al. 2010). Their engineering effects operate across both non-outbreak and outbreak phases. By creating spatially heterogeneous patches of mortality—from single trees to large stands—TKBB generate canopy gaps that alter microclimatic conditions and increase landscape heterogeneity.

These openings enhance light and moisture availability, promoting microbial activity, nutrient cycling, and understory productivity. Increased understory complexity supports diverse assemblages of birds, insects (including pollinators, Davis et al. 2020), and other invertebrates, and provides habitat for edge- and open-area-dependent species and those associated with early successional habitats (Beudert et al. 2015). Changes in hydrology and biogeochemistry often include elevated soil nitrogen that can persist for years, facilitating regeneration and recovery (Boggs Lynch et al. 2021).

The ecological influence of TKBB extends to the creation of deadwood legacies. Beetle-killed trees, both standing and fallen, generate structurally complex substrates that support abundant tree-related microhabitats (TreMs) and diverse biotic communities (Przepióra and Ciach 2025). Deadwood is a major driver of productivity and biodiversity in TKBB-adapted conifer forests (Müller et al. 2010), providing habitat and resources for a wide range of organisms, including invertebrates, fungi, bryophytes, and lichens. It supplies nesting sites for birds and bats, functions as nurse logs for regeneration, and contributes to nutrient cycling, including inputs of N and P (Przepióra et al. 2020). Notably, TKBB preferentially kill larger-diameter trees which host the greatest diversity of TreMs, support higher biodiversity, and persist longer, sustaining habitat complexity over extended decay trajectories.

Outbreaks also leave a legacy of surviving trees. In structurally heterogeneous forests, many trees persist following TKBB disturbance, including genetically resistant individuals, smaller mature trees below preferred diameter thresholds, saplings, and seedlings (Six et al. 2021). These residual structures facilitate rapid recovery from a “pre-existing” resilient forest template (Olsen

et al. 1996; Collins et al. 2011; Diskin et al. 2011; Kayes and Tinker 2012). Because only a subset of trees (of the preferred size and age, and likely genotype) becomes susceptible at any given time, this structure dampens the severity and spatial extent of subsequent outbreaks (Diskin et al. 2011; Donato et al. 2012; Seidl et al. 2016; Sommerfeld et al. 2021). It also maintains genetic heterogeneity, contributing to adaptive capacity. The resulting mosaic of early- and late-seral conditions maximizes landscape-level biodiversity and resilience.

Finally, the selective nature of bark beetle outbreaks contributes directly to forest evolution. By selectively removing trees that are poorly adapted to current conditions and/or highly susceptible to attack, TKBB act as agents of natural selection. Each outbreak can shift population genetic structure, effectively accelerating adaptation in a stepwise manner. Thus, the role of TKBB as ecosystem engineers extends beyond immediate ecological effects to influence long-term forest resilience, structure, and evolutionary trajectories.

TKBB are primary agents of disturbance and selection in conifer forests, shaping successional trajectories and forest evolution. Despite this, their ecological functions are often overlooked and underappreciated. Instead, they are commonly treated only as pests and targeted for broadscale suppression. However, as demonstrated for fire in western forests, suppression of natural disturbance can disrupt key ecological and evolutionary processes (Rogers 1996). In the context of rapid environmental change, natural disturbances including TKBB, and the evolutionary dynamics they sustain should be recognized as integral components of ecosystem resilience and adaptation.

649 **Management to support adaptation in complex evolving forests**

650 A major goal of forest management is often to prevent or dampen disturbance rather than to
651 foster the key ecological processes, including natural disturbance. Most forest management plans
652 include suppressive active management followed by replanting programs meant to speed forest
653 regeneration or control forest successional trajectories. For example, the USDA Forest Service
654 “Forest Health Protection (FHP) staff works to protect America’s forest and tree resources from
655 damaging outbreaks of forest insects” (USDA FS 2026) and the National Forest Foundation
656 supports large planting efforts on public lands after bark beetle outbreaks (NFF 2026). These
657 approaches often do not support adaptation and can impede forest survival in the long run. To
658 understand why requires us to look at forests in a different way.

