

Distressed Woods

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PHOTOGRAPHS BY JEFFRY B. MITTON

What explains the unprecedented epidemic of mountain pine beetles?

A small black beetle flew through a forest high in the western mountains of North America and landed on the trunk of a mature lodgepole pine. She walked about the bark for several minutes, assessing the tree's fragrance with receptors on her antennae, and perhaps nibbling the bark. Finding the tree to her liking, she began to bore horizontally into the bark to initiate a gallery where she would mate and then lay her eggs in the tree's phloem, the vascular tissue beneath the bark that distributes nutrients made in the needles. As she chewed through the bark, she severed canals that produce and store a sticky defensive resin, a pine's primary defense against burrowing insects. Resin poured from the severed canals into the borehole, filled it, and began to spill out of the tree, pos-

sibly expelling the invader. Once outside of the tree the resin began to dry and congealed into a "pitch tube," the telltale sign of the attack of a mountain pine beetle, *Dendroctonus ponderosae*.

When the female mountain pine beetle chose this pine, a battle between tree and beetle began, with lives on both sides in danger. The tree summoned resources in an attempt to mire the beetle in resin, and finding herself inundated, the beetle moved in and out of the tree, using her body to clear resin from the borehole. Left to a one-on-one skirmish, the tree would win, but during her attack the beetle inevitably swallowed some resin. In her body a defensive chemical in the tree's resin (a monoterpene known as α -pinene) was rapidly metabolized into a potent attraction pheromone. The pheromone formed plume



Swaths of dead trees stretch for miles in the Williams Fork Mountains (foreground) and the Gore Range in northern Colorado. From the Alaska Panhandle south to New Mexico and to Southern California's San Bernardino Mountains, recent surges of mountain pine beetle infestation have taken a toll.



Recently emerged from beneath the bark of a dead tree, where it lived as a larva, an adult mountain pine beetle will soon find a live pine tree to attack.

that extended hundreds of yards downwind, signaling an opportunity to both female and male pine beetles.

For females, the pheromone leads to a desirable tree under attack, a tree that has space for them and their egg galleries if they arrive in time to help the first attacker win the battle against tree defenses. For males the pheromone signals a chance for sex: following it leads to available females working hard to excavate egg galleries that will need filling after the fight is won. (Various predators of the mountain pine beetle also follow the pheromone plume: red-bellied clerid beetles attack adult mountain pine beetles on the surface of the tree, while darkling beetles and long-legged flies feed on the larvae beneath the bark.)

The critical struggle initiated with the first borehole can have one of two outcomes: either attacking females muster sufficient numbers to kill the tree, or the tree repels and possibly kills the beetles. A tree loses the conflict when a large number of females have bored holes, lowering the tree's resin pressure to zero and halting the resin flow, which allows beetles to enter the tree en masse. To help ensure success, the females also inoculate the tree's phloem with species of fungi commonly known as "blue stain." A female beetle carries the spores of these symbiotic fungi in *mycangia*, shallow pits in her mouth and along her body adapted to hold them. The blue stain fungi spread through the gallery and into the outer portions of the wood, clogging the phloem and the deeper

vascular tissue, the xylem, which together transport nutrients and water between the roots and the crown. The females certainly damage the phloem while burrowing egg galleries, but the fungi block phloem and xylem, effectively strangling the tree.

Mountain pine beetles and blue stain fungi are locked in a mutualistic relationship—each depends on and benefits from the other. The fungi do more than help the beetles kill trees: larval beetles feed on bits of the fungi growing in the phloem. Without that fungal food source, beetle offspring would struggle to eat and grow. For most organisms, wood is a poor resource, marked by small amounts of nitrogen needed to make proteins and by great quantities of nearly indigestible carbon compounds. Yet fungi like the various species of blue stains are specialized to break down wood cellulose and lignin into useful nutrients. For their part, blue stain fungi benefit from mountain pine beetles that introduce fungal spores into their boreholes. Indeed, blue stain fungi are found in just two places in nature: in or on mountain pine beetles and some other bark beetle species, and flourishing beneath the bark of trees the fungi have helped the beetles kill.