659 A good starting point is to consider how we view the trees themselves. In traditional silviculture,
660 trees of the same species are often regarded as relatively homogenous entities, varying primarily
661 in size, age, health, and spacing within a stand. Each tree is expected to respond predictably to
662 shifts in the environment including changes in nutrients, moisture, temperature and competition.
663 Silvicultural treatments can be applied to remove inferior trees (from a human perspective, e.g.,
664 exhibiting traits such as low stature or slow growth), to reduce competition, encourage vigorous
665 growth, produce a desired distribution of size classes and spacings, and to reduce the potential
666 for natural disturbances such as bark beetle outbreaks (Nyland 1996). Success may be measured
667 as an increase in growth rate, greater drought tolerance, and a lack or dampening of bark beetle
668 activity. In contrast, from the ecological/evolutionary perspective, a tree species is viewed as a
669 diverse collection of individuals with a variety of genotypic and phenotypic trait expressions and

high standing genetic diversity. Genetic sub-structuring is expected due to differential selection from stage/age specific selection pressures. Evolutionary change (adaptation) is seen as an ongoing response to manifold pressures over the long term, including natural disturbances, climate, and shifts in interactions with other members of the biotic community that are themselves responding and adapting to change. Natural selection is expected to remove trees that are less adapted to their current abiotic and biotic environment. For instance, slower growing stout trees with less demand for water may be better adapted than fast growing trees in some places. Ecological-evolutionary management would tend toward being passive or semi-passive, allowing natural selection to cull genetically inferior trees, shifting allele frequencies towards combinations better suited to local and new conditions. Thus, in traditional silviculture, humans choose the trees that live or die, whereas in an ecological-evolutionary approach natural selection is the acting agent. This difference is not trivial.

Thinning is a means by which trees are removed from a forest naturally or artificially via human actions. Self-thinning (a type of natural thinning) reduces density over time due to competition and maladaptation. The self-thinning rule relates plant mass to plant density and applies across the plant kingdom; populations decline in a density-dependent manner until they stabilize near carrying capacity (Li et al. 2000). Natural thinning also occurs when pathogens, insects, or drought remove damaged or genetically susceptible trees. This is a particularly active process during seedling and sapling stages but affects older trees as well.

While natural thinning supports natural selection and fosters genetic resilience, artificial thinning can reduce genetic resilience and dampen the intensity of natural selection depending on the

type, severity, frequency, and tactics and strategy of the thinning treatment (Schueler et al. 2021; Godineau et al. 2023). Artificial thinning can target young trees in the understory or older trees in the overstory or a mix of the two. It may be light or heavy and may be done once or repeatedly. It can be indiscriminate or selective for or against trees with particular traits. Each of these approaches affects stand trajectories, genetic diversity and structure, and consequently the potential for long-term adaptation. When thinning is intense, adaptation can be slowed in several ways. For example, relaxation of competition for water relieves selection pressure against trees with low drought tolerance maintaining them and their genes in the breeding population. The arbitrary removal of trees is as likely to remove trees with the best gene combinations as those with inferior genotypes and can lead to a loss in genetic diversity directly via the loss of rare alleles and indirectly through genetic drift (Danusevicius et al. 2016).

Thinning is widely applied in conifer forests as a broad strategy for fuels reduction, restoration, and mitigating insect impacts, and is increasingly promoted as a climate adaptation tool by reducing competition for water (e.g., Sankey and Tatum 2022). Meta-analyses and recent studies generally report positive short-term effects of thinning on tree growth and drought response (Sohn et al. 2016; Chagnon et al. 2025), leading to recommendations for its use in drought adaptation. However, these studies do not directly address adaptation. Although trees often show increased vigor after thinning, this response is transient as faster growing and larger trees demand more water (D'Amato et al. 2013). While beneficial for short-term wood production, increased growth and leaf area may be maladaptive under drier conditions. Thinning can also elevate evapotranspiration by increasing solar radiation and wind exposure (Lagergren et al. 2008; Brooks and Mitchell 2011). Accordingly, thinning may function only as a short-term

measure (Chagnon et al. 2025) and could even hinder long-term adaptation by reducing natural selection against drought sensitivity and genetic diversity.

Exploiting the genetic basis of drought tolerance or resistance in trees is appealing, but it is important to recognize that tree responses to drought are complex and highly context dependent and often involve polygenic traits. Populations within a species frequently differ in their performance under drought, and even a single population may respond inconsistently across drought events. This variability is partly driven by genetic diversity but also the timing of drought relative to seasonal phenology and developmental stage (Schueler et al. 2021) (Depardieu et al. 2020; Six et al. 2021; Alverson and Six 2026). Drought characteristics, including duration, intensity, and frequency, also strongly influence tree survival and response, yet they are underrepresented in empirical studies which often focus on recovery from single events.