Unlike most destructive forest pests, which are often introduced from far-off regions—for example, the gypsy moth that has ravaged deciduous forests of eastern North America—mountain pine beetles are native to the coniferous forests of western North America. The beetles utilize more than a dozen species of pines as hosts across a diverse range of environments from northern Mexico to Canada. Their populations typically alternate between endemic phases with very low densities and epidemic phases with high densities and conspicuous tree mortality.

Endemic populations rely on only the most susceptible trees, such as those weakened by lightning strikes, infected with harmful root fungus, or heavily parasitized by dwarf mistletoe (*Arceuthobium* spp.), a plant that roots itself on tree limbs and trunks and siphons off nutrients. These endemic populations of mountain pine beetles cause very little damage, and most people are not even aware of their presence, but every forty to sixty years, typically when drought reduces the resin defenses of pines, making them more susceptible to attack, mountain pine beetle populations erupt into an epidemic that can last for years.

Historically, a mountain pine beetle epidemic passes with hardly a comment, for epidemics have occurred in western forests for millions of years and typically remain restricted to one or two river valleys or sub-ranges of the vast mountainous west. However, a recent epidemic of mountain pine beetles has raged across the west, killing

fifty times more trees each year during its peak than all wildfires combined. Assessments of the geographic range impacted and the number of trees killed indicate that this epidemic is more than ten times larger than any previous epidemic. It has left well over a billion dead trees across pine forests from the mountains of New Mexico and southern California to Canada's Yukon Territory, and from the forests as far east as South Dakota's Black Hills to those standing above the coast of the Pacific Ocean. Furthermore, mountain pine beetles are killing trees at higher elevations and latitudes than ever before, bringing the threat of forest decline to treasured ski areas high in the Rocky Mountains and to Canadian forests once hundreds of miles beyond the reach of the beetles.

The consequences of this epidemic for mountain ecosystems and the regional economies they support remain poorly understood. Ecologically speaking, the death of trees from mountain pine beetle attack is neither novel nor certain to be negative, as most organisms in western forests have adapted to various levels of disturbance over their evolutionary histories. However, the unprecedented loss of living trees that pull carbon from the atmosphere and move it into woody materials and deep soil layers could, in the long term, tip some areas of the epidemic from carbon sinks to carbon sources as microbes decompose wood and organic materials.

More immediate concerns surround the consequences of tree death on regional water cycles. When mature conifers are lost in mountain forests, the increase in solar radiation striking the understory can have a large effect on understory climate and snowmelt throughout the winter and spring. Changes in snow accumulation depths and spring melt dates have already been reported following mountain pine beetle outbreaks—an unwanted impact on seasonal hydrology in a region where people already worry about the future of their water resources.

While the ecological effects of the moun-



Mountain pine beetles use pheromones to attract others of their kind to join in killing trees. Those chemicals also draw unwanted predators, like this mating pair of red-bellied clerid beetles.

tain pine beetle epidemic are now inevitable, scientists are still doggedly trying to understand why the epidemic is so much bigger than previous ones. While a complete explanation will have several facets, it is best to start with the impact of rapidly changing climate on the insect's life cycle. Historically, mountain pine beetle adults in the Colorado Rocky Mountains, one of the hardest-hit regions of the epidemic, began to emerge from trees in mid- or late July, with most beetles emerging the sec-



Mountain pine beetles that chew boreholes into a tree's bark elicit a formidable tree defense—an exudation of sticky, chemical-laden resin. Mass attacks, apparent on this tree, will overcome a tree's resistance. Inset: As it dries on the bark, the resin forms a "pitch tube."





A brood of beetles—both larvae and recently emerged adults—are revealed beneath a tree's bark. Mountain pine beetles have historically taken a full year to develop from eggs to adults. Increasing temperatures now allow some beetles to mature in just a few months, leading to multiple generations each year.