Natural thinning during drought, often mediated or amplified by bark beetles, can act as a selective filter that disproportionately removes drought-sensitive genotypes (Depardieu et al. 2020). In this context, TKBB function as agents of natural selection, accelerating the loss of poorly adapted individuals and reinforcing evolutionary processes. In contrast, artificial thinning is largely nonselective. Even when final stand densities are similar, artificially thinned stands may retain a higher proportion of drought-sensitive genotypes and exhibit reduced drought resistance over time. These dynamics underscore how drought and bark beetle disturbance interact to shape forest structure, genetic composition, and adaptive capacity, reinforcing the role

of TKBB as both ecosystem engineers and positive agents of selection under changing climatic conditions.

Recent simulation studies provide evidence that silvicultural interventions alter evolutionary trajectories. Godineau et al. (2023) found that artificial thinning reduced the evolution of tree vigor depending on its frequency and intensity and reduced genetic variability by as much as 84%. In contrast, stands undergoing self-thinning under natural selection showed continuous increases in mean vigor both within and across generations. Fririon et al. (2024) used simulation experiments integrating forest dynamics (growth, competition, drought, and regeneration) with genetic variation in quantitative traits to assess long-term adaptation. They found that thinning reduced natural selection pressures from both competition and drought relative to unthinned stands. Increasing thinning intensity further weakened selection against drought sensitivity, potentially hindering long-term adaptation. Avoiding early thinning promoted natural selection, resulting in improved stand performance while maintaining long-term evolvability. Overall, natural selection produced more favorable outcomes than silvicultural treatments aimed at reducing drought stress. Notably, more severe drought increased genetic gains for reduced drought sensitivity but decreased gains for vigor, revealing an antagonistic relationship between these traits. This tradeoff may be adaptive when rapid growth, which demands higher water availability, is disadvantageous. These findings highlight how management practices that favor one trait (e.g., rapid growth) may inadvertently constrain adaptation in complex environments. Collectively, they suggest that human interventions that dampen natural selection may lead to long-term erosion of tree fitness.

A growing body of evidence from the field suggests biomass removal through thinning or harvest alters forest genetic structure and, consequently, adaptive capacity. For example, shelterwood cutting in western hemlock significantly reduced both observed and expected heterozygosity compared to uncut stands (El-Kassaby et al. 2003). In white pine, phenotypic selection cuts increased inbreeding and genetic drift (Finkeldey and Ziehe 2004). Similarly, white spruce stands subjected to a 75% reduction cut had 25% fewer genes, 33% fewer polymorphic loci, and an 80% reduction in rare alleles compared to untreated stands (Rajora 1999). Danusevicius et al. (2016) also found that thinning in Scots pine (*P. sylvestris*) led to the loss of rare alleles when more than 30% of trees were removed.

The long-term effects of tree removal on forest adaptability remain uncertain, but available evidence suggests they may be substantial. Schaberg et al. (2008) compared genetic diversity in unmanaged eastern hemlock stands with those subjected to selection cuts over 40 years. Harvested stands contained fewer rare alleles and lower genetic multiplicity than unthinned controls. When large trees were removed, most rare alleles declined, although some increased in frequency, possibly because they were associated with slower-growing individuals that became proportionally more common after harvest.

Rare alleles are particularly important. Although some may be rare due to selection against them under current conditions, they can represent a critical reservoir of genetic diversity to support adaptation under changing environments (Schaberg et al. 2008). Their conservation value should not be overlooked, especially in the context of climate change. It is often assumed that high pollen dispersal ensures sufficient gene flow to offset localized losses of genetic diversity due to

thinning or harvest (Hamrick 2004). However, gene flow in conifer forests is often more limited than widely believed. While pollen can travel hundreds of kilometers, its effective reproductive success at such distances is often low due to phenological mismatches and competition with local pollen (Smouse et al. 2001). Effective pollination more commonly occurs over tens to hundreds of meters (Smouse et al. 2001; Rajora et al. 2002; Robledo-Arnuncio et al. 2004; Savolainen et al. 2007). In addition, many western forests now lack nearby uncut, unmanaged stands that could serve as sources of genetic diversity.

Tree additions can also alter forest adaptation. Artificial regeneration via plantings with seeds or seedlings from a non-autochthonous source can introduce new genetic diversity but comes with a risk of restricting the genetic base, swamping local adaptation, and introducing maladaptive genotypes that can hinder or reverse adaptive processes and spread through neighboring populations with broadscale long-term negative consequences (Ledig 1992; Aravanopoulos 2018). The literature on the negative effects of artificial regeneration and ‘offsite planting’ is rich in examples of adverse effects. To avoid such problems, seed zones have been developed for many tree species. The zones are meant to reflect natural genetic diversity and structure but only some are empirically based. For many, assignments are provisional and based on the expectation that similar climate equals similar genetic diversity and structure (Ledig 1992). Because populations of trees diverge at much smaller scales, seed zones can result in the use of poor substitutes for local seed.