The consequence has been a fundamental change in the beetle life cycle. Females emerging in early June are laying eggs a few days later, and those eggs develop into larvae, then

and third week in August. The first eggs, deposited in galleries just days after attack by dispersing females, quickly hatched into larvae. Thus, larval development began in late summer but slowed as temperatures dropped through the fall.

Beetles tended to overwinter as fourth or fifth instars (a term referring to stages of larval growth) and resume development when temperatures in the dead tree's phloem rose above about 40 degrees Fahrenheit in the spring. Larvae transformed into pupae during the summer, metamorphosing into teneral (soft) adults by July and August. In just a few days, those teneral adults accumulated black pigment and hardened, and were then ready to emerge from beneath the tree bark and begin the next wave of attacks, aggregations, and egg laying. Historically, this life cycle took one year to complete.

With climate change, spring temperatures suitable for insect development have increased dramatically. We examined the long-term temperature records maintained by the University of Colorado's Mountain Research Station to calculate spring days above 40 degrees over the last six decades. Those data show that at an elevation of 10,000 feet in the Front Range of Colorado, the heat energy measured in "growing degree days"—the cumulative temperature sufficient for growth, or in this case, for beetle development—have increased by 58 percent during the spring season alone over the last four decades. Concomitant with that increase in temperature, the beetles were emerging four to six weeks earlier than they had historically, increasing the number of days suitable for flight and reproduction from 50 to more than 110 days.

pupae, then adults that emerge and lay eggs in August. The second batch is able to complete development about ten months later, in June. Thus, the beetle, developing in a warmer climate, is now able to reproduce twice per year in particularly warm years, rather than once per year. A change from one to two generations per year results not in a simple doubling of beetles, but leads to an exponential increase in their numbers.



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A rise in spring temperatures has also been associated with increases in the beetle's geographic range. When the Forest Service was monitoring mountain pine beetles in Colorado in the 1970s and 1980s, they did not establish sam-

Pulling back bark has revealed a female laying eggs, one of which can be seen near her right antenna. To lay eggs—fifty to sixty of them under the best of conditions—a female tunnels under a tree's bark, then chews a vertically oriented egg chamber in the phloem, the layer of vascular tissue that transports nutrients made in the needles.

pling stations above 9,000 feet, for that was the insect's upper elevational limit. But today in Colorado, the beetle is attacking trees far above 11,000 feet. Biologists in British Columbia have also documented not only the beetle's increase in elevation but also its expansion several hundred miles north beyond its historical limit.

This recent range expansion has brought mountain pine beetles to sites where lodgepole pines (*Pinus contorta*) intermingle with jack pine (*P. banksiana*)—a close evolutionary relative of the lodgepole pine that has historically been too far from the beetle populations to be used as a host. Lodgepole and jack pines hybridize, providing an inviting bridge to this new host. If mountain pine beetles spread through the geographic range of jack pines, the insect, till now exclusively a western species, could spread to pines in Nova Scotia and New England.

Warming temperature explains some aspects of this unprecedented epidemic, but not all. Without the proper habitat for reproduction and food, an organism cannot thrive and certainly will not rapidly increase in numbers. Thus, in addition to sufficiently warm temperatures, epidemics can only occur when mountain pine beetles gain access to many susceptible

Mountain pine beetles live in an agricultural symbiosis with various species of fungi that are collectively referred to as "blue stain" because of the way they color a tree's tissues. The beetles carry the fungal spores into their boreholes, and the fungi then help kill the host tree, detoxify the tree's defensive resin, and finally become a food source for the beetle larvae. This cross section of a trunk reveals that blue stain has spread into the xylem (the vascular tissue that transports water) and has become especially concentrated in the tree's resin ducts, which appear as dark spots.