The threat of inappropriate seed sources or extensive artificial regeneration is not trivial. The amount of planting that occurs in response to fire, insect outbreaks, and harvest is immense. A

recent publication reports that in the western US the replanting potential is approximately 24 million ha and would require 7.5 billion seedlings (Fargione et al 2021). Although only an estimated 15-20 percent of what is considered needed is typically achieved annually (Dumroese et al. 2019; Fargione et al. 2021), this still constitutes a massive number of seedlings being placed into forest environments. The seed to support these efforts may be sourced locally or in seed zones but even when seed is appropriately collected, nursery practices and the planting process circumvent the initial environmental (primarily climatic) filters that occur during germination and seedling establishment (Schlesselmann et al. 2025). Further, recommendations have been made to prioritize collections in areas at risk of large-scale fire or insect outbreaks (Kildesheva et al. 2023). Planting seeds post-outbreak that were collected pre-outbreak could potentially swamp any adaptation resulted from selective mortality due to TKBB while potentially narrowing the genetic base depending on collection methodology. Further, many bark beetle-affected stands are also salvage logged prior to planting which often includes removal of many or all green tree survivors. This combination of artificial regeneration and removal of resistant survivors that would otherwise act as ‘adapted’ seed sources could effectively result in a preponderance of less adapted genotypes.

Planting may also be done with genetically “improved” stock. “Improvement” can refer to traits such as enhanced wood quality, faster growth, or increased resistance to pathogens. However, directional selection for specific traits, combined with the use of limited breeding stock or seed sources, can substantially reduce genetic diversity (Vallejo-Reyna et al. 2024). In addition, phenotypic plasticity—and the genetic variation that underlies it—is often considered undesirable in improved trees which are expected to express target traits uniformly. Improved

trees also tend to have a simpler genetic architecture for the selected trait compared to natural populations. For example, drought tolerance is being considered for tree improvement programs but is often polygenic, arising from the cumulative effects of many genes and their interactions (Depardieu et al. 2020). Consequently, simplifying its genetic basis may not capture the full adaptive potential required under variable environmental conditions. Currently, marker-assisted selection, gene editing, and gene silencing can only target one or a small number of genes (Ahmar et al. 2021; Li et al. 2024).

Assisted migration is increasingly proposed as a climate adaptation strategy (Ste-Marie et al. 2011). This can involve assisted gene flow – the introduction of non-local genes into existing populations to increase climate-adaptive genetic diversity (Xu and Prescott 2024). This can be done by relocating trees (Aitken and Whitlock 2013), using composites of seeds from multiple sources (Aitken and Bemmels 2015), or introducing pollen (Chludil et al. 2025) within a species' current range. These approaches require balancing gene flow with the risk of introducing maladaptive genes and swamping local adaptations and depend on accurate climate predictions—knowledge that is currently limited. While assisted gene flow may offer benefits in rapidly changing environments, it warrants considerable caution.

Assisted migration can also involve moving a tree species to new areas expected to remain or become suitable (McLane and Aitkin 2012). However, introducing non-native trees can disrupt recipient ecosystems, add stress to already vulnerable native forests, and risk invasiveness, as seen with several conifers in South America (Ricciardi and Simberloff 2009; Fuentes-Ramirez et al. 2024). This type of assisted migration also moves species without their associated ecosystems

unless done at range edges where coincident migration of other associated organisms is more likely.

Effects of Management for TKBB on Forest Adaptation

Active management for tree-killing bark beetles (TKBB)—including sanitation logging, insecticide application, and widespread tree removal before, during, and after outbreaks—is commonly justified as necessary to protect timber resources (Six et al. 2014). However, these interventions are often ineffective and do more than alter forest structure and function: they disrupt coupled ecological and evolutionary processes that underpin forest adaptation (reviewed in Six et al. 2014). Because TKBB are a central focus of management in conifer forests, efforts to control them exert a disproportionate influence not only on disturbance regimes and forest trajectories, but also on the strength and direction of natural selection. Across much of the managed landscape, repeated intervention effectively replaces disturbance-driven selection with human-imposed selection, fundamentally altering eco-evolutionary dynamics (Lindenmayer et al. 2025).