Bighorn sheep retreat from the alpine tundra in fall to gain the protection of the spruce, fir, and lodgepole pine forests in winter. The effects of the beetle epidemic on bighorn sheep and elk have yet to be determined.

trees. The continuum from susceptible to resistant depends on each tree's defensive resin production, which changes dramatically during each year and over a tree's lifetime.

In recent years, much of western North America has experienced a decade-long drought. This, too, may in large part be a result of climate change, which not only affects air temperatures, but can alter precipitation patterns and amounts as well. Changes in major Pacific Ocean currents are additionally implicated, some of which may also be influenced by atmospheric temperature. In any case, a drought induces stress in trees, and one of the consequences is the inability of the tree to sustain resin volume and pressure.

So a tree suffering drought stress is highly susceptible to attack: as few as a dozen or two dozen females boring into it could drop its resin pressure to zero. How-

ever, that same tree might have high resin pressure after a rainy season or even a rainy week, and be able to repel hundreds to thousands of attacking beetles. Historically, most beetle epidemics are triggered by drought, and some seem to terminate when precipitation returns to normal levels. Yet all epidemics must end when the numbers of trees available for attacks have fallen so low that epidemic beetle population sizes can no longer be maintained.

The role of the pine trees themselves in the epidemics has been largely overlooked because trees are often taken to be largely uniform and static throughout their life spans. Few forest entomologists have considered pine defenses to be formidable enough to stop the spread of mountain pine beetles once their numbers have reached epidemic levels, and fewer still have considered variation among individual trees to be an important influence on mountain pine beetle populations. Yet even within a single stand of trees receiving the same amount of precipitation, rooted on similar soils, and growing under the same air temperatures, resistance from tree to tree

typically differs, much in the way that human immune responses might differ among even close relatives.

Much of this variation is likely genetic. Conifers are among the most genetically variable groups of species, and trees of the same species growing side by side can certainly differ in growth rate, form, frost tolerance, and cone production. Those with higher photosynthetic capacity and lower respiration rates will be more physiologically efficient and will have greater energy budgets to work with, imbuing them with the ability to grow faster, or to devote more energy to defense, or both.

Because resin is the primary if not the sole defense of a tree against mountain pine beetles, the number and size of resin ducts, which produce and store resin, might provide a good measure of the resistance of trees against mountain pine beetle attacks. In the past, biologists used resin pressure or resin flow to estimate resistance, but those variables fluctuate with the amount of precipitation in the recent past. Resin ducts have the advantage that they remain as a permanent record in the wood and can be counted in small cores of wood extracted from the trunk of the tree. Resin defense traits are known to be heritable in some conifers, meaning that the number and size of resin ducts produced is influenced by genetic variation.

Studies completed in diverse environments and using different species of pines have shown that trees with fewer resin ducts are more likely to be attacked by beetles. Those studies did not explicitly determine, however, whether attacked trees might resist mountain pine beetles if they had sufficient numbers of resin canals. We directly examined resistance to beetle attack in lodgepole pine and limber pine (*P. flexilis*) by examining only trees that had been attacked, comparing those that succumbed to those that survived. The surviving trees of both species had significantly

This least chipmunk eats a wide variety of seeds. In the near future it will see fewer lodgepole seeds but more seeds from grasses and shrubs.



Trees killed by the mountain pine beetle turn from green to red and eventually to gray, making the damage easy to spot from a distance. This trend raises concerns across the West over changes in ecosystems and even possible impacts on tourism. Yet, given enough time, openings in the canopy of western forests are typically filled by expansive clones of quaking aspen, which turn a beautiful, vibrant yellow each fall.





The death of mature pine trees increases light reaching the forest floor in mountain drainages, promoting the proliferation of deciduous shrubs such as willows, a primary food for moose. In this way, mountain pine beetle epidemics benefit some organisms by opening new habitats and diversifying the landscape.

more resin ducts in recent growth rings than those that were killed. This showed that the density of resin ducts can be used to predict, with high accuracy, which trees will live and which will die independently of tree species.