Management treatments are often predicated on the assumption that outbreaks arise from “unhealthy” forests. However, outbreaks are better understood as emergent eco-evolutionary events. TKBB populations persist at low, endemic levels for extended periods, even in forests with abundant suitable hosts in conditions often classified as “unhealthy” (e.g., dense or late-successional stands). Irruptive (not cyclic) outbreaks only occur when interacting thresholds—temperature, host defense capacity, and beetle reproductive success—are exceeded (Bentz et al.

2010). Climatic triggers, particularly warm drought, often initiate these dynamics, although population amplification may lag. Once thresholds are surpassed, outbreaks can become self-sustaining until susceptible hosts are depleted or abiotic conditions shift (Bentz et al. 2010). In this framework, outbreaks represent episodic pulses of strong selection embedded within broader ecological dynamics.

Climate plays a dual role in shaping these eco-evolutionary processes. Warm drought simultaneously enhances beetle performance and constrains host defenses, generating positive feedback that accelerates population growth and attack success. Tree responses to climatic conditions and their defenses vary genetically, and beetle attack is correspondingly non-random. Individuals with less effective or poorly timed defenses are more likely to be colonized and killed, whereas those with more effective defenses or greater drought tolerance or resistance are more likely to survive. As a result, outbreaks act as density-dependent selective filters that restructure populations. Survivors represent a non-random subset of genotypes with heritable traits linked to resistance (Millar et al. 2012; Six et al. 2021), and regeneration from these individuals can shift population-level trait distributions. Repeated outbreaks thus couple ecological disturbance with evolutionary change.

Pre-emptive management strategies—including thinning, daylighting (removal of vegetation around trees to increase light on the mainstem), conversion to non-host species, and preferential removal of large trees—are typically designed to reduce short-term susceptibility but with little consideration of their effects on these eco-evolutionary dynamics. In doing so, they often function as mechanisms of *selection override* (Figure 2), weakening or redirecting selective

pressures imposed by beetles and climate. Daylighting, for example, is hypothesized to deter beetles by altering microclimate and pheromone signaling yet lacks empirical support. However, if it is effective at reducing successful attacks, it may dilute selection on host defenses. Removal of large trees can reduce host availability but may also disproportionately eliminate individuals that have survived prior disturbance events and therefore may carry adaptive trait combinations. Thinning provides a particularly clear example of the divergence between management intent and evolutionary consequences. Although thinning sometimes reduces mortality under non-outbreak beetle populations, its effects under outbreak conditions are weak and inconsistent (reviewed in Six et al. 2014). More fundamentally, thinning replaces beetle-driven selection with human selection based on criteria such as size, spacing, or perceived vigor—traits not reliably associated with resistance to beetles or drought. In this way, thinning decouples survival from the traits under selection during outbreaks. Moreover, thinning frequently removes more trees than beetles or leaves behind a similar density (Six and Skov 2009; Hansen et al. 2010), but creates a distribution of age classes and genotypes different than would result from natural selection. Beetle-caused mortality is typically partial, leaving behind a structurally intact and genetically filtered cohort. Untreated stands therefore retain both the demographic and evolutionary legacies of disturbance, whereas treated stands may be reset in ways that slow both ecological recovery and adaptive change. Direct control measures applied during outbreaks—such as insecticide application, sanitation cutting, and fell-and-burn—further illustrate the consequences of selection override. While these approaches may protect individual trees or small areas, they are rarely effective or even possible

at landscape scales because they do not address the climatic drivers of outbreaks (reviewed in Six et al. 2014). From an evolutionary perspective, as with thinning, they can act to preserve genotypes that would otherwise be removed by selection, thereby reducing the intensity of selection and potentially increasing future population susceptibility.

Post-outbreak management extends these effects. Salvage logging often removes both dead and surviving trees, including individuals that resisted/repelled attack and thus represent the outcome of recent selection. This practice can disproportionately eliminate adaptive genotypes and truncate the transmission of those traits to subsequent generations. Replanting further modifies evolutionary trajectories, particularly when it relies on limited genetic stock or non-local seed sources, potentially disrupting locally adapted gene complexes. In contrast, natural regeneration following outbreaks is derived from the surviving population and is therefore enriched for traits that confer resistance to contemporary stressors. It also results in environmental filtering and avoids the influences of nursery selection. Salvage logging also removes biological legacies—forest soil, snags, coarse woody debris, and microsite heterogeneity—that shape the selective environment for regeneration and maintain a diverse biotic community.

Beyond their uncertain efficacy in reducing beetle impacts, active management treatments can consistently shift forests toward simplified, homogeneous structures. This homogenization reduces environmental heterogeneity and, consequently, the diversity of selective pressures acting on populations, limiting the potential for adaptive responses across variable conditions. Logging-related disturbances, including soil compaction and loss of advanced regeneration, further constrain regeneration pathways. Active management and salvage logging may also

increase short-term carbon emissions relative to natural recovery, altering climate–forest feedback that influences future selection regimes (reviewed in Lindenmayer et al. 2025).

In contrast, unmanaged forests maintain the coupling between ecological and evolutionary processes. Natural disturbances generate spatial and temporal heterogeneity, creating a mosaic of selective environments. Partial mortality during outbreaks preserves a genetically filtered cohort of survivors, which serve as the foundation for regeneration under shifting climatic conditions. In this context, bark beetles function not only as disturbance agents but also as agents mediating adaptation to interacting stressors such as drought and warming.

Framed in this way, management choices can be viewed along a continuum from *selection alignment* to *selection override*. Figure 2 illustrates the extremes of this continuum, although most contemporary forests and management approaches fall somewhere between them. As the climate continues to warm, the potential for *in situ* adaptation will increasingly be constrained. Even if the pace of climate change slows, active management may be needed in some places to sustain functional forests. The challenge, therefore, is not simply whether to intervene, but when intervention is appropriate, how to intervene in ways that best preserve adaptive processes.

Management actions that allow beetle-driven and climate-mediated selection to proceed can help maintain eco-evolutionary feedbacks and, in turn, long-term adaptive capacity. In contrast, interventions that broadly suppress mortality, homogenize forest structure, or replace locally derived regeneration with externally selected stock can disrupt these feedbacks and potentially increase vulnerability over time. A growing body of evidence suggests that, although bark beetle outbreaks can conflict with short-term human objectives, allowing outbreaks to function as both

ecological and evolutionary processes can contribute to long-term forest resilience and continuity (Collins et al. 2011; Six et al. 2021; Sommerfield et al. 2021; Przepióra and Ciach 2025).

Accordingly, suppression may be most appropriate when targeted to high-value areas—such as campgrounds, residential zones, and intensively managed commercial forests—while management across broader landscapes seeks to align with, rather than override, natural selection.

Selection alignment does not imply an absence of management. Treatments may be necessary in forests altered by fire suppression, repeated timber extraction, or other legacies of intensive management. In these cases, explicitly considering how fuels treatments and restoration strategies influence genetic diversity, selective pressures, and opportunities for regeneration could help maintain or increase adaptive capacity. Incorporating these considerations *a priori* into treatment design and implementation may allow even intensive restoration to better align with ongoing evolutionary processes rather than inadvertently constrain them.

Ultimately, however, selection-aligned management cannot compensate indefinitely for continued climate change. If warming is not addressed directly, climatic conditions may exceed the capacity of many tree populations to adapt or migrate, regardless of how well management supports natural selection. Under such conditions, many forests will increasingly transition to non-forest states.

The main point of this discourse is to stress that an understanding of the genetic impacts of silvicultural and forest management procedures is essential for conservation of these highly complex co-evolved systems. Forests are much more than trees of different sizes and spacings.

965 Forests are interactive networks of diverse organisms that shift dynamically over time in
966 response to one another and abiotic conditions as shaped by genetics and natural selection.
967 Conservation of the DNA toolkit inherent in forests via informed management practices needs to
968 become an explicit goal of management to retain productive functional forests and biodiversity.
969 Managers and ecologists alike must become proficient in evolutionary and conservation genetics,
970 something sadly lacking in most forestry curricula and training programs (Fady and Scotti-
971 Saintagne 2025). Funding availability for research that can aid foresters in decision making
972 based on selection alignment has been rare, but its need is clear. Additionally, this type of
973 knowledge must be infused throughout the entire conservation community. Importantly, we must
974 find a way to transfer this knowledge to the public and to influence policy.

976 **Conclusions**

977 Genetic resilience is one of the most important forces driving survival on Earth, yet it is one of
978 the least acknowledged and leveraged in forest management. Eco-evolution-oriented forestry is
979 badly needed to support adaptivity and long-term ability to evolve (Lefevre et al. 2014). This will
980 require a major shift in thinking away from current practices that prioritize short-term benefits
981 while neglecting evolutionary processes and effects on genetic diversity. All strategies of climate
982 mitigation for forests are heavy with uncertainties and risk but management without
983 consideration of long-term effects on adaptation may be one of the riskiest.