To the extent that variation in a trait that provides disease resistance is genetic, it becomes subject to natural

selection. In this way, the evolutionary history of trees, particularly their ancestors' exposure to mountain pine beetle or other insect attack, might be reflected in their level of resistance to pests in the present day. In the Colorado Rockies, where mountain pine beetle epidemics historically occurred below 9,000 feet, pines such as limber, lodgepole, and ponderosa (*P. ponderosa*) that grow below and above that elevation might have evolved different levels of resistance. If so, climate change may have opened the gate for the mountain pine beetle to enter inherently more susceptible forests.

Determining whether trees in high-elevation forests are less defended against mountain pine beetle attacks than trees at lower elevations is an ongoing topic of research that is greatly complicated by the long lifespan common to pines in western North American forests. Scientists studying a large range of plants, such as marsh grasses, goldenrods, and milkweeds, have long known that anti-insect defenses are at their peak when plants are young. Those defenses then decrease as the plants age and put greater amounts of resources into reproductive structures such as flowers, pollen, and seeds. How anti-insect defenses vary with tree age in pines that can live for centuries to millennia remains poorly understood.

Recently, we compared the resin defenses of young and old limber, lodgepole, and ponderosa pines and discovered that resin defenses rapidly decreased as trees aged. Foresters sometimes make the generaliza-

tion that mountain pine beetles only attack large trees, but it is the age, not the diameter, of the tree that seems to matter. Tree size is only a weak indicator of tree age. Our finding helps to explain why mountain pine beetle epidemics have skipped over forests of younger trees, adding another wrinkle to the challenge of characterizing tree defenses across elevations or latitudes.

The geographic extent of mountain pine beetle epidemics might also be complicated by the effects humans have had on forest structure across North

America. By harvesting trees selected for their economic value, altering the timing of disturbances such as fires, and introducing grazing animals such as sheep that influence forest regeneration, humans have vastly altered the age structure of trees across the landscape. And at lower elevations, where the climate is more conducive to human settlement throughout the year, the forests quite often have longer histories of human intervention and, in consequence, typically contain younger trees than forests at higher elevations. So the current ravaging of high-elevation forests, where trees are often more than a century old, might best be viewed as a legacy of human settlement and economy, not just a result of climate change.

It is also important to remember that mountain pine beetles are natives of North America. For millions of years, as is evident in alpine lake sediments and fossilized wood, they erupted in epidemics among western conifer forests. Given this long history as well as current events, we have no reason to expect or even hope that the epidemics will stop. But experimental studies, particularly those testing evolutionary hypotheses, are not only revealing how the beetle's life cycle is changing in response to climate change, but also throwing light on factors that enable trees to resist. We have gained insight, too, into why the beetle has been so successful in mowing down stands of trees at higher elevations. These new insights will hopefully inspire forest management techniques based around tree defenses.

One practical example would be for foresters to identify highly resistant trees by using pine resin canals as a measure of a tree's anti-insect defenses. Those trees could be left untouched during harvesting and also used as seed sources for future plantings. This method of "resistance thinning" during forest management might offer hope to future generations that their treasured campgrounds, parks, and mountain vistas will hold the necessary traits for reducing mountain pine beetle epidemics.



Scott M. Ferrenberg (far left) is an entomologist and ecologist who studies plant-insect interactions and forest ecology. Over the past decade, much of his research has focused on forest disturbances from wildfire and insect epidemics. He currently lives in Boulder, Colorado, where he is in the fourth year of his PhD studies in Ecology and Evolutionary Biology. **Jeffrey B. Mitton** is enjoying his fortieth year conducting research and teaching in the Department of Ecology and Evolutionary Biology at the University of Colorado in Boulder. His research examines adaptive genetic variation in natural populations of mountain pine beetles and in several species of conifers and cottonwoods, and he teaches lower and upper division courses in genetics. He also writes "Natural Selections," a biweekly science column in the *Boulder Daily Camera*.