984 Already three decades ago, Ledig (1992) was calling for “new programs to develop the baseline
985 data against which we can monitor future changes” and stressed that “research is particularly

needed to document changes in allele frequency under various types of management. Genetic surveys and genetic monitoring should be institutionalized to track the impacts of human driven environmental changes.” Schaberg et al. (2008) further warned nearly two decades ago “one of the greatest risks of anthropogenic selection might be its ability to overwhelm natural selection and flexibility that sustains ecosystem health across time scales”. It is time to take heed. The window of time within which changes to forest management practices can be adapted to facilitate adaptation is closing.

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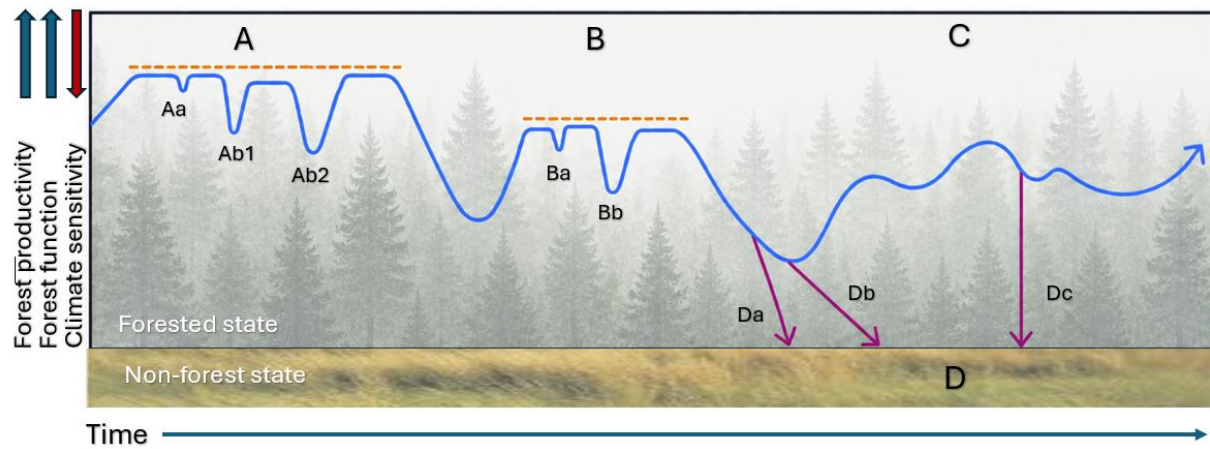
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1662

1663 Figures



1664 Time

1665 Figure 1. An example of how a forest's trajectory may shift with climate change. Forest

1666 characteristics and processes including physiological acclimation, phenotypic plasticity, selection

1667 on standing genetic diversity and new mutations, and migration of tolerant ecotypes and taxa are

1668 always in operation but vary in strength over time. Each process is influenced by feedback from

1669 the biotic community that is also changing. Dotted lines denote periods of relative climate

1670 equilibrium while dips are transient sensitive states. Sensitive states are characterized by reduced

1671 productivity and intensified natural selection leading to adaptation which in turn supports

1672 recovery of productivity. (Modified from conceptual models and concepts in Strickland et al.

1673 2024 and Stemkovski et al. 2025)

1674 A. The forest during climate equilibrium

1675 **Aa. Persistence/resistance** is characteristic of a stable climate and the forest undergoes no-to-

1676 little change when challenged by disturbance. This state develops with long-term forest

continuity and ecological legacies that are the outcome of evolutionary processes operating within a historical range of variation.

Ab. The forest experiences widespread mortality in response to disturbance/shifting climate but **resilience** supports recovery to its original state (**Ab1**) or one further from the original (**Ab2**), but with similar structure and functions. This property is present in forests operating within their historic range of variability under a stable climate as well as those undergoing early stage/weak transient sensitive states as climate changes. The type and/or severity of disturbance and degree of climate change affects the magnitude of the drop in productivity during sensitive states which influences the rate and degree of recovery.

B. The forest adapts via genetic resilience

As climate change continues and disturbance regimes shift, natural selection intensifies to remove intolerant ecotypes. The resulting altered niche space supports proliferation of adapted ecotypes and immigration of tolerant ecotypes and taxa. Concurrently, community reorganization is shaped by shifting interaction webs. If climate stability establishes, productivity increases and persistence (**Ba**) and resilience (**Bb**) of the adapted forest operate until a changing climate pushes it into yet another highly sensitive state.

C. The forest undergoes periods where equilibrium is not experienced

Some populations may never reach equilibrium due to frequent natural disturbance or a continually changing climate although processes continue to move the system to higher productivity via adaptation and immigration after each transient sensitive state.

- 1697 D. Collapse due to a lack of adaptive capacity.
- 1698 Standing genetic variation/ecological processes fail to support a return to productivity/function
- 1699 leading to rapid (**Da**) or continual slow decline (**Db**) resulting in a shift to a non-forest vegetation
- 1700 state. Collapse may also occur in response to climate change-driven megadisturbance (**Dc**).
- 1701

Accepted Review

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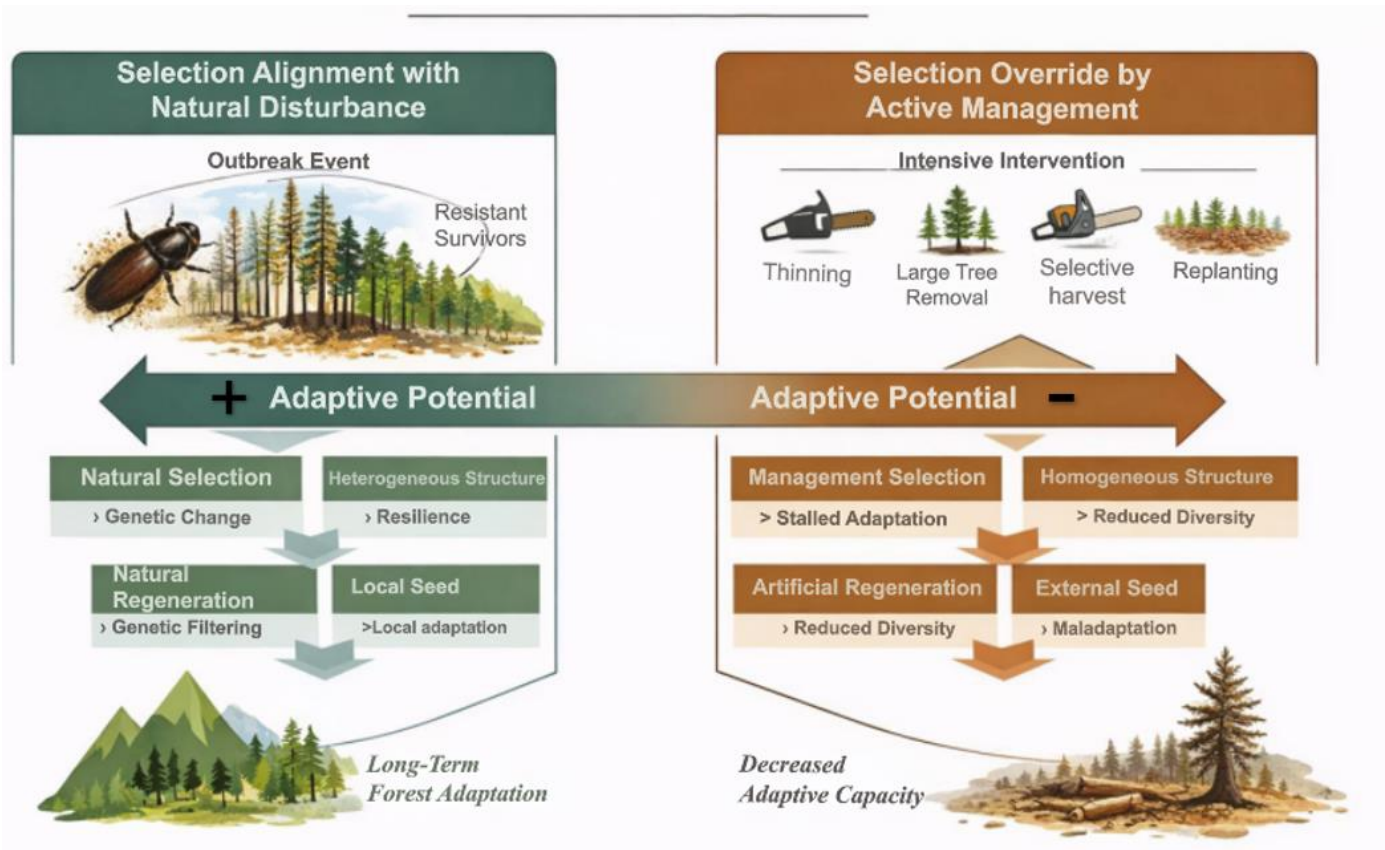


Figure 2. Comparison of natural selection alignment with natural selection override. Selection alignment facilitates adaptation via natural selection and is best supported by passive or semi-passive management. Selection override replaces natural selection with practices that suppress ecological processes, guiding forest trajectories to less adapted states. The more intensive the active management intervention, the less potential for adaptation remains.